

ARTICLE

Restoring function: Positive responses of carbon and nitrogen to 20 years of hydrologic restoration in montane meadows

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Abstract

Montane meadows are highly productive ecosystems that contain high densities of soil carbon (C) and nitrogen (N). However, anthropogenic disturbances that have led to channel incision and disconnected floodplain hydrology have altered the C balance of many meadows, converting them from net C sinks to net sources of C to the atmosphere. Restoration efforts designed to reconnect floodplain hydrology may slow rates of soil C loss from degraded meadows and restore the conditions for C sequestration and N immobilization, yet questions remain about the long-term impact of such efforts. Here, we used a 22-year meadow restoration chronosequence to measure the decadal impact of hydrologic restoration on aboveground and belowground C and N stocks and concentrations. Increases in herbaceous vegetation biomass preceded changes in soil C stocks, with the largest gains occurring belowground. Root biomass (0–15 cm) increased at a rate of 270.3 g m⁻² year⁻¹ and soil C stocks (0–15 cm) increased by 232.9 g C m⁻² year⁻¹ across the chronosequence. Increases in soil C concentration (2.99 g C kg⁻¹ year⁻¹) were tightly coupled with increases in soil N concentration (0.21 g N kg⁻¹ year⁻¹) and soil C:N did not vary with time since restoration. Fourier transform infrared spectroscopy results showed that the fraction of labile aliphatic C–H and carboxylate C–O (COO) compounds in the soil increased with the age of restoration and were positively correlated with soil C and N concentrations. Our results demonstrate that restoration of floodplain hydrology in montane meadows has significant impacts on belowground C and N stocks, soil C and N concentration, and soil C chemistry within the first two decades following restoration.

KEYWORDS

carbon sequestration, meadow, montane, peatland, reactive nitrogen, restoration, Sierra Nevada, soil carbon, soil nitrogen, subalpine, watershed, wetland

INTRODUCTION

Montane meadows are mineral soil wetlands that form in low-gradient valleys where fine sediment and water accumulate, creating extended periods of saturated soil conditions (Chambers & Miller, 2011; Wood, 1975). In mountainous regions, meadows provide critical habitat for wildlife, forage for grazing animals, late-season water storage, and filtration of chemical and organic contaminants for downstream water users (Kattleman & Embury, 1996; Peterson et al., 2001; Ratliff, 1985). Shallow depth to groundwater and saturated soil conditions during the growing season support hydric and mesic vegetation including sedges (*Carex* spp.), rushes (*Juncus* spp.), and other grasses and forbs (Castelli et al., 2000). The dense root mats of these herbaceous species trap fine sediments (Micheli & Kirchner, 2002b) and stabilize shallow, sinuous stream channels that saturate adjacent floodplains during periods of high flow (Chambers & Miller, 2011; Loheide & Gorelick, 2005).

Long histories of disturbance have led to widespread degradation of montane meadows in many regions. In the Sierra Nevada of California and Nevada, for example, anthropogenic activities including channel modification, road construction, grazing, and logging have resulted in the degradation of 60%–70% of meadows in the region (Hunsaker et al., 2015). These disturbances destabilize stream banks and increase the susceptibility of soil to erosive forces during high water flow events. The ensuing channel incision isolates streams from the surrounding floodplain, draining previously saturated meadows and creating extended periods of aerobic soil conditions (Germanoski & Miller, 2004). Increased depth to groundwater and drier soil conditions following stream channel incision result in decreased primary productivity, earlier senescence, and changes in vegetation community composition (Allen-Diaz, 1991; Dwire et al., 2006). These conditions also favor the replacement of hydric and mesic vegetation by xeric species with lower root biomass, further reducing stream bank stability and accelerating the rate of channel incision (Loheide & Gorelick, 2007; Micheli & Kirchner, 2002a; Toledo & Boone Kauffman, 2001).

Montane meadows are zones of enhanced biogeochemical activity at the terrestrial–aquatic interface (McClain et al., 2003) that contribute disproportionately to carbon (C) and nitrogen (N) cycles relative to their spatial extent. Meadows in the Sierra Nevada range cover <2% of the land surface area but may contain 12%–31% of total soil C stocks (Norton et al., 2011, 2014). Annual rates of C sequestration in undisturbed meadows of the Sierra Nevada may be three to six times higher than in the surrounding forest and commensurate with rates

reported for evergreen tropical forests, per unit land area (Reed et al., 2021). However, in meadows with disconnected floodplain hydrology, lower belowground C inputs coupled with high rates of microbial decomposition may convert ecosystems from net C sinks to net sources of C to the atmosphere (Reed et al., 2021). Decreased residence time of water following stream channel incision also reduces subsurface exchange between streams and floodplains, diminishing the potential for N retention (Kemmers et al., 2013; Peterson et al., 2001).

Restoration efforts in montane meadows designed to reconnect floodplain hydrology and increase the residence time of water have been ongoing for decades in the Sierra Nevada. These activities have been directed primarily at increasing late-season flows (Hammersmark et al., 2008), attenuating flood events, and improving habitat (Pope et al., 2015). However, recent California legislation (e.g., Assembly Bill 32) and the rise of voluntary and compliance C markets have sparked interest by policy makers and C accreditation agencies in the potential of meadow restoration to increase rates of soil C sequestration and mitigate climate change (California Air Resources Board, 2017; National Fish and Wildlife Foundation, 2010). Soil C sequestration is an important component of global C capture and storage strategies designed to counter rising global emissions (Fuss et al., 2018; Soussana et al., 2019). By some estimates, the capacity of soils to sequester C may be greater than afforestation and reforestation combined (Fuss et al., 2018).

In other wetland ecosystems, hydrologic restoration has been shown to yield rapid increases in vegetation biomass and decadal increases in soil C and N (Euliss et al., 2006; Moreno-Mateos et al., 2012; Walker et al., 2009; Yu et al., 2017). Field-validated hydrologic models in Sierra Nevada montane meadows project decreased depth to groundwater, extended periods of floodplain inundation (Hammersmark et al., 2008), and the re-establishment of hydric vegetation (Loheide & Gorelick, 2007) following hydrologic restoration of severely degraded meadows. These changes should, in theory, also restore conditions for soil C sequestration and N immobilization in montane meadows. Increased periods of soil saturation may impact methane and nitrous oxide fluxes as well, though even under saturated soil conditions methane emissions from Sierra Nevada montane meadows were a small fraction of the total C budget and lower than those reported for other wetland ecosystems (Reed et al., 2021). Higher mineral soil content in meadows relative to other types of wetlands may also afford physical protection to newly assimilated C through physicochemical interactions with the mineral matrix, potentially increasing the mean residence time of soil C (Dungait et al., 2018; Hemingway et al., 2019). Yet, uncertainty remains about long-term impacts of hydrologic restoration

in montane meadows on ecosystem C and N stocks (Moreno-Mateos et al., 2012; Pope et al., 2015).

The objective of this study was to assess the impact of hydrologic restoration on herbaceous biomass, below-ground biomass, soil C and N stocks and concentrations, and soil C chemical composition in six Sierra Nevada montane meadows comprising a 22-year restoration chronosequence. In addition to the traditional chronosequence approach, we compared the restored meadows to unrestored controls to better isolate the effects of hydrologic restoration from differences in disturbance histories. We hypothesized that: (1) restoration of floodplain hydrology would yield net gains in below-ground C stocks and concentration; (2) increases in aboveground and belowground herbaceous biomass would precede changes in soil C stocks and concentration; (3) changes in vegetation community composition combined with extended periods of saturated soil conditions following restoration would alter the chemical composition of soil C stocks; and (4) given biological coupling of C and N cycles, changes in soil N would mirror increases in soil C across the chronosequence.

METHODS

Study area

We used a chronosequence (space-for-time substitution; Pickett, 1989, Walker et al., 2010) of six restored meadows to assess the decadal impact of hydrologic restoration on aboveground and belowground C and N stocks and concentrations. The chronosequence sites are located within 20 km of each other in the northern Sierra Nevada range in California, USA. All sites were classified as riparian low-gradient meadows (Weixelman et al., 2011) with slopes ranging from 0.1% to 1%. Soils are poorly drained, clay loam alluvium derived from andesite parent material (Table 1; Horton, 2017, O’Geen et al., 2017). Vegetation in the watersheds above each meadow consists predominately of shrub communities (*Artemisia tridentata*, *Purshia tridentate*, *Ericameria nauseosus*) and forested hillslopes dominated by either ponderosa/Jeffrey pine (*Pinus ponderosa*, *Pinus jeffreyi*) or Sierra mixed conifer species (*Pinus contorta*, *Abies concolor*, *Pinus jeffreyi*). Forest cover in the upland ranges from 19% to 36% (Table 1; U.S. Geological

TABLE 1 Climate and watershed characteristics of restored chronosequence

Restored meadow	Age of restoration (years)	Latitude and longitude	Dominant soil type ^a	Upland Accumulated Area ^b (km ²)	MAT ^c (°C)	MAP ^c (mm)	Relief ^c (m)	Relative Relief ^b (m km ⁻¹)	Forest Cover ^b (%)
Poco	6	39° 58' 11" N 120° 31' 23" W	Clayey over loamy, smectitic over mixed, superactive, mesic Aquandic Endoaquolls	229.0	7.4	676.2	903.4	9.2	26.1
Dixie	9	39° 56' 05" N 120° 19' 55" W	Fine loamy, mixed, superactive, mesic Cumulic Endoaquolls	15.3	7.1	569.4	711.1	31.1	31.9
McReynolds	10	39° 57' 33" N 120° 29' 24" W	Clayey over loamy, smectitic over mixed, superactive, mesic Aquandic Endoaquolls	210.3	7.5	715.5	653.9	9.9	25.7
Alkali Flat	13	40° 05' 35" N 120° 20' 26" W	Loamy-skeletal, isotic Andic Humicryepts	105.2	8.6	425.5	606.2	8.9	19.0
Upper Clarks	15	40° 08' 06" N 120° 30' 29" W	Loamy-skeletal, isotic Andic Humicryepts	45.6	7.7	527.3	610.5	11.9	35.7
Big Flat	22	40° 08' 54" N 120° 27' 37" W	Loamy-skeletal, isotic Andic Humicryepts	9.6	7.8	512.7	302.3	16.7	20.8

Note: Climate characteristics include mean annual temperature (MAT) and mean annual precipitation (MAP). Watershed characteristics include dominant soil type within the meadow, area of the watershed above lowest point in the meadow (Upland Accumulated Area), maximum elevation change of the watershed above the meadow (Relief), basin relief divided by basin perimeter (Relative Relief), percentage cover of forest in the watershed above the meadow (Forest Cover), and mean basin elevation.

^aHorton (2017), O’Geen et al. (2017).

^bU.S. Geological Survey (2016).

^cPRISM Climate Group (2010).

Survey, 2016). Modeled 30-year averaged mean annual temperature ranged from 6.4°C to 8.1°C (4 km resolution; PRISM Climate Group, 2010). Modeled 30-year averaged mean annual precipitation (4 km resolution) ranged from 638 to 800 mm (Table 1; PRISM Climate Group, 2010). Most precipitation in the region falls during the winter months followed by a rain-free period during the growing season.

Stream channel incision (up to 6 m; Lindquist & Wilcox, 2000) was present in all meadows prior to restoration and historic reports suggested that major channel erosion in the area may have begun as early as the mid-1800s, primarily as a result of heavy grazing (Hughes, 1934; Hunsaker et al., 2015). By the early 1900s, stream channel incision had lowered the water tables by as much as 5 m, resulting in aerobic soil conditions, decreased primary productivity, and changes in vegetation community composition (Hughes, 1934). The meadows in this study were restored between 1995 and 2010 by Plumas Corporation using the pond-and-plug restoration technique (Appendix S1: Figure S1). Pond-and-plug restoration seeks to increase the residence time of water within the meadow and reconnect the floodplain by filling incised channels with soil excavated from on-site borrow ponds (Lindquist & Wilcox, 2000). All meadows are actively grazed; half under private management and the others grazed as part of United States Forest Service grazing allotments.

Sites were selected based on restoration type, soil parent material, vegetation community, and climate with the objective of controlling for soil forming factors other than time since restoration (Jenny, 1941). However, given the long and varied history of anthropogenic disturbance in montane meadows throughout the region, we were unable to control for disturbance type and level of

degradation prior to restoration. To minimize the impact of such legacies on experimental design, we identified unrestored sites within the same watershed, but outside the zone of impact of hydrologic restoration, and in similar condition as the restored meadow prior to restoration (Table 2; Appendix S1: Figure S2). Suitable unrestored comparisons were identified for five of the six meadows in the restoration chronosequence. Comparison of the relative difference between the restored and unrestored meadows across the chronosequence allowed us to control for site-specific differences and isolate the impact of restoration over time.

Undisturbed or “pristine” site comparisons were not included in this study design as we are unaware of any such meadows that have similar state factors as the meadows in the chronosequence. Furthermore, the aim of pond-and-plug restoration is to reestablish ecosystem function through reconnection of floodplain hydrology rather than to re-create predisturbance conditions. However, we make comparisons with literature values from undisturbed and lightly impacted meadows in other areas of the Sierra Nevada because these comparisons may contextualize biophysical differences between restored and undisturbed montane meadows.

Carbon and nitrogen stocks and concentration

In each meadow, we sampled 12 points within the zone of impact of hydrologic restoration (actualized impact in the restored meadows or potential impact in the unrestored meadows). Points were separated into three groups

TABLE 2 Climate and watershed characteristics of unrestored meadow comparisons

Unrestored meadow	Restored pair	Latitude and longitude	Dominant soil type ^a	Upland Accumulated Area ^b (km ²)	MAT ^c (°C)	MAP ^c (mm)	Relief ^c (m)	Relative Relief ^b (m km ⁻¹)	Forest Cover ^b (%)
Clover Valley	Poco	39° 57' 42" N 120° 24' 48" W	Fine loamy, isotic, frigid Ultic Argixerolls	83.1	7.3	559.0	872.9	14.7	26.9
Lower Dixie	Dixie	39° 56' 18" N 120° 20' 15" W	Fine loamy, mixed, superactive, mesic Cumulic Endoaquolls	15.8	6.9	579.2	714.4	30.9	31.8
Coyote Flat	Alkali Flat and Big Flat	40° 06' 36" N 120° 25' 02" W	Loamy-skeletal, isotic Andic Humicryepts	156.4	8.4	488.6	640.4	8.0	22.0
Lower Clarks	Upper Clarks	40° 07' 25" N 120° 30' 16" W	Loamy-skeletal, isotic Andic Humicryepts	47.7	7.9	599.0	621.8	11.6	34.9

Note: Climate characteristics include mean annual temperature (MAT) and mean annual precipitation (MAP). Watershed characteristics include dominant soil type within the meadow, area of the watershed above lowest point in the meadow (Upland Accumulated Area), maximum elevation change of the watershed above the meadow (Relief), basin relief divided by basin perimeter (Relative Relief), percentage cover of forest in the watershed above the meadow (Forest Cover), and mean basin elevation.

^aHorton (2017), O'Geen et al. (2017).

^bU.S. Geological Survey (2016).

^cPRISM Climate Group (2010).

of four points with 30 m between points (in a 2×2 arrangement) or two groups of six (in a 3×2 arrangement), depending on the size and shape of the meadow (please refer to Appendix S1: Figure S2 for examples of grid placement). Aboveground herbaceous vegetation biomass was sampled at six of the 12 points at peak productivity in 2016 by clipping all vegetation within a 25-cm^2 quadrat to within 1 cm of the soil surface. Aboveground herbaceous vegetation biomass was dried at 60°C to a constant mass and weighed to 0.01 g precision. Aboveground shrub biomass was not sampled as xeric shrubs were present only in the unrestored meadows and mesic shrubs in the restored meadows. Furthermore, sampling in a subset of meadows revealed that shrubs comprised $<0.5\%$ of the total ecosystem C (data not shown). Soil cores were taken to a depth of 45 cm using a 5-cm diameter AMS slide-hammer with a 15-cm corer (AMS Equipment Corp, American Falls, Idaho).

Twelve soil cores were taken at the 0–15 cm depth, eight from 15 to 30 cm, and four from 30 to 45 cm at each site. Sampling intensity was higher in the top 15 cm because we expected spatial heterogeneity and restoration impact to be greatest at that depth (Euliss et al., 2006; Knops & Bradley, 2009; Meyer et al., 2008). Soil cores were wet sieved to separate the >2 mm fraction and roots. A subsample of <2 mm fraction was dried at 105°C to calculate soil gravimetric water content. A subsample of the <2 mm fraction was also set aside for analysis of soil C and N concentrations using a Costech 4010 Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA). Root biomass was washed and dried at 60°C to a constant mass and weighed to 0.01 g precision. Bulk density was calculated as the mass of the dry <2 mm fraction divided by the entire core volume to correct for the impact of rock and root volume on soil C and N stocks (Throop et al., 2012). Mean values from the nearest points sampled were used to extrapolate values for unsampled points at deeper depths. Extrapolated values were used only to calculate stocks from 0 to 45 cm and were not included in statistical analyses. Means and standard deviations of aboveground and belowground measurements for each site are included in Appendix S1: Table S1 (aboveground) and Appendix S1: Table S2 (belowground).

Diffuse reflectance mid-infrared Fourier transform spectroscopy

To characterize changes in the chemical composition of the soil organic matter as a result of restoration, we used diffuse reflectance mid-infrared Fourier transform spectroscopy (DRIFTS), which provides an index of the

abundance of organic and inorganic substances by measuring the excitation of molecular bonds when exposed to infrared radiation (Parikh et al., 2014). Samples from six points in each restored meadow were homogenized, dried at 60°C to prevent interference from water, and ground to a fine powder. Only samples from 0 to 15 cm and 15 to 30 cm were analyzed because the low sample size from 30 to 45 cm limited statistical inference. Samples were not diluted with potassium bromide (KBr) as preliminary analysis indicated that this was unnecessary. We measured absorption in the mid-infrared range from 400 to 4000 cm^{-1} using a Bruker IFS 66v/S vacuum FTIR spectrometer (Bruker Corporation, Billerica, MA, USA) and a Praying Mantis DRIFTS sampler (Harrick Scientific Corporation, Ossining, NY). Finely ground and oven-dried KBr (Aldrich Chemical Company, Saint Louis, MO, USA, FT-IR grade) was used as a background reference for all FTIR analyses. Each sample was the average of 32 scans taken with a 6-mm aperture. All spectra were tangentially baseline corrected. Please refer to Appendix S1: Figure S3 for spectra by depth for each site.

Given that that meadow soils in this study were derived of predominately andesitic parent material, we excluded the spectral regions impacted by Fe- and Al-(oxyhydroxides and silicates from analyses (<1200 , $1700\text{--}2000$, >3000 ; Parikh et al., 2014). We assigned the peaks located between $2898\text{--}2986\text{ cm}^{-1}$ (centered at 2925 cm^{-1}) and $2839\text{--}2870\text{ cm}^{-1}$ (centered at 2850 cm^{-1}) to aliphatic C–H asymmetric and symmetric stretch (Parikh et al., 2014), associated with low-molecular-weight compounds and light fraction organic matter (Calderón et al., 2011). The area of each aliphatic peak was measured separately and the values summed for analysis. We interpreted the peak spanning $1570\text{--}1710\text{ cm}^{-1}$ (centered at 1648 cm^{-1}) as C=O stretch of amides, quinones, and ketones with contribution from C=C aromatic stretch (Parikh et al., 2014). Amides and quinones are present in microbial cell walls and may be indicative of microbially processed organic matter (Kögel-Knabner & Amelung, 2014), whereas ketones and aromatic compounds are long-chained lipids and complex C molecules primarily derived from plant lignin and woody debris (Parikh et al., 2014). There was a distinguishable shoulder from 1360 to 1450 cm^{-1} (centered at 1405 cm^{-1}) that we attributed to carboxylate C–O (COO) stretch and aliphatic C–H bend. We considered another peak between $1220\text{--}1320\text{ cm}^{-1}$ (centered at 1270 cm^{-1}) to be indicative of phenols and carboxylic acid C–O (Margenot et al., 2015; Parikh et al., 2014). Carboxylic acids are putative products of decomposition and may provide evidence of microbial processing (Perez et al., 2002). Please refer to Figure 1 for mean spectra and peak assignments. We also calculated an index of aromaticity as the ratio of peak areas assigned to aromatic (1648 cm^{-1}) and

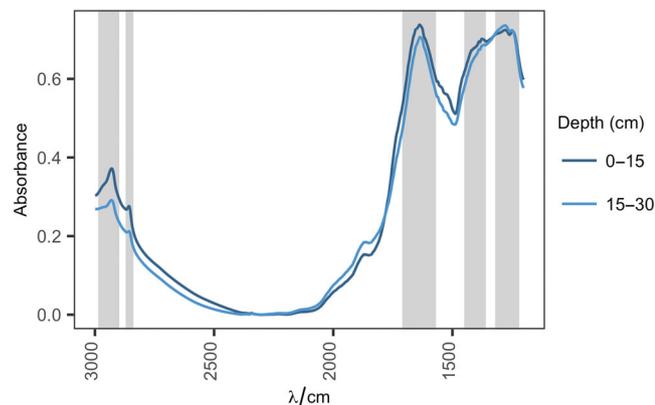


FIGURE 1 Mean diffuse reflectance infrared Fourier transform spectroscopy (DRIFTS) spectrum of soil from 0 to 15 cm ($n = 35$) and 15 to 30 cm ($n = 25$) depths for all restored meadows. Spectral features used to analyze organic functional groups are indicated by vertical gray bars.

aliphatic ($2925 + 2850 + 1405 \text{ cm}^{-1}$) functional groups. Similar ratios of band values have been shown to increase with microbial transformation and degree of decomposition (Demyan et al., 2012; Hsu & Lo, 1999; Margenot et al., 2015).

Peak areas were measured by drawing a baseline between the high and low values of each range using the “approxfun” function in R version 4.0.3 (R Core Team, 2020). The area under the curve was integrated after baseline correction using the “auc” function in the *MESS* package (Ekström, 2019). Establishing local baselines allowed us to separate peaks from larger spectral features. By calculating corrected peak areas, we were further able to remove assumptions about peak shape relative to the local baseline (Hall et al., 2018). Relative peak areas were then calculated by dividing the area of each corrected peak by the sum of all the peak areas. This approach allowed us to assess changes in the relative concentrations of functional groups across samples.

Statistical analysis

The aim of our statistical approach was to assess the impact of hydrologic restoration on aboveground and belowground C and N stocks and concentrations through time. We recognize that restoration ages were unreplicated across the chronosequence. Similar unreplicated chronosequences have been used to provide information on ecosystem development during secondary succession in forests (Mund et al., 2002), grasslands (Baer et al., 2002; Knops & Bradley, 2009), and wetlands (Ballantine & Schneider, 2009), yet we caution against extrapolation of these results to other sites without

discretion. As the site (or age of restoration) was the main experimental unit in this study, we used mean values from each site to measure trends through time. The 12 replicates at each site allowed us to account for spatial heterogeneity within the meadow. We used linear regression to assess the relationships between age of restoration and aboveground and belowground biomass, soil C and N stocks and concentrations, and DRIFTS absorbance ratios. The slope of the linear relationship was used to determine average annual rates of change across the chronosequence. Differences among restored sites were assessed using analysis of variance and Tukey’s honestly significant difference post hoc tests. Relationships among C and N concentrations, root biomass, and soil physical and chemical characteristics were assessed using plot-level measurements and analyzed using general linear mixed-effects models with site as a random effect to account for the nested sampling design (*nlme* package in R; Pinheiro et al., 2020). The difference in mean values between restored and un-restored meadow comparisons was used to measure the effect size of restoration at different time points across the chronosequence. Given that small sample sizes can result in larger p -values even under large effects (Wasserstein & Lazar, 2016), we set statistical significance a priori to $\alpha = 0.1$ for all meadow-level analyses. For plot-level comparisons we adopted the more traditional $\alpha = 0.05$. All statistics were conducted using R version 4.0.3 (R Core Team, 2020).

RESULTS

Restoration chronosequence

Aboveground herbaceous biomass in the restored meadows ranged from 516.3 to 719.1 g m^{-2} , but did not increase with time since restoration ($p = 0.72$, $r^2 = 0.21$, $n = 6$; Figure 2a). Root biomass was an order of magnitude larger than aboveground herbaceous biomass, with site means ranging from 3.0 to 7.6 kg m^{-2} in the top 45 cm. Root biomass in the top 15 cm increased significantly across the chronosequence, or with increasing age of restoration ($p = 0.06$, $r^2 = 0.54$, $n = 6$; Figure 2b), at a rate of $270.3 \pm 102.9 \text{ g m}^{-2} \text{ year}^{-1}$. However, there was no significant change in root biomass with time since restoration at deeper soil depths (15–30 cm: $p = 0.15$, $r^2 = 0.31$, $n = 6$; 30–45 cm: $p = 0.14$, $r^2 = 0.33$, $n = 6$). The ratio of aboveground to belowground biomass (0–15 cm) decreased exponentially with increasing age of restoration (log-transformed values, $p = 0.03$, $r^2 = 0.63$, $n = 6$).

Soil C stocks in the top 45 cm ranged from 9.4 to 18.3 kg C m^{-2} . In the top 15 cm, there was a positive

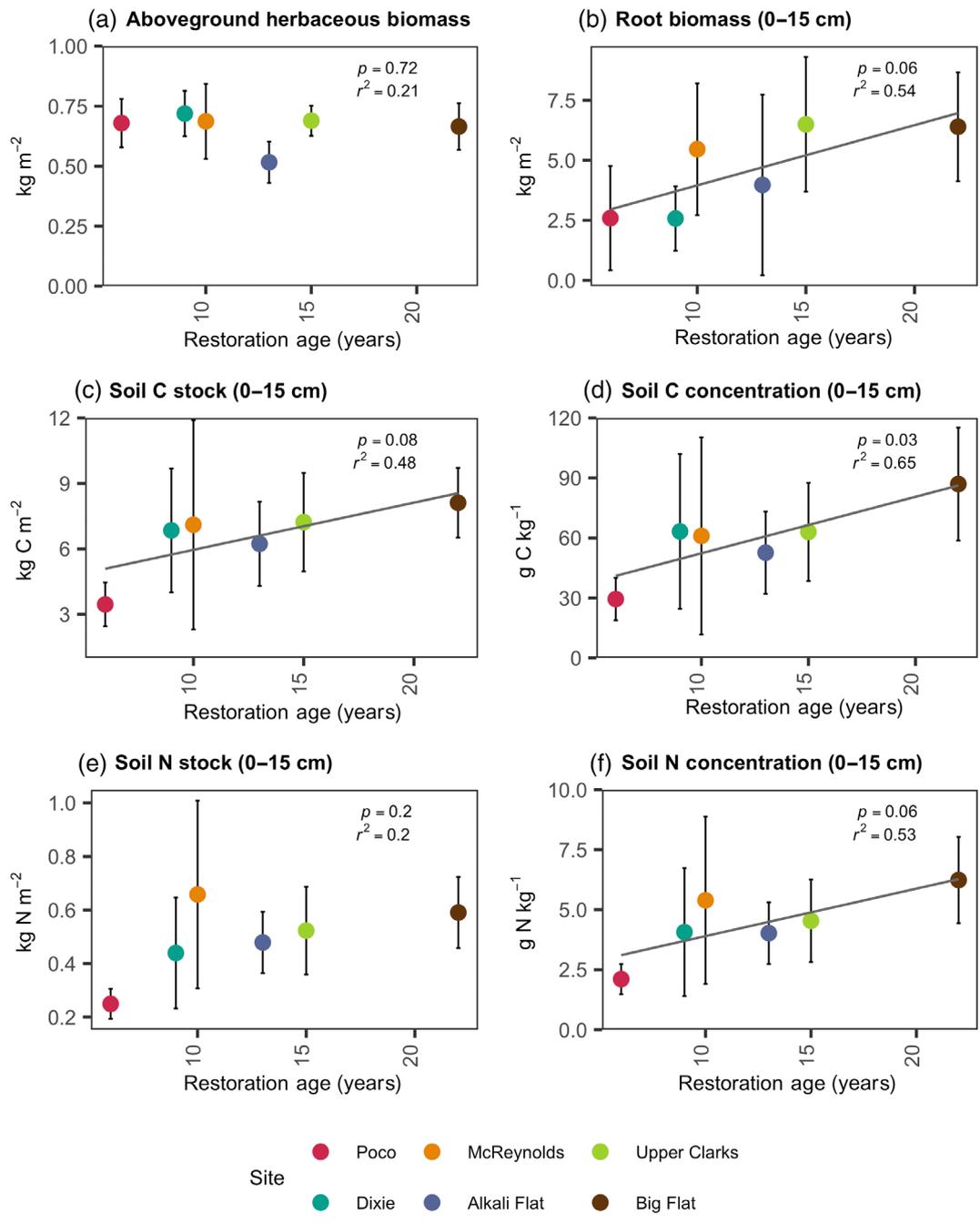


FIGURE 2 Across the chronosequence of restored sites, aboveground biomass (a) displayed no trend with age of restoration. Root biomass (b), soil carbon (C) stock (c), and soil C concentration (d) all increased with increasing age of restoration. Changes in soil nitrogen (N) stock (e) did not vary across the chronosequence, but soil N concentration (f) increased with age of restoration.

relationship between soil C stock and age of restoration ($p = 0.08$, $r^2 = 0.48$, $n = 6$; Figure 2c). Soil C stock at this depth increased at a rate of $232.9 \pm 98.3 \text{ g C m}^{-2} \text{ year}^{-1}$ across the chronosequence. There were no relationships between soil C stock and time since restoration from 15 to 30 cm ($p = 0.99$, $r^2 = 0.25$, $n = 6$) or 30–45 cm ($p = 0.34$, $r^2 < 0.01$, $n = 6$). Soil C concentration in the top 15 cm ranged from 29.4 to 87.0 g C kg^{-1} and increased at a rate of $3.0 \text{ g C kg}^{-1} \text{ year}^{-1}$ ($p = 0.03$, $r^2 = 0.65$, $n = 6$; Figure 2d). Similar to soil C stock, no relationships were

observed between soil C concentration and time since restoration at deeper depths (15–30 cm: $p = 0.61$, $r^2 = 0.16$, $n = 6$; 30–45 cm: $p = 0.68$, $r^2 = 0.19$, $n = 6$).

Soil bulk density did not vary with age of restoration from 0 to 15 cm ($p = 0.12$, $r^2 = 0.37$, $n = 6$), 15–30 cm ($p = 0.35$, $r^2 = 0.02$, $n = 6$), or 30–45 cm ($p = 0.77$, $r^2 = 0.22$, $n = 6$). At the plot level, soil bulk density was negatively correlated with soil C concentration across all restored meadows from 0 to 15 cm ($p < 0.01$, $t = 7.56$, groups = 6 $n = 72$) and 15–30 cm ($p = 0.04$, $t = 2.1$,

groups = 6, $n = 48$) but not 30–45 cm ($p = 0.18$, $t = 1.42$, groups = 6, $n = 24$).

Soil N stocks in the top 45 cm of the restored sites ranged from 0.79 to 1.75 g N m⁻² and displayed no trend with time since restoration at any of the depths sampled (0–15 cm: $p = 0.20$, $r^2 = 0.21$, $n = 6$; 15–30 cm: $p = 0.97$, $r^2 = 0.25$, $n = 6$; 30–45 cm: $p = 0.97$, $r^2 = 0.25$, $n = 6$; Figure 2f). Soil N concentration at the 0–15 cm depth ranged from 2.1 to 6.2 g N kg⁻¹ and increased at a rate of 0.18 g N kg⁻¹ year⁻¹ across the chronosequence ($p = 0.06$, $r^2 = 0.53$, $n = 6$; Figure 2e). There was no relationship between soil N concentration and time since restoration from 15 to 30 cm ($p = 0.59$, $r^2 = 0.15$, $n = 6$) or from 30 to 45 cm ($p = 0.67$, $r^2 = 0.19$, $n = 6$). At the plot level, soil N concentration was negatively correlated with soil bulk density from 0 to 15 cm ($p < 0.01$, $t = 6.29$, groups = 6, $n = 72$) but not from 15 to 30 cm ($p = 0.16$, $t = 1.43$, groups = 6, $n = 48$), or from 30 to 45 cm ($p = 0.63$, $t = 0.50$, groups = 6, $n = 24$). The ratio of C:N did not vary with time since restoration at any depth (0–15 cm: $p = 0.79$, $r^2 = 0.23$, $n = 6$; 15–30 cm: $p = 0.76$, $r^2 = 0.22$, $n = 6$; 30–45 cm: $p = 0.86$, $r^2 = 0.24$, $n = 6$) and the slope of the relationship between log-transformed values of C and N concentration was not significantly different from one at any depth (0–15 cm: $p = 0.52$; 15–30 cm: $p = 0.65$; 30–45 cm: $p = 0.22$).

We observed a significant increase with time since restoration in the relative area of the peaks associated with aliphatic C–H (2925 + 2850 cm⁻¹) and carboxylate C–O (COO) stretch and/or aliphatic C–H bend (1400 cm⁻¹) in the surface soil (Table 3 and Figure 3a,b). Conversely, there was a age of restoration was negatively

correlated with the relative area of carboxylic acid and phenols (1270 cm⁻¹) from 0 to 15 cm and aromatic C=O/C=C stretch from 15 to 30 cm (Table 3 and Figure 3c). At the plot level, the relative area of aliphatic C–H (2925 + 2850 cm⁻¹) was positively correlated with both soil C and N concentrations from 0 to 15 and 15 to 30 cm (Table 3). The relative area of carboxylate C–O (COO) stretch (1400 cm⁻¹) was positively correlated with soil C concentration at both depths but only significantly correlated with soil N concentration at the 15–30 cm depth (Table 3). The relative area of carboxylic acid (1270 cm⁻¹) was negatively correlated with soil C concentration from 0 to 15 and 15 to 30 cm, but the relationship with soil N concentration was only significant at the 0–15 cm depth (Table 3). There were no relationships between the relative area of aromatic C=O and/or C=C stretch bonds (1648 cm⁻¹) and soil C or N concentration at either depth (Table 3). The ratio of aromatic to aliphatic compounds did not vary linearly with age of restoration, but was significantly higher in the youngest restored meadow relative to the older sites (Table 3 and Figure 4a). Furthermore, the ratio of aromatic to aliphatic compounds decreased exponentially with increases in both C and N concentrations at the plot level (Table 3 and Figure 4b,c).

Unrestored–restored meadow comparisons

The results of the unrestored–restored meadow comparisons largely mirrored those of the restoration chronosequence. Aboveground herbaceous biomass was higher in all restored

TABLE 3 DRIFTS results

Depth	Aliphatic C–H (2925 + 2850 cm ⁻¹)	Aromatic C=O and C=C stretch (1648 cm ⁻¹)	Carboxylate C–O and aliphatic C–H (1400 cm ⁻¹)	Carboxylic acid and phenols (1270 cm ⁻¹)	Aromatics: Aliphatics (2925 + 2850/1648)
Age of restoration					
0–15 cm	$r^2 = 0.45^*$...	$r^2 = 0.51^*$	$r^2 = 0.66^{**}$...
15–30 cm	...	$r^2 = 0.40^*$
Soil carbon concentration					
0–15 cm	$t = 6.09^{***}$...	$t = 2.91^{***}$	$t = -4.81^{***}$	$t = -4.21^{***}$
15–30 cm	$t = 4.05^{***}$...	$t = 2.89^{***}$	$t = -1.75^{**}$	$t = -3.93^{***}$
Soil nitrogen concentration					
0–15 cm	$t = 5.38^{***}$	$t = -4.13^{***}$	$t = 2.85^{***}$
15–30 cm	$t = 3.43^{***}$...	$t = 3.80^{***}$...	$t = -3.86^{***}$

Note: Relationships between the relative area of the soil carbon compounds identified using diffuse reflectance infrared Fourier transform spectroscopy (DRIFTS) and age of restoration (y), soil concentration (g C kg⁻¹) and nitrogen concentration (g N kg⁻¹) in the soil. For comparisons with age of restoration, $n = 6$ at both depths. For comparisons with soil carbon and nitrogen concentrations, $n = 35$ from 0 to 15 cm and $n = 25$ from 15 to 30 cm.

... No significant relationship.

*Significant at $p < 0.1$. **Significant at $p < 0.05$. ***Significant at $p < 0.01$.

meadows relative to the unrestored controls and the effect size ranged from 367.8 to 635.2 g m⁻². However, the difference between restored and unrestored meadows did not vary with time since restoration ($p = 0.63$, $r^2 = 0.22$, $n = 5$). Root

biomass in the top 45 cm of soil was 1.3–6.5 kg m⁻² higher in the restored sites than the unrestored controls. The difference in root biomass increased significantly with time since restoration at the 0–15 cm ($p < 0.01$, $r^2 = 0.92$, $n = 5$;

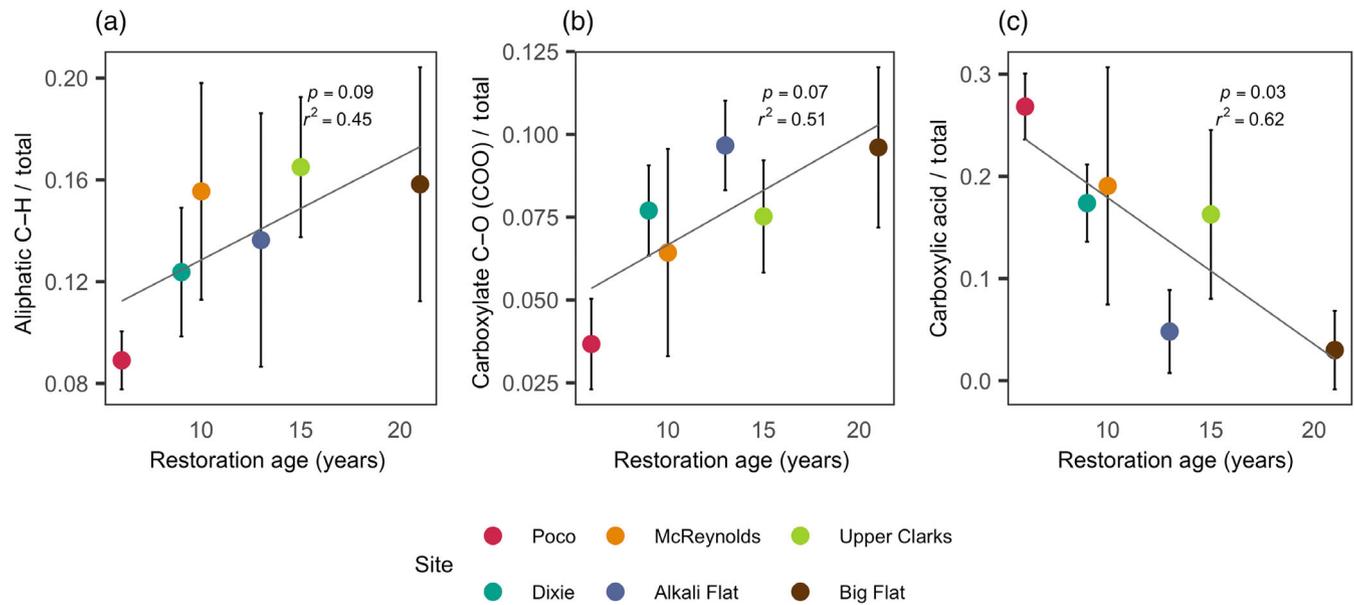


FIGURE 3 Changes in soil carbon (C) chemistry across the chronosequence of restored sites. The relative area of aliphatic C–H bonds (2925 + 2850 cm⁻¹; [a]) and carboxylate C–O (COO stretch; 1400 cm⁻¹; [b]) increased with time since restoration, whereas the relative area of carboxylic acid and phenols (1270 cm⁻¹) decreased with age of restoration (c). The relative area of C=O/C=C (1648 cm⁻¹) did not vary significantly with age of restoration. All relationships are for the top 15 cm of soil.

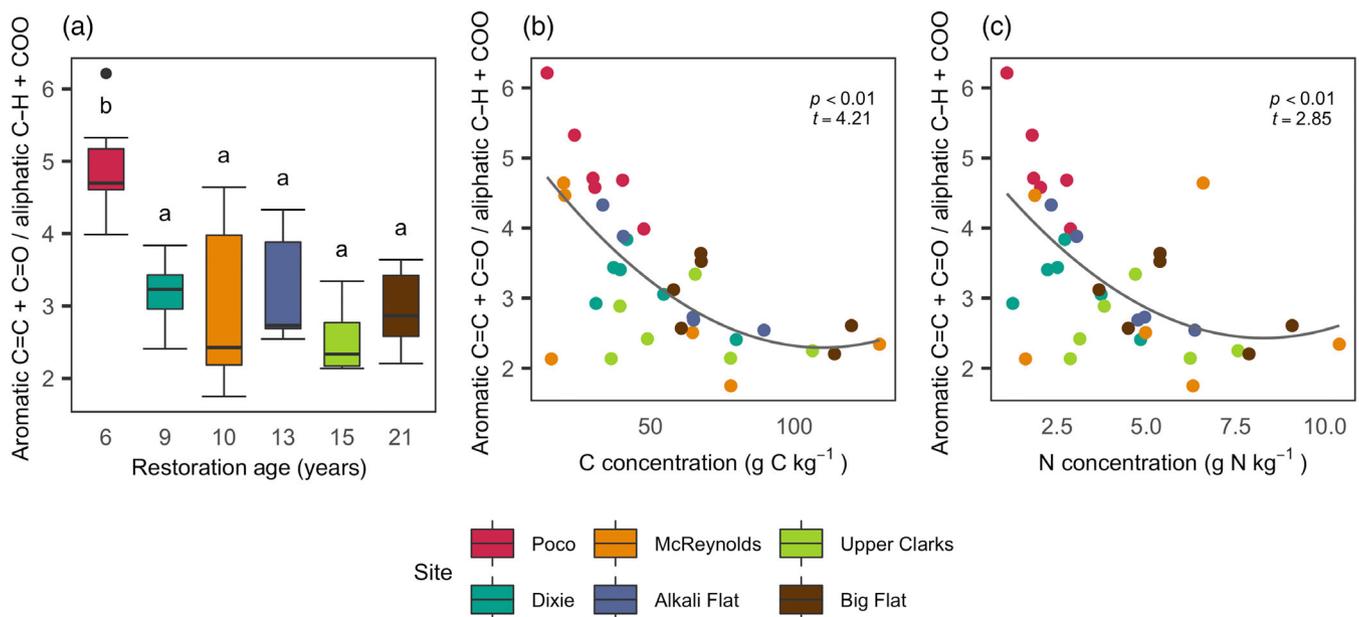


FIGURE 4 Ratio of aromatic to aliphatic DRIFTS peak areas. The ratio of aromatic to aliphatic compounds did not vary significantly with age of restoration but was significantly higher in the youngest restored meadow relative to the others (a). At the plot level, the ratio of aromatic to aliphatic compounds decreased exponentially with increases in both soil C concentration (b) and soil N concentration (c) across all meadows. All relationships are for the top 15 cm of soil.

Figure 5a) and 15–30 cm depths ($p = 0.1$, $r^2 = 0.53$, $n = 5$), but not from 30 to 45 cm ($p = 0.31$, $r^2 = 0.10$, $n = 5$). Across the chronosequence, the difference in root biomass between restored and unrestored meadows increased by $305.5 \pm 43.5 \text{ g m}^{-2} \text{ year}^{-1}$ from 0 to 15 cm and $40.8 \pm 17.3 \text{ g m}^{-2} \text{ year}^{-1}$ from 15 to 30 cm. On average, soil bulk density from 0 to 15 cm was 17.1% lower in the restored meadows ($0.80 \pm 0.08 \text{ g cm}^{-3}$) than the unrestored controls ($0.96 \pm 0.1 \text{ g cm}^{-3}$). However, the difference in soil bulk density between the restored and unrestored meadows did not vary

with age of restoration from 0 to 15 cm ($p = 0.98$, $r^2 = 0.33$, $n = 5$), 15–30 cm ($p = 0.50$, $r^2 = 0.11$, $n = 5$), or 30–45 cm ($p = 0.46$, $r^2 = 0.08$, $n = 5$).

Soil C stock in the restored meadows was $0.04\text{--}2.93 \text{ kg C m}^{-2}$ higher relative to the unrestored comparisons in the top 0–15 cm. The impact of restoration on soil C stock increased across the chronosequence at a rate of $186.2 \pm 49.1 \text{ g C m}^{-2} \text{ year}^{-1}$ from 0 to 15 cm ($p = 0.03$, $r^2 = 0.77$, $n = 5$; Figure 5b). The difference in soil C stock between restored and unrestored meadows did not vary

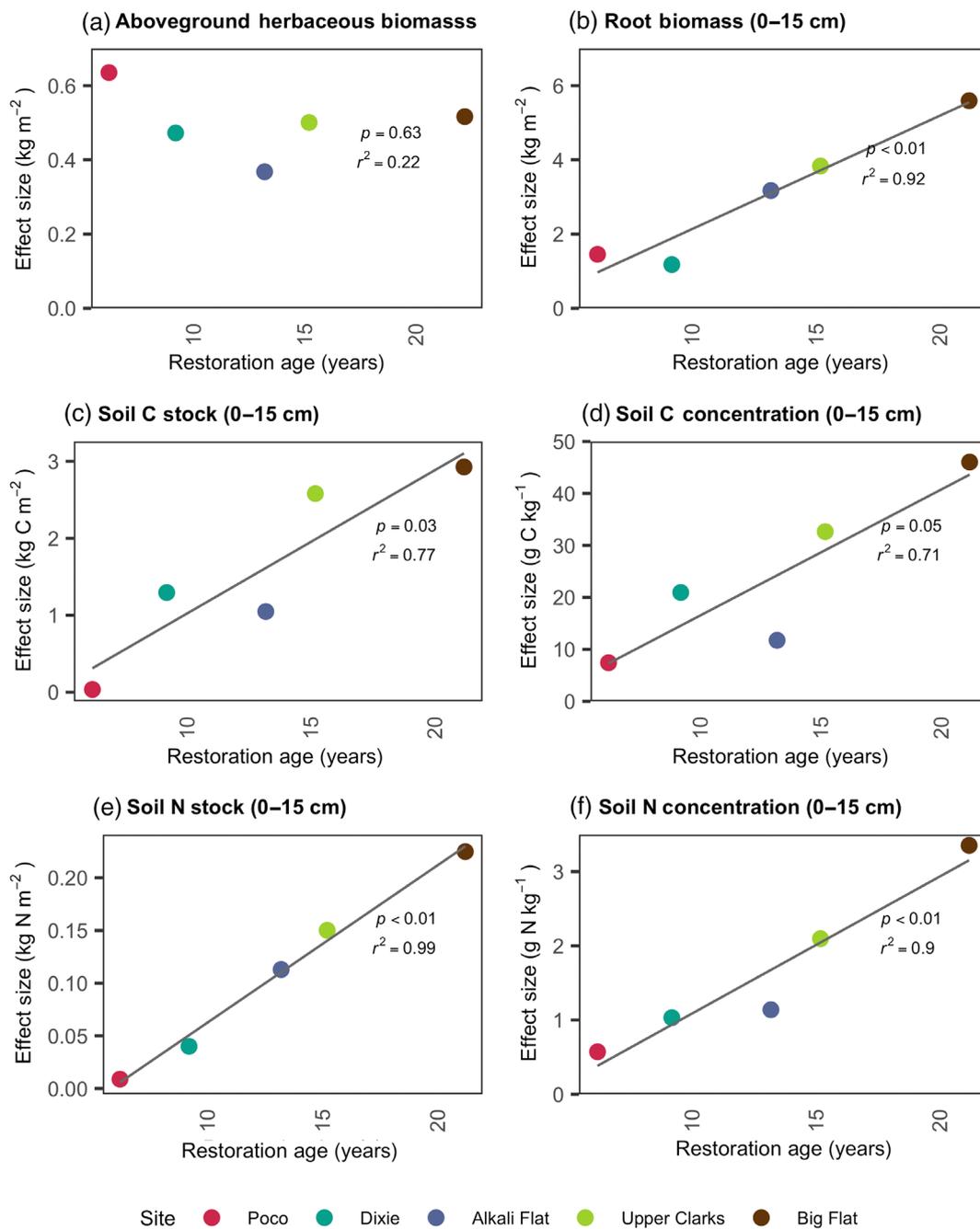


FIGURE 5 The difference between restored meadows and unrestored comparisons. Differences between restored and unrestored meadow comparisons increased with age of restoration for herbaceous vegetation biomass (a), root biomass (b), soil carbon (C) stock (c), soil C concentration (d), soil nitrogen (N) stock (e), and soil N concentration (f).

significantly with time since restoration from 15 to 30 cm ($p = 0.16$, $r^2 = 0.38$, $n = 5$) or 30–45 cm ($p = 0.29$, $r^2 = 0.37$, $n = 5$). Soil C concentration in the top 15 cm was 7.4–46.0 g C kg⁻¹ higher in the restored meadows relative to the unrestored comparisons and increased at a rate of 2.4 ± 0.74 g C kg⁻¹ year⁻¹ across the chronosequence ($p = 0.05$, $r^2 = 0.71$, $n = 5$; Figure 5c). The difference in soil C concentration between restored and unrestored meadows did not vary significantly with time since restoration from 15 to 30 cm ($p = 0.15$, $r^2 = 0.40$, $n = 5$) or 30–45 cm ($p = 0.60$, $r^2 = 0.20$, $n = 5$).

Soil N stocks in the top 15 cm were 8.9–224.7 g N m⁻² higher in the restored meadows than the unrestored controls and the difference increased linearly with time since restoration ($p < 0.01$, $r^2 = 0.99$, $n = 5$; Figure 5d) at a rate of 14.9 g N m⁻² year⁻¹. The difference in soil N stock between restored and unrestored meadows did not vary with time since restoration at deeper depths (15–30 cm: $p = 0.46$, $r^2 = 0.08$, $n = 5$; 30–45 cm: $p = 0.71$, $r^2 = 0.26$, $n = 5$). Soil N concentration in the restored meadows was 0.57 to 3.35 g N kg⁻¹ higher than in the unrestored comparisons in the top 15 cm and the difference increased across the chronosequence ($p < 0.01$, $r^2 = 0.89$, $n = 5$; Figure 5e) at a rate of 0.18 ± 0.03 g N kg⁻¹ year⁻¹. The difference in soil N concentration did not vary with time since restoration from 15 to 30 cm ($p = 0.42$, $r^2 = 0.04$, $n = 5$) or 30–45 cm ($p = 0.99$, $r^2 = 0.33$, $n = 5$). Additionally, the difference in C:N ratio between restored and unrestored meadows did not vary with time since restoration at any depth (0–15 cm: $p = 0.70$, $r^2 = 0.26$, $n = 5$; 15–30 cm: $p = 0.95$, $r^2 = 0.33$, $n = 5$; 30–45 cm: $p = 0.90$, $r^2 = 0.33$, $n = 5$).

DISCUSSION

Restoration of floodplain hydrology in montane meadows leads to increases in herbaceous biomass, altering the ecosystem C balance and creating conditions for substantial soil C sequestration within two decades following restoration. Consistent with our first hypothesis, both soil C stock and root biomass increased significantly with time during the first two decades following restoration. Combining increases in root C with increases in soil C stock yields annual belowground C increases of 332 g C m⁻² year⁻¹ across the chronosequence, amounting to C gains of 6.64 kg C m⁻² over a 20-year period. Soil C stocks (0–45 cm) in all but the youngest restored site were equal to or greater than values reported for similar depths in relatively “pristine” Sierra Nevada meadows with connected floodplain hydrology (Norton et al., 2011; Reed et al., 2021) and wetlands across the conterminous United States (Euliss et al., 2006; Nahlik & Fennessy, 2016). The rate of increase

in soil C stock in the top 15 cm was similar to values reported for restored wetlands (Euliss et al., 2006; Knox et al., 2015) and roughly seven times higher than values reported for grassland restoration chronosequences (Baer et al., 2002; Knops & Bradley, 2009; Matamala et al., 2008).

Soil C concentration remained lower than values reported in Sierra Nevada meadows with undisturbed floodplain hydrology, despite significant increases with time since restoration. Mean soil C concentration in the top 15 cm of the oldest restored site was 87.0 g C kg⁻¹, whereas values have been reported as high as 174.0 g C kg⁻¹ in the top 15 cm of meadows with undisturbed floodplain hydrology (Norton et al., 2011; Reed et al., 2021).

Our results suggested that C concentrations in the top 15 cm of soil could approach values reported for undisturbed meadows within 45 years following restoration, assuming that the consistent rate of annual increase we measured continues. This increase in soil C concentration could lead to lower soil bulk density, greater hydrologic connectivity between ground and surface water, and better conditions for root growth (Vereecken et al., 1989). The negative relationship between soil bulk density and C concentration that we observed in this study suggests this trajectory may already be occurring, despite the fact that overall soil bulk density did not change across the chronosequence. Even so, it may take longer than 45 years for soil bulk density to approach possible predisturbance conditions. Twenty-two years after restoration, soil bulk density was 18%–45% higher in these restored sites than other Sierra Nevada meadows with undisturbed floodplain hydrology (Norton et al., 2011; Reed et al., 2021), though this comparison is limited by the fact that sites were not located in the same region of the Sierra Nevada and did not have the same soil parent material. Long-lasting legacies of land-use on soil bulk density have been observed in other ecosystems (Dambrine et al., 2007; Douglas et al., 2018), raising the possibility that soil compaction or altered biophysical processes following drainage and rewetting of meadows might lead to persistently high soil bulk density. Studies conducted in wetland (Besasie & Buckley, 2012) and grassland (Baer et al., 2002) restoration chronosequences have similarly found higher bulk density in restored relative to pristine sites, suggesting that this may be the case.

Assuming a constant rate of C accumulation beyond the 22-year timeframe of this study may be tenuous, however. Saturation of C on mineral soil surfaces (Stewart et al., 2007) may result in lower rates of C storage over time, unless these gains can be offset by accumulation of C in particulate organic matter (POM). Lower bulk density in pristine meadows relative to the restored meadows in this study may be an indication of additional C stored as POM, though more data are needed to determine how

soil C pools and mechanisms of soil C storage differ between restored and undisturbed montane meadows. Regardless, centennial scale changes in soil C stocks in these sites will be the result of complex interactions among hydrology, bulk density, vegetative C inputs, microbial processing of soil organic matter, and soil adsorptive properties, among other things, making precise projections impossible.

Consistent with our second hypothesis, increases in aboveground biomass preceded increases in soil C across the chronosequence. Aboveground biomass in even the youngest restored meadow was equal to or greater than values reported for undisturbed meadows in the Sierra Nevada (McIlroy & Allen-Diaz, 2012; Micheli & Kirchner, 2002b; Ratliff, 1985; Reed et al., 2021) and other montane regions (Kato et al., 2006; Wu et al., 2013; Yang et al., 2008), suggesting that aboveground biomass may reach predisturbance levels within a few years following restoration of floodplain hydrology. However, contrary to our expectation, increases in root biomass did not appear to precede increases in soil C stock; both increased linearly across the 22-year chronosequence and approached values reported for undisturbed meadows in the Sierra Nevada (Reed et al., 2021) and similar montane regions (Dwire et al., 2004; Toledo & Boone Kauffman, 2001) within 15 years following restoration. Similar decoupling of aboveground and belowground recovery trajectories have been reported in grassland chronosequences (Matamala et al., 2008), highlighting the importance of independently assessing belowground C dynamics.

Consistent with our third hypothesis, changes in soil C chemical composition occurred with increasing time since restoration and were correlated with both C and N concentrations. Although it is difficult to conclusively translate DRIFTS spectral features to soil organic C compounds, relative increases in the proportion of aliphatic bonds are commonly associated with increases in light fraction organic matter with lower rates of microbial processing (Demyan et al., 2012; Haberhauer et al., 1998; Ryals et al., 2014). The increase in the relative area of peaks associated with aliphatic compounds with increasing C concentrations and age of restoration in this study may be indicative of vegetative C inputs with lower degrees of microbial processing. Without physical or chemical protection on mineral surfaces, this labile C may be susceptible to future loss under changing climate conditions or management. However, labile C from aboveground and belowground sources has also been shown to contribute disproportionately to mineral-associated organic matter (MAOM; Cotrufo et al., 2015; Haddix et al., 2020) and Ramírez et al. (2021) found aliphatic C–H bonds to be highly correlated with both POM and MAOM. Adsorption of C onto mineral soil particles

can increase turnover times by an order of magnitude or more relative to POM (Balesdent et al., 2000). More work is needed to determine whether the increase in C concentration and the relative area of aliphatic compounds with time since restoration in montane meadows are associated with increases in POM or MAOM. It should be noted, however, that Cotrufo et al. (2019) found that the largest fraction of C in grasslands was stored in MAOM. Given the higher N requirement of MAOM relative to POM (Cotrufo et al., 2019), potential increases in the fraction of mineral-associated C may depend, in part, on rates of N accumulation.

Consistent with our fourth hypothesis, C and N increased together across the chronosequence. Nitrogen is considered the limiting nutrient in many ecosystems, ultimately restricting C inputs to the soil from primary productivity (LeBauer & Treseder, 2008; Vitousek & Howarth, 1991) in addition to constraining microbial conversion of POM to MAOM (Cotrufo et al., 2019; Daly et al., 2021; Schimel & Weintraub, 2003). Although changes in soil N stock were not significantly different from zero across the traditional chronosequence, the difference in soil N stock between restored and unrestored meadow comparisons increased significantly with time since restoration at a rate similar to the values reported for restored wetlands and salt marshes (Meyer et al., 2008). It is important to note that the 10-year site was not included in the restored–unrestored meadow comparisons because we could not identify a suitable unrestored control. If that site was removed from the chronosequence of restored meadows, the increase in soil N stock through time would closely match the change in the difference between the restored–unrestored meadows. Increases in soil N concentration were observed with both approaches, but values in even the oldest restored meadow (6.2 g N kg^{-1} , 0–15 cm) remained lower than those reported for undisturbed montane meadows (up to 12.0 g N kg^{-1} ; Norton et al., 2011). Higher soil C and N concentrations in undisturbed montane meadows and the tightly coupled response of C and N to restoration suggest that additional accumulation of C with time in restored meadows may be contingent on increases in soil N concentration.

The results of the unrestored–restored meadow comparisons in this study were largely consistent with those of the traditional chronosequence, apart from differences in the measured response of soil N stock. Estimates of rates of C gain between the two methods differed by $<50 \text{ g C m}^{-2} \text{ year}^{-1}$ for soil C stocks and $0.6 \text{ g C kg}^{-1} \text{ year}^{-1}$ for soil C concentration in the top 15 cm of soil. The general agreement between the two methods suggests our chronosequence is robust to differences in disturbance and management history. Although the most substantial changes were limited to the top 15 cm of soil over the

period studied, increases deeper in the profile may occur with increased age of restoration, though uncertainty remains about the timing and magnitude of such gains. These results are consistent with findings from other wetland (Meyer et al., 2008) and grassland (Baer et al., 2002) chronosequences, and underscore the need for long-term monitoring to accurately assess the impact of restoration activities.

Could physical processes such as sediment deposition contribute substantially to the rates of C accumulation we measured, or were rates of C accumulation likely to be driven by biological activity? Stratified alluvium in meadow soils highlights the importance of sediment deposition over geologic time scales. However, the United States Soil Conservation Service (1989) measured rates of upland erosion for the watersheds containing Poco/McReynolds and Alkali Flat, and estimated rates of deposition from forest sheet erosion to be 2.06 and 10.5 Mg km⁻² year⁻¹, respectively, whereas roads contributed 163.9 and 291.2 Mg km⁻² year⁻¹ respectively. Assuming a C concentration of 30 g C kg⁻¹, a high estimate for Sierra Nevada forest soils, this amounts to annual C inputs of 4.9 and 8.7 g C m⁻² year⁻¹, or 1.5%–2.6% of the annual belowground C gains measured across the restoration chronosequence. Disturbances that often lead to increased rates of sediment deposition (e.g., wildfire, logging, new road construction) were minimal or not present over the course of the study period, suggesting that biological processes were the dominant driver of the belowground C accumulation we measured.

CONCLUSION

Our results suggest that restoration of floodplain hydrology in montane meadows may yield annual gains in soil C that exceed global C sequestration targets for at least two decades following restoration. In 2015, the 21st Conference of Parties (COP21) of the United Nations Framework Convention on Climate Change set the goal of increasing global soil C stocks by 0.4% annually to improve food security and combat climate change (Soussana et al., 2019). Across the chronosequence of restored meadows in this study, the annual rate of increase was $3.9 \pm 1.4\%$ of soil C stocks from 0 to 15 cm and $1.6 \pm 0.5\%$ of soil C stocks from 0 to 45 cm (mean of all restored sites), highlighting the potential value of meadow restoration for climate change mitigation. These increases in belowground C stocks are further augmented by the prevention of ongoing soil C loss from degraded meadows (Reed et al., 2021). In addition to increasing ecosystem water storage and revitalizing critical habitat (Loheide & Gorelick, 2007), our findings demonstrate that

hydrologic restoration of montane meadows could be a valuable component of regional C mitigation strategies.

AUTHOR CONTRIBUTIONS

Cody C. Reed and Benjamin W. Sullivan collected field data and collected laboratory analyses; Cody C. Reed, Kimber C. Moreland and Asmeret A. Berhe conducted DRIFTS analyses, Cody C. Reed and Benjamin W. Sullivan conducted statistical analyses; Cody C. Reed wrote the manuscript with assistance from Benjamin W. Sullivan and substantial input from all authors.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Reed et al., 2022) are available from Dryad at <https://doi.org/10.5061/dryad.4j0zpc8dp>.

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