University of Nevada, Reno

Maintaining soil carbon in semiarid meadows: inputs, retention, and resulting carbon stocks

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Natural Resources and Environmental Science.

By

Brian Morra

Dr. Benjamin W. Sullivan/Dissertation Advisor

December 2022

THE GRADUATE SCHOOL

We recommend that the dissertation prepared
under our supervision by

BRIAN M. MORRA

Entitled

Maintaining soil carbon in semiarid meadows: inputs, retention, and resulting carbon stocks

Be accepted in partial fulfilment of the
requirements for the degree of

DOCTOR OF PHILOSOPHY

Benjamin W. Sullivan

Advisor

Tamzen K. Stringham

Committee Member

Paul S. J. Verburg

Committee Member

Joanna R. Blaszczak

Committee Member

Joel S. Scheingross

Graduate School Representative

Markus Kemmelmeier, Ph.D.,

Dean Graduate School

December, 2022

Abstract

Soil carbon (C) provides ecosystem services and can function as a C sink to mitigate climate change. Soil C is the result of inputs facilitated by autotrophs and respiratory losses caused by heterotrophic soil microbes. Inputs and outputs occur unevenly across the landscape creating soil C hotspots such as meadows and riparian areas. Maintaining soil C and the associated ecosystem services requires consideration of how annual weather, plant communities, edaphic characteristics, and land use interact to change the magnitude of annual C inputs and outputs. My dissertation considers the impact of these factors on annual C inputs to soils of grazed meadows in central Nevada, and the retention of C sorbed to mineral surfaces from meadows across climates. Applying insights gained from studying C inputs and outputs to management, I also present the impact of grazing management on soil and ecosystem C stocks following 27 years of grazing management. My results show that semiarid meadows have large gross inputs (580 ± 103 g C m^{-2} y^{-1}) that can be comparable to more humid ecosystems such as Mediterranean grasslands (639 ± 210 g C m^{-2}). These large inputs are likely driven by driven by antecedent root mass which is incorporated into soil C stocks consistently among years, plant communities and grazing intensities. Under years of below average precipitation, inputs to soils decreased most with high grazing intensity and remained constant where grazing was eliminated. In meadows located in humid and semiarid climates, the retention of C inputs sorbed to mineral surfaces of meadow soils is greatest in regions with high productivity. This may be due to microbial use of mineral sorbed C occurring under low productivity conditions. This work shows that grazing management consisting of grazing exclusion or changes to the timing and intensity of grazing is an effective tool to increase C inputs to soils, resulting annual gains of ecosystem C ranging from 80 to 303 g C m^{-2} annually. The impact of grazing management in riparian ecosystems can increase C stocks on geomorphic surfaces extending from the stream channel the valley edge. My dissertation shows that meadows and riparian ecosystems found in semiarid ecosystems have the potential to be large C sinks while still providing resources for grazing. Management that considers annual weather, hydrology, and plant productivity can contribute to the recovery and retention of C contained in these ecosystems.

Acknowledgements

I am thankful for the many people in my life who made this dissertation possible. The support provided both professionally and personally impacted all aspects of my dissertation. Roughly four years ago I was passing through Reno and met Ben Sullivan on the side of the highway for a free sandwich and an informal interview. At the time I was working for the forest service and felt conflicted about going back for more graduate school, having recently finished my master’s degree. He offered me the opportunity to earn a PhD in soil ecology, something I knew almost nothing about. His passion for mentoring and enthusiasm for the science his lab group conducted was contagious. I left our meeting feeling excited about going back to school. Four-years and one global pandemic later, I’m still excited about science and sandwiches. This excitement has been fuelled by the opportunities to learn new skills that ranged from building CO_2 sensors to using isotopes to study carbon cycling. Ben provided ample opportunities to learn, problem solve, and spent countless hours pushing me to become a better writer. His insight and dedication to science communication shine through every page of this document. I am also grateful for my committee, Tamzen Stringham, Joel Scheingross, Paul Verburg, and Joanna Blaszczak. In particular, I want to thank Tamzen, who has a love and understanding of rangelands that can only come from many years of experience. She is an incredible ecologist and an inspiring advocate for science-based management. I offer my thanks to the lab members, both past and present, who provided manual labour during their free time, my family who have been supportive and encouraging throughout this process, and the land managers who allowed us to work on their lands. I am also grateful for my partner Erin, who has stepped up multiple times to help me when I bit off more than I could chew with lab work. I feel lucky to have such a caring partner who is willing to come into the lab at 11 pm and spend several hours helping me finish processing samples. This work was funded by a Hatch Grant given to the Nevada Agricultural Experiment Station.

Table of contents

List of Tables

Chapter 1

Chapter 2

Chapter 3

List of Figures

Chapter 1

Chapter 2

Chapter 3

Preface

Despite the large landmass occupied by semiarid ecosystems, carbon cycling is often thought to occur at low rates in these regions. As a result, these lands are frequently overlooked in carbon cycle research. This work seeks to quantify the importance of carbon cycling in meadows and riparian areas of semiarid landscapes. I hope this dissertation will help others gain a similar appreciation for the Great Basin that I developed doing this work. Many of the areas presented in this dissertation are public lands, and it gives me great pleasure to collect and share research related to improving their management in the three chapters of my dissertation. Each chapter consists of a manuscript formatted for publication in a peer reviewed journal. References are formatted to meet the requirements of each respective journal, but paragraph heads have been edited for consistency. Since the chapters are designed for publication, I use, “we” when I refer to work that involves coauthors.

Chapter one: Carbon stocks and total belowground carbon fluxes are large, differ by plant community, and respond to weather and grazing in surface soils of semiarid montane meadows. Status: In review at Ecosystems.

Chapter two: Productivity drives mineral associated organic matter formation and the relative contribution of sorption capacity across climates. In preparation for submission to Soil Biology and Biochemistry.

Chapter three: Ecosystem carbon and nitrogen gains following 27 years of grazing management in a semiarid alluvial valley. Status: in review at Journal of Environmental Management.

Introduction

The biological carbon (C) cycle consists of inputs from photosynthesis and outputs from decomposition. The difference between inputs provided by plants and gaseous losses from decomposition dictates the size of C stocks that develop. Photosynthesis converts inorganic carbon dioxide (CO_2) to organic C. Annually, terrestrial plants fix 8.1 Gt of CO_2 (Le Quéré et al., 2014). The fate of C fixed during photosynthesis is to return to the atmosphere or be retained in soil organic matter which provides ecosystem services such as water and nutrient storage. Organic C molecules are returned to the atmosphere primarily as CO_2 or methane (CH_4). These gases trap the heat reflected off Earth's surface and have caused natural fluctuations in Earth's climate. However, human activity has transformed the C cycle through the combustion of fossil fuels and changes in land use that have sped the release of C from soils and biomass. Annually, human activity contributes an additional 2.7 Gt of C to the atmosphere as CO_2 or CH_4 (Le Quéré et al., 2009), causing an unprecedented rise in global temperatures and the depletion of soil C stocks. Understanding how to offset C emissions from fossil fuels or restore C stocks found in plants and soils may be a critical step to mitigate the impacts of an altered C cycle.

The rapid rise in greenhouse gases has caused many companies to strive to be net C neutral through the purchase of voluntary C credits (Black et al., 2021). The new revenue source that results from selling C credits may give restoration projects that sequester C monetary value (Kreibich and Hermwille, 2021). Management to restore soil C in rangelands and croplands has the potential to remove as much as 4-5 Gt CO_2 per year from the atmosphere (Paustian et al., 2019). While the potential of soils to mitigate the effects of elevated atmospheric CO_2 have been considered for decades (Lal, 2004), the incorporation of soils into voluntary carbon markets has been slow (especially outside of croplands), partly due to the difficulty associated with monitoring and verifying C fluxes to soils (Smith et al., 2020) and observations of differing permanence among soil C stocks (Bailey et al., 2019; Dynarski et al., 2020). Research that can highlight where management increases C stocks, or show what ecosystem properties build stable soil C is therefore useful to voluntary C markets and land managers seeking to gain ecosystem services associated with soil C.

This dissertation seeks to show the potential role meadows located in managed lands of Nevada can play in C sequestration. Managed lands, which are primarily used for grazing, make up 61% of Nevada (BLM, 2022). These rangelands may represent an opportunity to sequester C locally through changes in the timing and intensity of grazing. Livestock consumption of forage is commonly standardized per animal per unit time and is referred to as an animal unit month (AUM). Here, grazing management reduced the use of specific pastures but retained similar AUMs by spreading cattle into other regions not considered in this study. I therefore describe grazing treatments as managed or changed rather than reduced. Consideration of the role grazing plays in local economies (Jonathan et al., 2006) is critical for creating realistic plans that use rangelands as C sinks. This work shows the potential C stock or flux changes that can occur in conjunction with grazing as well as additional C gains that may occur under grazing exclusion. Grazing management approaches that lead to C sequestration have the potential to augment rancher income with C credits. In some cases, grazing exclusion may sequester more C but cause negative impacts to ranching communities. In Chapters 1 and 3, I provide information on the possible outcomes of changes to grazing or exclusion but the merit of one approach or another is a social policy issue and is outside the scope of this work.

I focus on C cycling in meadows and riparian areas found in rangelands as they are focal points for grazing (Trimble and Mendel, 1995; Wu et al., 2010), contain soil C stocks that respond to management (Matzek et al., 2020; Reed et al., 2022) and have been shown to sequester or emit C at rates disproportionate to their spatial extent when compared to their surrounding upland ecosystems (Norton et al., 2014; Reed et al., 2021). The stark contrast between C cycling of meadows and their surrounding uplands makes them hotspots of C on the landscape. Hotspots are thought to be the result of converging hydrologic flow paths (Mcclain et al., 2003). As groundwater dependent ecosystems, meadows form where water provided by the landscape creates seasonally inundated regions of montane ecosystems. The moisture found in meadows is provided by groundwater upwelling and surface flows generated by spring snow melt. In riparian meadows, water is supplied to floodplains adjacent to stream channels (Weixelman et al., 2011). Access to shallow water during the growing season helps support plant communities characterized by herbaceous vegetation that forms dense root mats. In hydrologically functioning meadows, roots supply C to soils as root turnover and exudation, allowing for soil C inputs to outpace gaseous losses from heterotrophic respiration (Reed et al., 2021; Schwieger et al., 2021). The following three chapters contain research about the impact of grazing and annual weather on C inputs to soils, how climate, soil characteristics, and productivity control the retention of those inputs within soil C pools, and decadal trends in ecosystem C following changes to grazing practices.

In Chapter 1, I measured total belowground C flux (TBCF) to soils in three different meadow plant communities to quantify how C inputs to soils change with grazing intensity among plant groups. This study captured the impact of grazing management during years of reduced precipitation, a trend likely to continue as a result of climate change (Abatzoglou and Kolden, 2011).

In Chapter 2, I measured the allocation of plant C inputs to soils into different soil C fractions. I explored how this allocation to soil C fractions changed between high and low productivity regions of meadows from humid or semiarid climates. Using C isotopes, I quantified the retention of C inputs in different soil C fractions that have been shown to contribute to long-term and short-term soil C storage. These fractions are known as mineral associated organic matter (MAOM) and particulate organic matter (POM) respectively. Long-term storage is provided by charges found on mineral surfaces, which may limit the amount of C held as MAOM.

In Chapter 3, I explore the potential of grazing management to restore ecosystem C stocks, and the uncertainty associated with gains following management change. This chapter uses the measurements of uncertainty to estimate the time required to see significant changes in ecosystem C relative to unmanaged regions.

Collectively, the chapters of this dissertation were designed to provide estimates of changes to C stocks and fluxes under different land use scenarios. While policy decisions related to C management in Nevada are still in development, collecting data showing the impact of management on C stocks found in the understudied meadows located in semiarid rangelands of Nevada may help guide future legislation. In the absence of policy changes, voluntary C markets may provide monetary incentives for land managers interested in changing their grazing management to improve the ecosystem services provided by healthy soils.

References

Abatzoglou, J.T., Kolden, C.A., 2011. Fire and Invasive Plants Special Feature Climate Change in Western US Deserts : Potential for Increased Wildfire and Invasive Annual Grasses. Rangeland Ecology and Management 64, 471–478. doi:10.2111/REM-D-09-00151.1

Bailey, V.L., Pries, C.H., Lajtha, K., 2019. What do we know about soil carbon destabilization? Environmental Research Letters 14, 83004. doi:10.1088/1748-9326/ab2c11

Black, R., Cullen, K., Fay, B., Hale, T., Lang, J., Smith, S., 2021. Taking Stock: a global assessment of net zero targets. Energy & Climate Intelligence Unit and Oxford Net Zero 1–30.

BLM, 2022. NEVADA RANGELAND MANAGEMENT AND GRAZING [WWW Document]. URL https://www.blm.gov/programs/natural-resources/rangeland-and-grazing/rangeland-health/nevada

Dynarski, K.A., Bossio, D.A., Scow, K.M., 2020. Dynamic Stability of Soil Carbon: Reassessing the “Permanence” of Soil Carbon Sequestration. Frontiers in Environmental Science 8. doi:10.3389/fenvs.2020.514701

Jonathan, A., Elizabeth, F., Harris, T., 2006. ANALYSIS OF IMPACTS OF PUBLIC LAND GRAZING ON THE ELKO COUNTY ECONOMY : PART III : ECONOMIC IMPACTS OF FEDERAL GRAZING IN ELKO COUNTY. Reno Nevada.

Kreibich, N., Hermwille, L., 2021. Caught in between: credibility and feasibility of the voluntary carbon market post-2020. Climate Policy 21, 939–957. doi:10.1080/14693062.2021.1948384

Lal, R., 2004. Soil carbon sequestration impacts on global climate change and food security. Science 304, 1623–1627. doi:10.1126/science.1097396

Le Quéré, C., Peters, G.P., Andres, R.J., Andrew, R.M., Boden, T.A., Ciais, P., Friedlingstein, P., Houghton, R.A., Marland, G., Moriarty, R., Sitch, S., Tans, P., Arneth, A., Arvanitis, A., Bakker, D.C.E., Bopp, L., Canadell, J.G., Chini, L.P., Doney, S.C., Harper, A., Harris, I., House, J.I., Jain, A.K., Jones, S.D., Kato, E., Keeling, R.F., Klein Goldewijk, K., Körtzinger, A., Koven, C., Lefèvre, N., Maignan, F., Omar, A., Ono, T., Park, G.-H., Pfeil, B., Poulter, B., Raupach, M.R., Regnier, P., Rödenbeck, C., Saito, S., Schwinger, J., Segschneider, J., Stocker, B.D., Takahashi, T., Tilbrook, B., van Heuven, S., Viovy, N., Wanninkhof, R., Wiltshire, A., Zaehle, S., 2014. Global carbon budget 2013. Earth System Science Data 6, 235–263. doi:10.5194/essd-6-235-2014

Le Quéré, C., Raupach, M.R., Canadell, J.G., Marland, G., 2009. trends in the sources and sinks of carbon dioxide. Nature Geoscience 2, 831–836. doi:10.1038/ngeo689

Matzek, V., Lewis, D., O'Geen, A., Lennox, M., Hogan, S.D., Feirer, S.T., Eviner, V., Tate, K.W., 2020. Increases in soil and woody biomass carbon stocks as a result of rangeland riparian restoration. Carbon Balance and Management 15, 1–15. doi:10.1186/s13021-020-00150-7

Mcclain, M.E., Boyer, E.W., Dent, C.L., Gergel, S.E., Grimm, N.B., Groffman, P.M., Hart, S.C., Harvey, J.W., Johnston, C.A., Mayorga, E., Mcdowell, W.H., Pinay, G., 2003. Biogeochemical Hot Spots and Hot Moments at the Interface of Terrestrial and Aquatic Ecosystems 301–312. doi:10.1007/s10021-003-0161-9

Norton, J.B., Olsen, H.R., Jungst, L.J., Legg, D.E., Horwath, W.R., 2014. Soil carbon and nitrogen storage in alluvial wet meadows of the Southern Sierra Nevada Mountains, USA. Journal of Soils and Sediments 14, 34–43. doi:10.1007/s11368-013-0797-9

Paustian, K., Larson, E., Kent, J., Marx, E., Swan, A., 2019. Soil C Sequestration as a Biological Negative Emission Strategy. Frontiers in Climate 1, 1–11. doi:10.3389/fclim.2019.00008

Reed, C., Berhe, A., Moreland, K., Wilcox, J., Sullivan, B., 2022. Restoring function: Positive responses of carbon and nitrogen to 20 years of hydrologic restoration in montane meadows. Ecological Applications 0–2. doi:10.1002/eap.2677

Reed, C., Merrill, A., Drew, M., Christman, B., Hutchinson, A., Keszey, L., Swanson, S., 2021. Montane Meadows: A Soil Carbon Sink or Source? Ecosystems. doi:10.1007/s10021-020-00572-x

Schwieger, S., Kreyling, J., Couwenberg, J., Smiljanić, M., Weigel, R., Wilmking, M., Blume-Werry, G., 2021. Wetter is better: rewetting of minerotrophic peatlands increases plant production and moves them towards carbon sinks. Ecosystems. doi:10.1007/s10021-020-00570-z

Smith, P., Soussana, J.F., Angers, D., Schipper, L., Chenu, C., Rasse, D.P., Batjes, N.H., van Egmond, F., McNeill, S., Kuhnert, M., Arias-Navarro, C., Olesen, J.E., Chirinda, N., Fornara, D., Wollenberg, E., Álvaro-Fuentes, J., Sanz-Cobena, A., Klumpp, K., 2020. How to measure, report and verify soil carbon change to realize the potential of soil carbon sequestration for atmospheric greenhouse gas removal. Global Change Biology 26, 219–241. doi:10.1111/gcb.14815

Trimble, S.W., Mendel, A.C., 1995. The cow as a geomorphic agent — A critical review. Biogeomorphology, Terrestrial and Freshwater Systems 13, 233–253. doi:10.1016/b978-0-444-81867-6.50019-8

Weixelman, D., Cooper, D., Hill, B., Berlow, E., Viers, J., Purdy, S., Merrill, A., Gross, S., 2011. A field key to meadow hydrogeomorphic types for the Sierra Nevada and Southern Cascade Ranges in California. Vallejo, CA.

Wu, Y., Tan, H., Deng, Y., Wu, J., Xu, X., Wang, Y., Tang, Y., Higashi, T., Cui, X., 2010. Partitioning pattern of carbon flux in a Kobresia grassland on the Qinghai-Tibetan Plateau revealed by field 13C pulse-labeling. Global Change Biology 16, 2322–2333. doi:10.1111/j.1365-2486.2009.02069.x

Chapter 1: Carbon stocks and total belowground carbon fluxes are large, differ by plant community, and respond to weather and grazing in surface soils of semiarid montane meadows.

Authors: Brian Morra[1], Will Richardson[2], Tamzen Stringham[2], Benjamin W. Sullivan[1,3]

[1] Department of Natural Resources & Environmental Science, The University of Nevada, Reno,

1664 N. Virginia St., Reno, NV 89557

[2] Department of Agriculture, Veterinary, and Rangeland Sciences, The University of Nevada, Reno, 1664 N. Virginia St., Reno, NV 89557

[3] The Global Water Center, The University of Nevada, Reno, 1664 N. Virginia St., Reno, NV 89557

Abstract

Montane meadow ecosystems are regional carbon (C) hotspots relative to surrounding uplands and can be substantial C sinks or sources. In the semiarid Great Basin region of the western United States, meadows are vital to hydrology, livestock production, and wildlife. To elucidate factors contributing to meadow C cycling in the Great Basin, we measured the impact of interannual weather, grazing, vegetation communities, and edaphic characteristics on carbon stocks and total belowground C flux (TBCF) in meadows. Meadow carbon stocks were three times larger than the total ecosystem carbon found in their surrounding uplands. This makes Great Basin meadows a stronger hotspot than meadows in other regions. The surface (0-15 cm) soil was the main source of TBCF change and surface soil TBCF rates were high and varied from -6.78 kg C m^{-2} y^{-1} to 8.18

kg C m^{-2} y^{-1} depending on precipitation, grazing, and vegetation community. Because TBCF is a gross C flux, values near or below zero likely indicate soil C loss. Belowground carbon fluxes differed by plant community, decreased during drier years, and benefited from grazing reduction during periods of below average precipitation. Soil C change dominated TBCF and was associated with antecedent root mass. Roots consistently contributed 40% of their biomass to soil C. Per mole, carbon dioxide dominated the flux of greenhouse gases when accounting for warming potential of methane and nitrous oxide. Grazing management and interannual weather variation can influence the C sink of Great Basin meadows, which should be considered in regional C inventories.

Introduction

Soils contain more carbon (C) than plants and the atmosphere combined (Hiederer and Köchy 2012) and soil C provides ecosystem services like soil stability, atmospheric carbon dioxide (CO_2) sequestration, and storage of nutrients and water (Schmidt and others 2011). Soil C is unevenly distributed across Earth’s surface primarily because of imbalances between autotrophic inputs and heterotrophic outputs. Fluxes of C in or out of soils have different climatic and edaphic drivers that can change with management. Because ecosystems with large C stocks and fluxes can have a disproportionate contribution to regional C budgets (Dutta and others 2006), understanding C fluxes in managed ecosystems with large C stocks is important for maintaining ecosystem services.

Per unit area, montane meadows appear to be C hotspots relative to surrounding upland ecosystems. For example, meadow soil C stocks in the Sierra Nevada in the states of California and Nevada, USA exceed 20 kg m^{-2}, more than 1.5 times the soil C contained in the surrounding upland (Norton and others 2014). Is the degree to which meadows contrast with their surrounding uplands consistent among climates? Climate might alter the degree to which meadow C stocks differ from their surrounding uplands by either altering upland C stocks or meadow C stocks. Total ecosystem C stocks in upland montane forests surrounding meadows in the Sierra Nevada mountains of California, USA can be 32 kg C m^2 (Mattson and Zhang 2019), while drier and warmer upland montane ecosystems found at similar elevations of the Great Basin, USA have ecosystem C stocks as low as 4 kg C m^2 (Rau and others 2011). Alternatively, climate may impact meadow C stocks themselves: soil C stocks decreased with increasing mean annual temperature (MAT) and increased with mean annual precipitation (MAP) in grassland meadows of Yunnan Province, China (Balasubramanian and others 2020). As groundwater-dependent ecosystems, meadows exist in semiarid regions (regions receiving less than 50 cm of rain annually) because their hydrogeomorphic landscape position accumulates water from the surrounding watershed, which is sensitive to climate. Therefore, relative to uplands, meadows in semiarid ecosystems may be “hotter” hotspots, “cooler” hotspots, or may not be different than meadows in more humid regions.

The accumulation of soil moisture in meadows from the surrounding watershed can result in extended periods of shallow groundwater levels. Spatial and temporal variation in depth to groundwater influences the distribution of plants within meadows (Allen-Diaz 1991, Castelli and others 2000). Meadow plant distribution drives C cycling and storage by creating an imbalance between C inputs and outputs (Norton and others 2014, Reed and others 2021). Though meadow vegetation is diverse, it can be grouped into communities based on a tolerance of, or reliance on, shallow groundwater. Plant communities range from wetland-obligate herbaceous plants to upland shrubs (Castelli et al., 2001; Stringham et al., 2001; Darrouzet-Nardi et al., 2006) These communities may differ in their annual productivity and proportion of C allocated belowground (De Deyn and others 2008, Norton and others 2011, Reed and others 2021). Meadows with more wetland-obligate or facultative plants experienced net C sequestration, whereas meadows with more upland plants experienced net C loss. This difference was attributed to different rates of plant inputs to soil, not respiratory losses of soil C (Reed and others 2021).

Shallow groundwater may cause anoxic soil conditions that slow decomposition and promote the use of alternative terminal electron acceptors such as CO_2 or NO_3^- by soil bacteria and archaea. These metabolic pathways are responsible for the production of methane (CH_4) and nitrous oxide (N_2O), which have 30 and 200 times the warming potential of CO_2 respectively (Myhre and Shindell 2011). The production of potent climate warming gases has the potential to offset the net C fixed by plants (Hemes and others 2018). In some meadows, fluxes of CH_4 and N_2O were substantially smaller than fluxes of CO_2 (Reed and others 2021). However, because C fluxes to soil in semiarid ecosystems might be smaller than C fluxes in more humid ecosystems, the possibility remains that some meadow C sinks could be offset by CH_4 or N_2O production.

Belowground C fluxes can be further altered by management activities such as grazing via direct impacts to plant communities or indirect effects on plants due to changes in hydrology - and grazing impacts may change with climate (Milchunas and others 1988, Trimble and Mendel 1995, Enriquez and others 2015). In some cases, grazing may cause a compensatory growth response and belowground C stocks are increased (Hafner and others 2012). The compensatory growth response can be decreased (Zhao and others 2008) or increased by low soil moisture (Van Staalduinen and Anten 2005). Grazing was associated with lower C stocks in drier portions of meadows than wetter ones (Norton and others 2011) and grazing reduced meadow soil C stocks in dry climates with fine textured soils (Mcsherry and Ritchie 2013, Enriquez and others 2015). In severe cases, grazing can contribute to the establishment of shrubs or annual plants (McIlroy and Allen-Diaz 2012) by altering hydrology through the formation of dominant flow paths, leading to incised channels (Trimble and Mendel 1995, Darrouzet-Nardi and others 2006, Loheide and Gorelick 2007). Following incision, increased depth to groundwater allows shrubs to replace bank-stabilizing herbaceous vegetation, allowing for further erosion and continued channel incision (Debinski and others 2010). This shift in vegetation may convert meadows from net C sinks to net C sources. While less-impacted meadows can gain soil C at rates of 300-850 g C m^{-2} y^{-1}, hydrologically impacted meadows in the California Sierra Nevada, USA lost soil C at an average rate of ~400 g C m^{-2} y^{-1} and had greater depth to groundwater, less root biomass, more bare ground, and more xeric vegetation (Reed and others 2021).

It is likely meadows disproportionately contribute to the C cycle and forage production of semiarid regions. These areas remain productive long after upland areas experience annual water limitations and concentrate wild and domesticated herbivores due to dense communities of herbaceous vegetation. To understand how grazing interacts with moisture availability to impact soil C cycling in semiarid meadows, we designed this study to address the following questions:

a. How do meadow C stocks in semiarid meadows differ from surrounding upland ecosystems and meadows in more humid climates?

b. What are the gross rates of belowground C flux in semiarid meadows, and how do they differ among different meadow vegetation communities, grazing regimes, and years with different antecedent winter precipitation? Do trace gases such as CH_4 and N_2O mitigate meadow C sequestration rates?

c. What are the ecosystem characteristics associated with changes in carbon flux in semiarid meadows?

Methods

Site description

This research was conducted in four meadows in the Desatoya Mountains in central Nevada (Figure 1A), USA, a semiarid region of the Great Basin which has a mean annual precipitation of 315 mm, a mean annual temperature ranging from 4.6 to 7.6 °C, and a 30-year average of 5.8 °C (Prism Climate Group, 2022). Our study meadows ranged in size from 0.2 ha to 1.4 ha and were located between 2280 and 2400 meters above sea level (Figure 1B). Similar meadows can be found throughout the Great Basin (Germanoski and Miller, 2004). Our study captured the wettest (419 mm in 2019) and driest (175 mm in 2020) conditions in the last 30 years (Prism Climate Group 2022).

Data collection began in the spring of 2019 and captured one season of consistent grazing across the four meadows. Grazing by wild horses (*Equus ferus)* was uncontrolled while cattle (*Bos taurus)* grazed in late spring. In November 2019, fences were built to split three of the four meadows into grazing exclusion and managed grazing treatments (Figure 1C). Managed grazing excluded horses all year; cattle grazing began in mid-June and continued until forage species were consumed to a stubble height of 10 cm (Hall and Bryant 1995). The fourth meadow was left unfenced and maintained year-round use by wild horses and seasonal cattle grazing (unmanaged grazing). With two grazing levels across three meadows and one meadow with unmanaged grazing, we established a total of seven sites (Figure 1B). Within each of the seven sites, three plant communities were delineated by Richardson and others (2021) based on degree of dependence on shallow water tables. Defined here as wet, mesic, and edge plant communities, each community contained a set of three replicated plots creating a total of 63 plots where data were collected to measure C fluxes (Figure 1C; Figure S1).

Soil, plant, and greenhouse gas sampling

We collected soil cores in the spring of 2019, 2020, 2021 and the fall of 2020 and 2021 to assess soil and root C stocks. We cored 0-45 cm soil in each of the three replicated plots with a five cm-diameter slide hammer (AMS Equipment Corp, American Falls, Idaho) in stratified 15-cm depth increments (see Appendix A Methods for more detail). Following sample collection, bulk density was calculated using the rock-free, root-free mass of dry soils that passed through a 2 mm sieve. Soil C stock (g C cm^{-2}) was the product of the measurement depth, bulk density and soil percent C measured using a Costech 4010 Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA). To minimize uncertainty associated with changes in bulk density and soil moisture, we applied the mean plot level bulk densities from the Fall 2020 and Fall 2021 sampling events, when soils were driest, to all seasonal C stock estimates. Comparing the average fall bulk density to the bulk density we measured at each time point gave a mean square error of 0.01, giving us confidence that annual changes in bulk density due to sampling events were minimal. By using the average plot-level bulk density, we compared changes in soil C concentration and used bulk density to standardize measurements for comparison with the other components of belowground C flux (Equation 1).

Each year, we collected aboveground herbaceous plant biomass at peak biomass and at the end of the growing season at each location where a soil core was taken. Herbaceous plant biomass was oven dried at 60 °C and a subset of three aboveground tissue samples and three root samples from each of the 3 plant groups were ground using a Wiley Mill (Thomas Scientific, Philadelphia, PA, USA) and analyzed for C concentration with elemental analysis. We used percent C measurements to convert grams of herbaceous biomass (aboveground tissues and roots) to grams C.

We measured greenhouse gas (GHG; CO_2, CH_4 and N_2O) fluxes approximately every three weeks during the growing season in 2019, 2020, and 2021 for a total of 18 GHG sampling events. We measured GHG fluxes using the same static chamber and gas chromatography methods described in Reed and others (2018); see Appendix A Methods for more detail. During gas sampling, we measured soil moisture and temperature using two methods: time domain reflectometry (TDR) and analog thermometers for high spatial resolution (n = 63 per sampling event) and soil moisture and temperature probes deployed at the plant community level (n = 21) for high temporal resolution. See

Appendix A Methods for instrumentation details. We used the high temporal resolution data to interpolate daily values between monthly measurements taken at high spatial resolution as explained in Appendix A Methods.

We used C gas fluxes, root C, soil C, and aboveground herbaceous C to calculate total belowground C flux (TBCF; Equation 1). Total belowground C flux is a mass balance approach which uses the sum of gaseous losses of C from soils (CO_2 and CH_4) (respired soil C) and changes in C stored in roots (Δ Root C) and soils (Δ Soil C) to estimate the gross flux of C to soils from plants (Raich and Nadelhoffer, 1989; Giardina and Ryan, 2002)

$$\mathrm{TBCF} = \frac{\Delta\ \mathrm{soil\ C} + \Delta\mathrm{Root\ C} + \mathrm{respired\ soil\ C} - \Delta\mathrm{litter\ C}}{\mathrm{time}} \qquad \text{(Equation 1)}$$

We estimated TBCF for the three growing seasons of 2019, 2020, and 2021. The growing season lengths were based on site access due to snowpack in spring and temperature and water content in the fall. Growing seasons lasted 115, 116, and 138 days for 2019, 2020, and 2021 respectively. For 2019, the change in soil C stock and root C stock was calculated as the difference between stocks measured in spring 2019 and spring 2020, while changes in soil C stock for 2020 and 2021 were calculated as the difference between spring and fall soil C stocks. We justify the difference in pretreatment sampling and post treatment sampling with the assumption that there would be very little difference between soil C stocks (root and soil C) measured in late October of 2019 and at the start of the 2020 growing season in early May of 2020, and the impact of grazing was likely minimal over the winter months. Following the implementation of different grazing treatments, we increased the temporal resolution of our sampling to capture soil and root

C stocks leading up to and following annual grazing. Our plots never developed a litter layer and we assumed end of season standing biomass C was equal to change in litter C. We ignored aboveground litter inputs from woody plants (*Artemisia* spp.) because their contribution to litter in our plots was minimal.

Upland C stocks

To contextualize the importance of meadow C in the Great Basin region relative to potential surrounding Great Basin upland vegetation C stocks, we conducted a literature review of C stocks in ecosystems characterized by dominant species common to semiarid regions of the Great Basin: *Artemesia* spp., *Bromus tectorum*, and *Pinus monophyla*. We used five data sets that contained 11 mean values to represent an average soil C stock, four data sets containing nine mean values to represent an average root C stock, and four data sets containing nine mean values to represent an average aboveground biomass C stock in regional upland vegetation that might surround a Great Basin meadow. A full list of studies and mean values can be found in Table S1.

Statistics

All statistical tests were performed using R (R Core Team, 2021). In the effort to prioritize effect sizes, we report *p* values associated with the results and allow the reader to determine the strength of the evidence against null hypotheses.

To assess differences among meadow C stocks and compare meadow C stocks to those measured in upland ecosystems reported in our literature review, plot-level measurements were averaged across all five sample dates. We used analysis of variance (ANOVA) and Tukey's honest significance test (Tukey's HSD) to measure differences among C pools.

Our TBCF approach is based upon a before-after-control-impact (BACI) study design. In a similar low-replication, complex BACI design, Ellison and others (2010) recommended presenting the slope of the line of the response variable (TBCF) as a function of time as the effect size to integrate change following the implementation of a treatment. We fit linear mixed models to plot-level data (plant level data nested within grazing intensity) that included a random intercept for the individual plot as a way of accounting for dependence among repeatedly sampled plots. We present the slopes of the mixed linear models as the effect size associated with the plot level data. We then compared the slopes among linear models using an analysis of covariance (ANCOVA) (Gotelli and Ellison, 2004). The results of the ANCOVA were used to show the main effects (plant community, grazing treatment, and time) as well as the interactions among grazing intensity, plant community, and time. We used t-tests to determine the probability of TBCF and change in soil C stock being different than zero (positive) for a given plant community experiencing a particular grazing intensity.

We wanted to quantify the importance of properties within the soil environment as drivers of TBCF. We selected eight variables associated with the soil environment to analyze for their importance in explaining TBCF: peak biomass, days of vegetative growth, average volumetric water content (VWC) for the growing season, average soil temperature for the growing season, soil drought days, soil drying rate, average VWC in the first month of observation, and average soil temperature for the first month of observation. The calculation of these values is explained in the supplementary materials. We focused this analysis on shallow soils (0-15 cm) because soil temperature and moisture measurements were confined to shallow soil depths. These nine variables were evaluated using backward stepwise linear regression and ranked based on their Akaike information criterion (AIC) score. To explore the role of roots in TBCF we used linear models to explore the relationships between antecedent root mass and soil C stocks.

Results

Meadow C stocks

Soil C in the 0-45 cm depth was consistently the largest component of ecosystem C stocks, followed by root C and aboveground C (Figure 2). Soil C stocks were different among the three plant communities ($p < 0.001$): mesic and wet plant communities had similar soil C stocks (13.00 ± 0.18 and 12.03 ± 0.24 kg C m^{-2}, respectively) while the edge plant community had smaller soil C stocks (9.50 ± 0.21 kg C m^{-2}) (Figure 2). In each vegetation group, soils contained nearly six times the C found in the other pools combined. Root C and aboveground C stocks were similar among the three meadow plant communities.

Per unit area, these meadows had larger C stocks than literature-derived estimates for typical surrounding upland Great Basin ecosystems dominated by *Artemesia* spp., *Bromus tectorum,* and *Pinus monophyla* (Figure 2). Compared to upland Great Basin ecosystems, meadows hold proportionally more of the total C stock in soil and roots than aboveground vegetation. These meadow soil C stocks were three times greater; root C stocks were two times greater, and aboveground C stocks were six times lower than in upland Great Basin ecosystems.

Components of TBCF

Total belowground C flux varied between -6.78 kg C m^{-2} y^{-1} and 8.18 kg C m^{-2} y^{-1} across all growing seasons, plant communities, and grazing treatments. Averaged across growing seasons, the edge, mesic, and wet plant communities had TBCF rates of 0.35 ± 0.03, 0.75 ± 0.03, and 0.65 ± 0.03 kg C m^{-2} y^{-1}, respectively. Overall, the largest individual flux that contributed to TBCF was change in soil C stock, followed by soil respiration and root C change (Figure 3A). End of season herbaceous biomass, which represents aboveground plant litter flux to meadow soil, was the smallest flux and was an order of magnitude smaller than changes in soil C stock (Figure 3A). We primarily saw annual gains in soil C stocks occurring in shallow soils (0-15 cm), during 2019, an abnormally wet year, while losses only occurred in the edge community of unmanaged grazing (Figure 4). By 2021, change in soil C stock was not different than zero across grazing intensities and plant communities. When we averaged TBCF across growing seasons and grazing treatments, TBCF in the top 15 cm of soil accounted for over 75% of the TBCF measured in the 0-45 cm depth in all three vegetation communities (Fig. 3B). Therefore, we will focus on shallow soil (0-15 cm) TBCF when exploring the impacts of vegetation community, grazing, and the physical environment on TBCF.

Total belowground C flux among plant communities and grazing regimes

In shallow soils (0-15 cm), TBCF was generally highest in 2019 and declined through 2021 (growing season main effect: $p < 0.001$). Surface soil TBCF differed by grazing intensity (grazing main effect: $p = 0.008$) and among plant communities (plant community main effect: $p = 0.059$). The 2019-2021 interannual decline in TBCF showed modest differences with grazing intensity (grazing by growing season interaction: $p = 0.063$) but not by plant community (plant community by growing season interaction: $p = 0.12$) or the interaction of grazing intensity and plant community (plant community by grazing by growing season interaction: $p = 0.58$).

Shallow soil TBCF was positive in all three plant communities in 2019 (when all meadows were grazed prior to fencing, which occurred after the 2019 growing season) (Figure 5; $p < 0.1$). In 2020, we measured positive TBCF in the wet plant community experiencing managed grazing ($p = 0.04$). By 2021, TBCF was not different from zero under any grazing treatment or plant community (p values ranged from 0.26 to 0.96).

Linear models estimated a minimal decline in TBCF of 0.31 kg C m^{-2} y^{-1} from 2019 to 2021 where grazing was excluded in 2020 and 2021, averaged across all plant communities (Figure 5; $p = 0.14$). Relative to grazing exclusion, the average decline in TBCF between 2019 and 2021 was two times higher under managed grazing (0.84 kg C m^{-2} y^{-1}; $p < 0.001$) and almost four times higher under unmanaged grazing (1.2 kg C m^{-2} y^{-1}; Figure 5; $p = 0.003$). Under unmanaged grazing, the wet vegetation community had the largest decrease in TBCF between 2019 and 2021, decreasing by 2.13 kg C m^{-2} y^{-1} (Figure 5; $p = 0.04$). This interannual decrease in TBCF was twice as large as the next largest decrease which occurred in the mesic plant community of managed grazing (1.01 kg C m^{-2} y^{-1}; $p = 0.02$).

Mechanisms controlling TBCF

We sampled each plot for soil C and root biomass five times between 2019 and 2021, allowing us to correlate soil C stocks and antecedent root mass at four time points during this study (Table 1). At a meadow level (n=4) in shallow soils (0-15 cm), we found positive correlations (Table 1) between C stock and antecedent root mass during three out of the four sampling dates. Where correlations existed, soil C stocks consistently changed, positively or negatively, by ~40% of antecedent root mass. When we combined wet and mesic plant communities (and excluded the edge community), only spring soil C stock was correlated to antecedent root mass ($p = 0.08$ and 0.04) (Table 1). Root mass in the spring contributed little to fall soil C stocks with slopes ranging from 0.03 to -0.06 kg y^{-1} ($p = 0.76$ and 0.70; Table 1). In the edge community, antecedent root mass predicted soil C stocks in one spring sampling and one fall sampling.

Stepwise linear model selection showed different environmental controls on TBCF among plant communities. However, the most parsimonious models for each plant community only explained a fraction of variation in TBCF (r^2 values between 0.07 and 0.20; Table S3). Peak aboveground herbaceous biomass was the most important variable for predicting changes in belowground C fluxes in edge and wet communities. Additionally, the best models for wet and edge plant communities omitted soil drying rate and percent drought days. In the mesic plant community, the models with the lowest AIC were those related to water availability, including spring VWC, number of growing days, and soil drying rate.

Soil greenhouse gas fluxes

Soil CO_2 efflux was the largest component of total greenhouse gas flux measured during the growing season, even when accounting for higher radiative forcing capacities of CH_4 and N_2O (Table 2). The next largest gas flux, CH_4, was between three and four orders of magnitude smaller than soil CO_2 flux. The average growing season CH_4 production rates were 2%, 1%, and 6%, of the annual CO_2 flux in the edge, mesic and wet plant communities, respectively, when converted to eCO_2. Across grazing treatments and years, only the wet vegetation community was a net CH_4 source. Soil N_2O fluxes were between five and six orders of magnitude smaller than CO_2 fluxes.

Discussion

Meadows are a hotspot of the C cycle of the semiarid Great Basin, beginning with large soil C stocks which rival stocks found in more humid meadow ecosystems, and continuing with large and dynamic gross soil C fluxes. Total belowground C flux in meadows was largely made up of change in soil C stock resulting from root turnover. Along with changes in soil C and root mass, TBCF was driven by edaphic characteristics that varied among plant communities, reflecting different patterns in groundwater and root morphology within meadows. We observed the integrated effects of annual weather, plant community, and grazing intensity to show how TBCF differed among plant communities, decreased during drier years, and benefited from grazing reduction during periods of below average precipitation. Given management and weather, meadows in semiarid ecosystems are a potential atmospheric C sink even when considering trace gases such as CH_4 and N_2O.

The importance of semiarid meadows to the regional C cycle

Our meadow C stocks were only ~20% lower at equivalent depths to meadows in more humid montane regions (Reed and others 2021), but three times greater than surrounding semiarid upland ecosystem C stocks. Montane meadows in more humid regions contain only half the C stock of surrounding forests (32.30 kg C m^{-2}; Mattson and Zhang 2019). Because meadow C is largely belowground, it is less vulnerable to fire, a common montane disturbance, than aboveground C.

Total belowground C fluxes from mesic and wet plant communities were three times larger than upland rates of gross primary productivity (GPP) measured in the Great Basin, which ranged from 0.38 to 0.51 kg C m^{-2} y^{-1} (Pandit and others 2019). Given TBCF must be smaller than GPP, TBCF in meadows vastly exceeds TBCF in regional upland ecosystems. Gross C fluxes to soils measured in these meadows are large and dynamic relative to measurements of TBCF found in more humid ecosystems. For example, from 2019 through 2021 we measured mean (across vegetation groups) annual meadow TBCF values of 1.2 ± 0.22, 0.61 ± 0.23, and -0.11 ± 0.18 kg C m^{-2} y^{-1}, values which are among the lowest and highest TBCF rates identified in a meta-analysis by Gill and Finzi (2016). Such high gross flux rates are supported by high net C flux rates in other meadows. Using different methodologies, Blackburn and others (2021) and Reed and others (2020) estimated net belowground C fluxes between -0.59 to +0.85 kg C m^{-2} y^{-1}, placing meadows among both the largest terrestrial net C sinks (Baldocchi, 2008) and sources like degraded peatlands (Kareksela and others 2015).

Meadow TBCF in context

Methodological approaches challenge comparisons between this and other studies of TBCF and its constituent fluxes. Most TBCF measurements have occurred in forests (Gill and Finzi, 2016). In forest studies, changes in soil and root C have often been assumed to be negligible and are omitted, making TBCF equal to the difference between soil respiration and litterfall (Gill and Finzi 2016). In studies that have included change in soil C, it was the smallest component of TBCF, increasing by 0.01 kg C m^{-2} y^{-1} in eucalyptus plantations (Giardina and Ryan, 2002) and decreasing by 0.01 kg C m^{-2} y^{-1} in temperate grasslands (Adair and others 2009).

While change in soil C was the largest flux involved in meadow TBCF here, the consistent correlations showing 40% of root mass contributes to soil C stock helps explain dynamic meadow soil C stocks. This proportional contribution of biomass to soils has also been observed by Parsons and others (1983), who found that 42% of GPP was recovered as dead tissue in perennial ryegrass pastures. Differences in the timing of root contributions to soil C among plant communities shows the different patterns in C allocation among functional groups. In the herbaceous-dominated communities, roots at the end of the previous growing season were responsible for changes in soil C stock in the subsequent year, rather than the roots present in the current spring. Similar fall season contributions of roots to soil C have been reported by Hooker and Stark (2012), who found root litter from perennial grasses in semiarid regions was the dominant flux to stable soil C pools. They proposed this was due to the higher moisture content of the recently abscised root tissue relative to the surrounding soil. By contrast, in the shrub-dominated edge plant community, root mass may have a more consistent contribution to soil C stock throughout the growing season, as there were no consistent seasonal patterns between antecedent root mass and soil C stocks. The differences in the role of roots for soil C among plant communities are likely due to differing root morphologies of shrubs found in the edge plant community (characterized by woody coarse roots) and the herbaceous dominated wet and mesic plant community containing short-lived fine roots (Zhang and Wang 2015).

While the bulk of meadow TBCF variability can be explained by roots changing the soil C stock, as groundwater dependent ecosystems, other ecosystem characteristics explain limited variability (<15%) of meadow C flux, though in different ways among vegetation communities. Spring VWC was the only variable common among the most parsimonious models for wet, mesic, and edge plant communities, and TBCF was higher with wetter soil, highlighting spring snowmelt as an overall driver of TBCF among meadow plant communities. The most parsimonious models for the wet and edge plant communities both included aboveground biomass despite different water availabilities in each community. Wet and edge plant communities may have similar controls on TBCF because they experience longer periods of consistent depth to groundwater – either shallow (wet) or deep (edge). However, the mesic plant community might experience a wider range of rooting depths as wet conditions limit rooting depth for a portion of the growing season, followed by periods of drying where downward root growth must keep pace with increasing depth to groundwater (Darrouzet-Nardi and others 2006). The differing drivers of TBCF among plant communities are likely due to groundwater effects similar to those described by Castelli and others (2001), who found that the distribution of plants in semiarid meadows was the result of integrative variables that incorporated the number of days groundwater spent at less than 30 cm and less than 70 cm, as well as the number of days that roots were subject to anaerobic conditions.

TBCF variation among years, plant communities, and grazing intensities

This study occurred during the wettest year in over 30 years followed by two years of below-average precipitation, allowing us to observe the impact of sustained year-over-year soil drying on TBCF under different grazing intensities. As the stepwise model selection results indicated, total belowground C flux was highest when meadows received above-average precipitation and decreased during the following two years of below-average precipitation. After the second year of below-average precipitation, TBCF hovered near or below zero. A negligible or negative gross flux means these meadows were almost certainly net sources of CO_2 during these dry years. Meadows in other regions can be large net C sources to the atmosphere (Reed and others 2021), though it is surprising that we observed such a large change in a gross flux over only three years.

In some meadow ecosystems, light grazing induces higher belowground C fluxes, commonly referred to as a compensatory growth response (Hafner and others 2012). Here, we saw little evidence for the compensatory growth response. Compensatory growth responses decreased with increasing aridity in a global synthesis (Mcsherry and Ritchie, 2013) and within a given location may be muted by reduced precipitation (Guo and others 2021). Our results show a negative relationship between grazing intensity and TBCF during this period, suggesting that matching grazing intensity to annual precipitation may prevent soil C loss, which can occur more rapidly than its replenishment (Sanderman and Baldock 2010). Important feedbacks may be involved with soil C loss and soil water, which can decrease water retention of soils - in some cases shortening the growing season by as much as 35 days (Ankenbauer and Loheide 2017).

To better understand the mechanisms by which grazing impacted TBCF, we recommend that future studies control for the timing of grazing with respect to the availability of water and plant phenology. Here, grazing occurred across plant communities with different moisture availability and phenological timing (both among plant communities and years, Richardson and others (2021). The timing of grazing can alter how plants respond to biomass removal by altering their allocation of C (Luo and others 2015; Guo and others 2021). Differences in plant C allocation may result in changes in root biomass (Veen and others 2014), soil water content via evapotranspiration (Lu and others 2011), and physical properties of soils (Sun and others 2017) that impact TBCF and soil C.

Soil greenhouse gas fluxes did not offset the C sink

Trace gases (CH_4 and N_2O) have the potential to offset sequestration of CO_2 in soil. In the San Joaquin delta wetlands of California, the annual net C sink in soil and sediment was offset by large CH_4 emissions (9,000-21,000 moles eCO_2 m^{-2} y^{-1}; Hemes and others 2018). We saw no evidence of substantial CH_4 or N_2O flux in these meadows. When it occurred, CH_4 production consistently occurred in several hotspots within the wet plant community. Most of the time, meadow soil was a net CH_4 sink as a result of methanotrophic soil microbial activity, producing net CH_4 uptake rates similar to those measured by Craig (2019) across an elevational gradient in the central Great Basin. The total N_2O released during a growing season was highest in the wet plant community and was only one-ten thousandth of soil eCO_2 efflux. This growing season flux was similar to daily fluxes reported in coastal wetlands by Morse et al (2012). We recognize that site access may have limited our ability to measure the largest fluxes of CH_4 and N_2O occurring when soils were wettest in early spring, though we observed small variation in trace gas production across the ranges of soil moistures captured during this 3-year study.

Conclusions

In addition to being C hotspots, meadows serve other important ecosystem functions, such as hosting the majority of the region’s biodiversity while covering 1% of the land surface in the Great Basin (Chambers and Miller 2004). Quantifying the response of meadows to land use and climate is critical for identifying conservation strategies. Here, we show the importance of available moisture in groundwater dependent ecosystems within semiarid ecosystems, evidenced by large decreases in TBCF following years with below average precipitation. These decreases were highest in meadows experiencing unmanaged grazing and likely resulted in the loss of soil C. The importance of moisture in semiarid ecosystems has prompted the implementation of landscape treatments such as removal of pinion juniper woodlands to increase water availability to meadows and riparian ecosystems (Huxman and others 2005). However, increases in water availability will not offset moisture deficits created by years with low precipitation and higher temperatures (Carroll and others 2017). As annual weather becomes less reflective of historical climate, our results show the importance of matching grazing intensity to annual precipitation as an important step to mitigate losses of soil C and associated benefits of healthy soils under years of varying precipitation.

References

Adair, C. E., P. B. Reich, S. E. Hobbie, and J. M. H. Knops. 2009. Interactive effects of time, CO2, N, and diversity on total belowground carbon allocation and ecosystem carbon storage in a grassland community. Ecosystems 12:1037–1052.

Allen-Diaz, B. H. 1991. Water Table and Plant Species Relationships in Sierra Nevada Meadows. American Midland Naturalist 126:30.

Ankenbauer, K. J., and S. P. Loheide. 2017. The effects of soil organic matter on soil water retention and plant water use in a meadow of the Sierra Nevada, CA. Hydrological Processes 31:891–901.

Balasubramanian, D., W. J. Zhou, H. L. Ji, J. Grace, X. L. Bai, Q. H. Song, Y. T. Liu, L. Q. Sha, X. H. Fei, X. Zhang, J. Bin Zhao, J. F. Zhao, Z. H. Tan, and Y. P. Zhang. 2020. Environmental and management controls of soil carbon storage in grasslands of southwestern China. Journal of Environmental Management 254:109810.

Baldocchi, D. 2008. TURNER REVIEW No. 15. “Breathing” of the terrestrial biosphere: Lessons learned from a global network of carbon dioxide flux measurement systems. Australian Journal of Botany 56:1–26.

Blackburn, D. A., A. J. Oliphant, and J. D. Davis. 2021. Carbon and Water Exchanges in a Mountain Meadow Ecosystem, Sierra Nevada, California. Wetlands 41.

Carroll, R. W. H., J. L. Huntington, K. A. Snyder, R. G. Niswonger, C. Morton, and T. K. Stringham. 2017. Evaluating mountain meadow groundwater response to Pinyon-Juniper and temperature in a great basin watershed. Ecohydrology 10:1–18.

Castelli, R. M., J. C. Chambers, and R. J. Tausch. 2000. Soil-plant relations along a soil-water gradient in great basin riparian meadows. Wetlands 20:251–266.

Castelli, R. M., J. C. Chambers, and R. J. Tausch. 2001. Soil-plant relations along a soil-water gradient in great basin riparian meadows. Wetlands 20:251–266.

Chambers, J., and J. Miller. 2004. Great Basin Riparian Ecosystems : Ecology, Management, and Restoration. Island Press, Washington, DC.

Craig, C. 2019. Rates and Controls of Greenhouse Gas Fluxes in the Great Basin, USA. Univeristy of Nevada, Reno.

Darrouzet-Nardi, A., C. M. D’Antonio, and T. E. Dawson. 2006. Depth of water acquisition by invading shrubs and resident herbs in a Sierra Nevada meadow. Plant and Soil 285:31–43.

Debinski, D. M., H. Wickham, K. Kindscher, J. C. Caruthers, and M. Germino. 2010. Montane meadow change during drought varies with background hydrologic regime and plant functional group. Ecology 91:1672–1681.

De Deyn, G. B., J. H. C. Cornelissen, and R. D. Bardgett. 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecology Letters 11:516–531.

Dutta, K., E. A. G. Schuur, J. C. Neff, and S. A. Zimov. 2006. Potential carbon release from permafrost soils of Northeastern Siberia. Global Change Biology 12:2336–2351.

Enriquez, A. S., R. A. Chimner, M. V. Cremona, P. Diehl, and G. L. Bonvissuto. 2015. Grazing intensity levels influence C reservoirs of wet and mesic meadows along a precipitation gradient in Northern Patagonia. Wetlands Ecology and Management 23:439–451.

Germanoski, D., and J. R. Miller. 2004. Great Basin Riparian Ecosystems—Ecology, Management, and Restoration. Page (J. Chambers and J. R. Miller, Eds.). Island Press, Covelo.

Giardina, C. P., and M. G. Ryan. 2002. Total belowground carbon allocation in a fast-growing Eucalyptus plantation estimated using a carbon balance approach. Ecosystems 5:487–499.

Gill, A. L., and A. C. Finzi. 2016. Belowground carbon flux links biogeochemical cycles and resource-use efficiency at the global scale. Ecology Letters 19:1419–1428.

Gotelli, N., and A. Ellison. 2004. A Primer of Ecological Statistics. 2nd edition. Sinauer Associates Publishers, Sunderland.

Guo, C., D. Zhao, D. Zheng, and Y. Zhu. 2021. Effects of grazing on the grassland vegetation community characteristics in Inner Mongolia. Journal of Resources and Ecology 12:319–331.

Hafner, S., S. Unteregelsbacher, E. Seeber, B. Lena, X. Xu, X. Li, G. Guggenberger, G. Miehe, and Y. Kuzyakov. 2012. Effect of grazing on carbon stocks and assimilate partitioning in a Tibetan montane pasture revealed by 13CO 2 pulse labeling. Global Change Biology 18:528–538.

Hall, F. C., and L. Bryant. 1995. Herbaceous stubble height as a warning of impending cattle grazing damage to riparian areas. General Technical Report - US Department of Agriculture, Forest Service.

Hemes, K. S., S. D. Chamberlain, E. Eichelmann, S. H. Knox, and D. D. Baldocchi. 2018. A Biogeochemical Compromise: The High Methane Cost of Sequestering Carbon in Restored Wetlands. Geophysical Research Letters 45:6081–6091.

Hiederer, R., and M. Köchy. 2012. Global soil organic carbon estimates and the harmonized world soil database. Page EUR 25225EN, Luxembourg.

Hooker, T. D., and J. M. Stark. 2012. Carbon Flow from Plant Detritus and Soil Organic Matter to Microbes-Linking Carbon and Nitrogen Cycling in Semiarid Soils. Soil Science Society of America Journal 76:903–914.

Huxman, T., B. Wilcox, D. Breshears, R. Scott, K. Snyder, E. Small, K. Hultine, W. Pockman, and R. Jackson. 2005. Ecohydrological Implications of Woody Plant Encroachment. Ecology 86:308–319.

Kareksela, S., T. Haapalehto, R. Juutinen, R. Matilainen, T. Tahvanainen, and J. S. Kotiaho. 2015. Fighting carbon loss of degraded peatlands by jump-starting ecosystem functioning with ecological restoration. Science of the Total Environment 537:268–276.

Loheide, S. P., and S. M. Gorelick. 2007. Riparian hydroecology: A coupled model of the observed interactions between groundwater flow and meadow vegetation patterning. Water Resources Research 43:1–16.

Lu, N., S. Chen, B. Wilske, G. Sun, and J. Chen. 2011. Evapotranspiration and soil water relationships in a range of disturbed and undisturbed ecosystems in the semi-arid Inner Mongolia, China. Journal of Plant Ecology 4:49–60.

Luo, C., X. Bao, S. Wang, X. Zhu, S. Cui, Z. Zhang, B. Xu, H. Niu, L. Zhao, and X. Zhao. 2015. Impacts of seasonal grazing on net ecosystem carbon exchange in alpine meadow on the Tibetan Plateau. Plant and Soil 396:381–395.

Mattson, K. G., and J. Zhang. 2019. Forests in the northern Sierra Nevada of California, USA, store large amounts of carbon in different patterns. Ecosphere 10.

McIlroy, S. K., and B. H. Allen-Diaz. 2012. Plant community distribution along water table and grazing gradients in montane meadows of the Sierra Nevada Range (California, USA). Wetlands Ecology and Management 20:287–296.

Mcsherry, M. E., and M. E. Ritchie. 2013. Effects of grazing on grassland soil carbon: A global review. Global Change Biology 19:1347–1357.

Milchunas, D. . G. ., O. . E. . Sala, and W. . K. . Lauenroth. 1988. A Generalized Model of the Effects of Grazing by Large Herbivores on Grassland Community Structure. The American Society of Naturalists 132:87–106.

Morse, J. L., M. Ardón, and E. S. Bernhardt. 2012. Using environmental variables and soil processes to forecast denitrification potential and nitrous oxide fluxes in coastal plain wetlands across different land uses. Journal of Geophysical Research: Biogeosciences 117:1–14.

Myhre, G., and D. Shindell. 2011. Chapter 8 : Anthropogenic and Natural Radiative Forcing Presented by:1–124.

Norton, J. B., L. J. Jungst, U. Norton, H. R. Olsen, K. W. Tate, and W. R. Horwath. 2011. Soil Carbon and Nitrogen Storage in Upper Montane Riparian Meadows. Ecosystems 14:1217–1231.

Norton, J. B., H. R. Olsen, L. J. Jungst, D. E. Legg, and W. R. Horwath. 2014. Soil carbon and nitrogen storage in alluvial wet meadows of the Southern Sierra Nevada Mountains, USA. Journal of Soils and Sediments 14:34–43.

Pandit, K., H. Dashti, N. F. Glenn, A. N. Flores, K. C. Maguire, D. J. Shinneman, G. N. Flerchinger, and A. W. Fellows. 2019. Developing and optimizing shrub parameters representing sagebrush (Artemisia spp.) ecosystems in the northern

Great Basin using the Ecosystem Demography (EDv2.2) model. Geoscientific Model Development 12:4585–4601.

Parsons, A. . J., E. . L. Leafe, B. Collett, P. . D. Penning, and J. Lewis. 1983. The Physiology of Grass Production Under Grazing . II . Photosynthesis , Crop Growth and Animal Intake of Continuously-Grazed Swards. Society, British Ecological Ecology, Applied 20:127–139.

Prism Climate Group. 2022. Prism. https://prism.oregonstate.edu.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raich, J., and K. Nadelhoffer. 1989. Belowground Carbon Allocation in Forest Ecosystems : Global Trends. Ecology 70:1346–1354.

Rau, B. M., D. W. Johnson, R. R. Blank, R. J. Tausch, B. A. Roundy, R. F. Miller, T. G. Caldwell, and A. Lucchesi. 2011. Woodland expansion's influence on belowground carbon and nitrogen in the Great Basin U.S. Journal of Arid Environments 75:827–835.

Reed, C., A. Merrill, M. Drew, B. Christman, A. Hutchinson, L. Keszey, and S. Swanson. 2021. Montane Meadows: A Soil Carbon Sink or Source? Ecosystems.

Richardson, W., T. K. Stringham, W. Lieurance, and K. A. Snyder. 2021. Changes in meadow phenology in response to grazing management at multiple scales of measurement. Remote Sensing 13.

Sanderman, J., and J. A. Baldock. 2010. Accounting for soil carbon sequestration in national inventories: A soil scientist's perspective. Environmental Research Letters 5.

Schmidt, M. W. I., M. S. Torn, S. Abiven, T. Dittmar, G. Guggenberger, I. A. Janssens, M. Kleber, I. Kögel-Knabner, J. Lehmann, D. A. C. Manning, P. Nannipieri, D. P. Rasse, S. Weiner, and S. E. Trumbore. 2011. Persistence of soil organic matter as an ecosystem property. Nature 478:49–56.

Van Staalduinen, M. A., and N. P. R. Anten. 2005. Differences in the compensatory growth of two co-occurring grass species in relation to water availability. Oecologia 146:190–199.

Stringham, T. K., W. C. Krueger, and D. R. Thomas. 2001. Application of non-equilibrium ecology to rangeland riparian zones. Journal of Range Management 54:210–217.

Sun, G., X. Zhu-Barker, D. Chen, L. Liu, N. Zhang, C. Shi, L. He, and Y. Lei. 2017. Responses of root exudation and nutrient cycling to grazing intensities and recovery practices in an alpine meadow: An implication for pasture management. Plant and Soil 416:515–525.

Trimble, S. W., and A. C. Mendel. 1995. The cow as a geomorphic agent — A critical review. Biogeomorphology, Terrestrial and Freshwater Systems 13:233–253.

Veen, G. F. C., S. De Vries, E. S. Bakker, W. H. Van der Putten, and H. Olff. 2014. Grazing-induced changes in plant-soil feedback alter plant biomass allocation. Oikos 123:800–806.

Zhang, X., and W. Wang. 2015. The decomposition of fine and coarse roots: Their global patterns and controlling factors. Scientific Reports 5:1–10.

Zhao, W., S. P. Chen, and G. H. Lin. 2008. Compensatory growth responses to clipping defoliation in Leymus chinensis (Poaceae) under nutrient addition and water deficiency conditions. Plant Ecology 196:85–99.

Tables

Table 1. Pearson correlations between meadow soil carbon (C) stocks and root mass from the sampling event antecedent to the soil C measurement (Antecedent root mass) in shallow (0-15 cm) soils across all meadows. Bold text indicates *p* < 0.05 and italic text indicates *p* < 0.1.

		Antecedent root mass among plants	Antecedent root mass edge	Antecedent root mass mesic	Antecedent root mass wet	Antecedent root mass wet + mesic
C stock Spring 2020	Slope	0.41	0.55	0.18	0.41	0.36
	p	**0.01**	**0.01**	0.60	0.15	*0.08*
	r	0.33	0.58	0.14	0.33	0.26
C stock Fall 2020	Slope	0.16	0.28	-0.14	0.00	0.03
	p	0.17	0.19	0.48	0.98	0.76
	r	0.10	0.30	0.17	0.07	0.04
C stock Spring 2021	Slope	0.42	0.47	0.81	0.25	0.28
	p	**0.01**	0.22	**0.01**	0.21	**0.04**
	r	0.33	0.28	0.85	0.30	0.32
C stock Fall 2021	Slope	0.42	0.65	0.03	-0.14	-0.06
	p	**0.00**	**0.01**	0.91	0.48	0.70
	r	0.33	0.81	0.03	0.17	0.06

Table 2. Growing season fluxes of greenhouse gases (carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) from meadow soils, in CO_2 equivalents (eCO_2), among three plant communities. Values are the mean fluxes across the three growing seasons and grazing treatments ± standard error. Positive values indicate net gas release and negative values occur where gases were consumed. Letters indicate differences of gas flux among plant communities ($p < 0.05$).

Gas	Edge	Mesic	Wet
CO_2 (mol m^{-2} $season^{-1}$)	16.1 ± 1.30^c	22.3 ± 4.13^b	29.9 ± 5.12^a
CH_4 (mol eCO_2 m^{-2} $season^{-1}$)	-0.39 ± 0.03^a	-0.29 ± 0.07^a	1.65 ± 1.37^a
N_2O (µmol eCO_2 m^{-2} $season^{-1}$)	25.4 ± 3.45^a	133 ± 64.1^a	146 ± 99.2^a

Figures:

Figure 1:

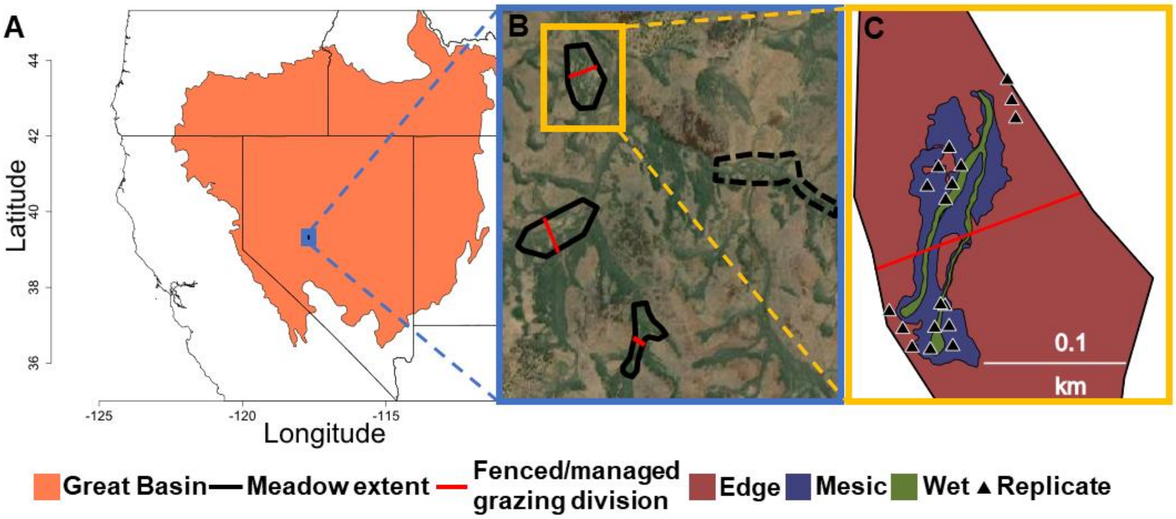

Figure 1. Hierarchy of the experimental design. A. We collected samples from four meadows in the semiarid Great Basin, Nevada, USA. B. In the late fall of 2019, after our first year of sampling, three of the meadows had fences installed that surrounded the meadows (solid black lines). Fences split the three meadows (red line) into grazing exclusion (no cattle or horse entry) or managed grazing (fenced, cattle entry controlled; horses excluded) pairs. A fourth meadow was left unfenced (dashed black line) and experienced unmanaged grazing – cattle and horses permitted throughout the growing season – which served as our reference meadow. C. Within each grazing treatment, three plant communities were delineated, which we term edge, mesic, and wet. Each plant community contained three replicated plots where measurements were conducted (equaling 63 plots total; Supplementary Figure 1).

Figure 2:

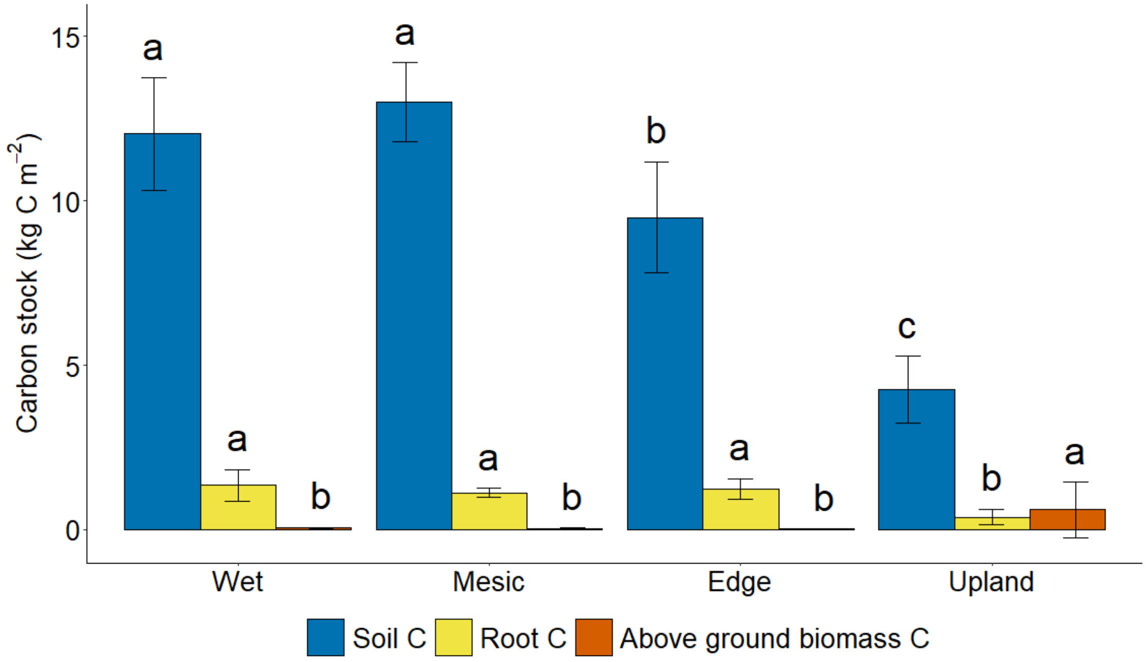

Figure 2. Belowground carbon stocks found in three meadow plant communities (wet, mesic, and edge) compared to literature-derived C stock estimates measured in non-meadow Great Basin ecosystems (upland). Values are the mean ± the standard error. Meadow C stocks are the mean value over the three growing seasons of this study for unmanaged, managed grazing, and fenced meadows. Letters indicate significant differences among plant communities ($p < 0.05$); letters do not indicate differences among C stocks.

Figure 3:

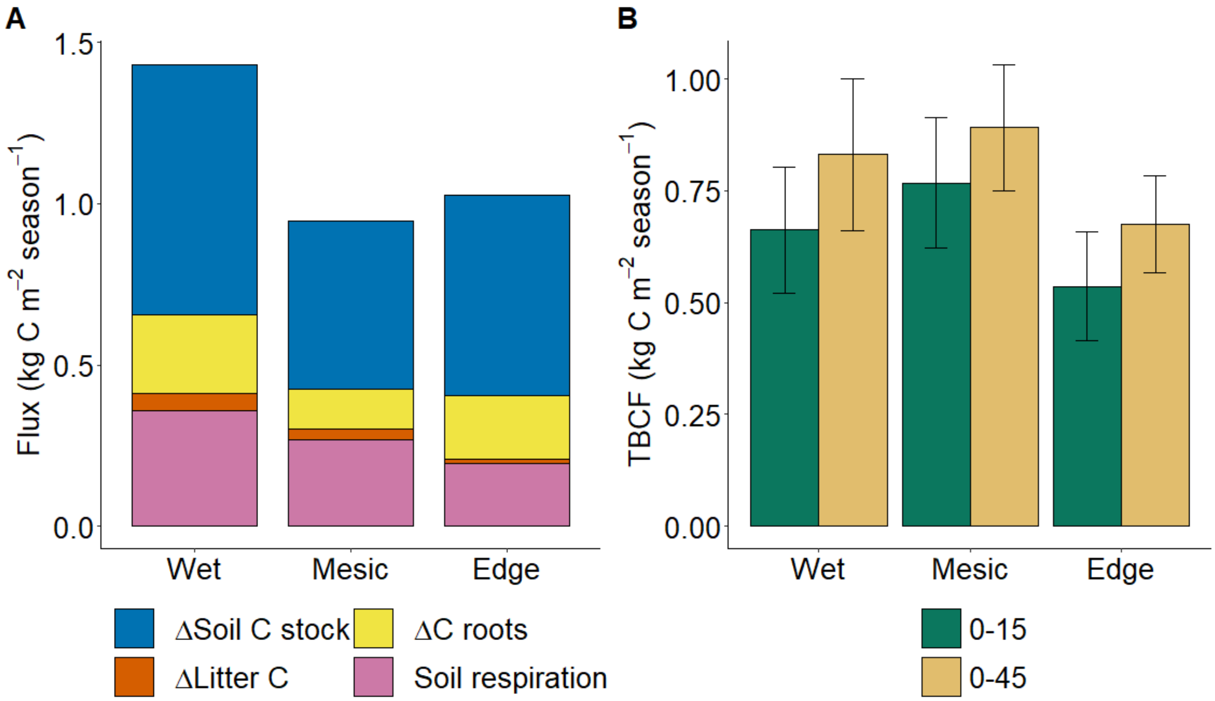

Figure 3**. A** Components of total belowground C flux (TBCF) in soils 0-15 cm in wet, mesic and edge vegetation communities within Great Basin meadows. **B** Comparison of TBCF measured in shallow soils (0-15 cm) to TBCF measured to the full soil depth (0-45 cm) in each of the three vegetation communities. In both panels, values are the plot-level means observed across 2019-2021; 2B includes the standard error among plots and years.

Figure 4:

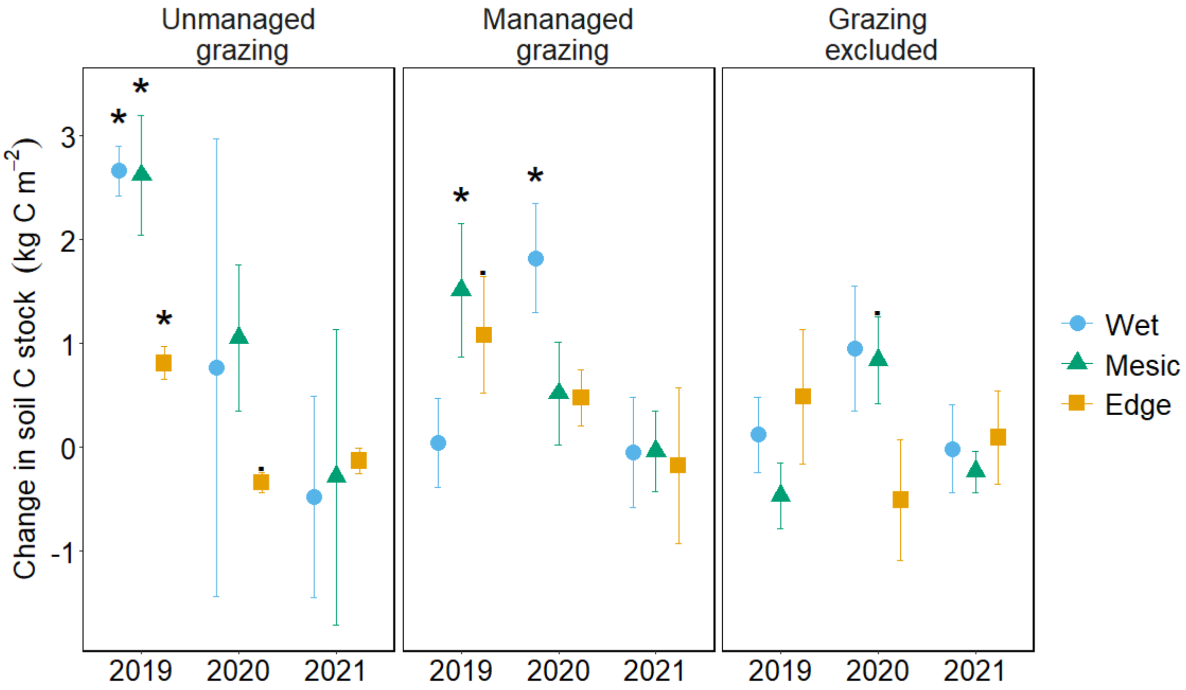

Figure 4. Changes in soil C stock in soils 0-15 cm in edge, mesic, and wet plant communities under unmanaged grazing, managed grazing, and grazing exclusion. Error bars show the standard error of the mean. An asterisk indicates $p < 0.05$ and a period indicates $p < 0.1$.

Figure 5:

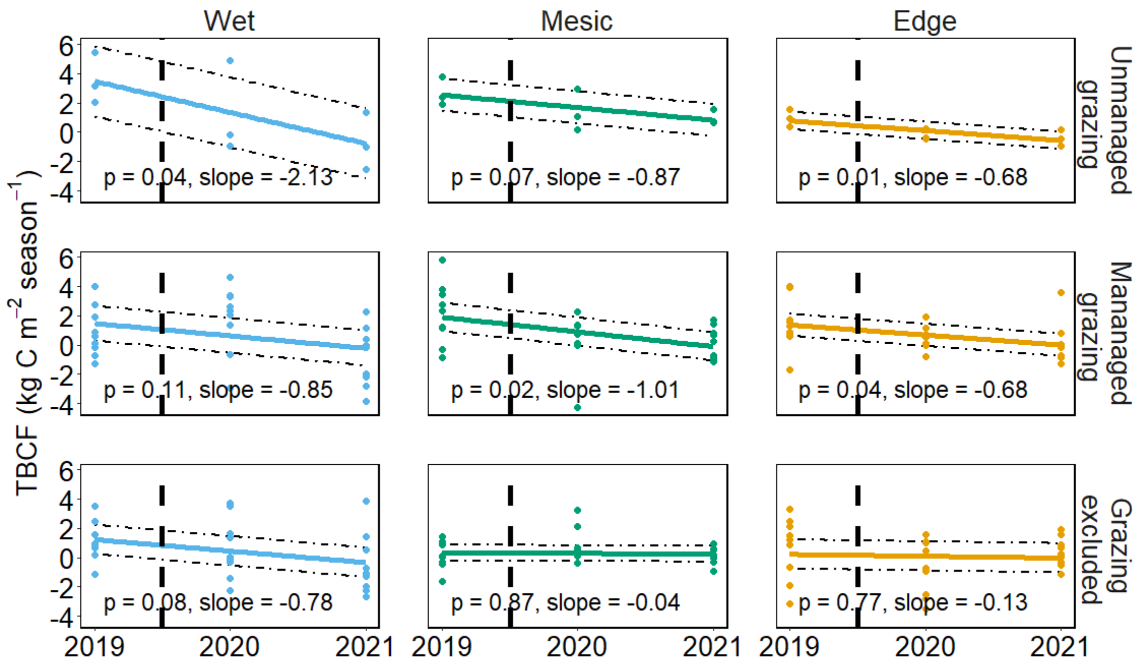

Figure 5. Changes in total belowground carbon flux (TBCF) for soils (0-15 cm) in wet, mesic, and edge plant communities under unmanaged grazing, managed grazing, and grazing exclusion. The dashed line separates pretreatment data from measurements taken after the installation of fences. Slopes and p-values are derived from linear models measuring the impact of plot level data on TBCF with respect to time. Dashed lines are the 95% confidence interval of the plant communities within the treatment. An asterisk or period under the year indicates a TBCF flux different from zero, with $p < 0.05$ and $p < 0.1$, respectively.

Chapter 2: Productivity drives mineral associated organic matter formation and the relative contribution of sorption capacity across climates.

Authors: Brian Morra[1], Cody Reed[1], Simon R. Poulson[2], Benjamin W. Sullivan[1,3]

[1] Department of Natural Resources & Environmental Science, The University of Nevada, Reno,

1664 N. Virginia St., Reno, NV 89557

[2] Department of Geological Sciences and Engineering, The University of Nevada, Reno,

1664 N. Virginia St., Reno, NV 89557

[3] The Global Water Center, The University of Nevada, Reno, 1664 N. Virginia St., Reno, NV 89557

Abstract

Mineral associated organic matter (MAOM) plays an important role in soil carbon storage due to its long-term residence in soils. It is understood that productivity, climate, and surface sorption capacity of minerals in the silt and clay fraction contribute to MAOM formation. Commonly MAOM formation is assumed to be controlled by landscape scale controls such as ecosystem type and climate. However, within climates and landscapes there can be variability in productivity and sorption capacity provided by soil minerals. To what degree are small-scales controls on MAOM formation responsible for rates of MAOM development in meadows found in humid and semiarid ecosystems? In this study, we combined an in-situ pulse ^{13}C labeling experiment with laboratory incubations designed to assess the additional organic C sorption potential of soils. By comparing ^{13}C label recovery and sorption potential in high and low productivity regions, located in humid and semiarid montane climates, we found productivity created the largest differences among plots. In low productivity plots, assimilated ^{13}C label was rapidly incorporated into the MAOM fraction but destabilized over the course of the study in both climates. Conversely, high productivity plots incorporated plant assimilate into MAOM more slowly and retained the labeled C one year later in both climates. The destabilization of MAOM in low productivity plots and the retention of MAOM in high productivity plots may impact the sorption potential of bulk soils, as low productivity plots were able to sorb ten times as much organic C as high productivity plots during laboratory incubations. When comparing high or low productivity plots between humid and semiarid regions, plots found in the humid climate had lower sorption potentials than those found in semiarid climates, revealing that MAOM fractions of semiarid climates

may be further from saturation than those found in humid climates. Overall, productivity may limit the relative contribution of mineral sorption in MAOM formation across climates, making it the most important driver in MAOM formation we measured.

Intro

Carbon (C) in soil organic matter (SOM) is often divided into particulate organic matter (POM) or mineral associated organic matter (MAOM). Because MAOM is chemically and physically protected by close association to mineral surfaces, it can remain in soil for centuries to millennia (Torn et al., 1997; Kleber et al., 2015). In grasslands, MAOM is the dominant form of soil C and consists of microbially processed C (Cotrufo et al., 2019). Concurrently, abiotic formation of MAOM can occur from the interaction of mineral surfaces and dissolved organic C (Mikutta et al., 2019). By contrast, POM is composed of organic fragments and has shorter residence times, often less than ten years under aerobic soil conditions (Lavallee et al., 2020). While the broad characteristics of MAOM and POM are well understood, there are multiple, non-mutually exclusive factors contributing to the formation and stabilization of MAOM or POM in soil, including mineral sorption capacity, plant inputs (quantity and quality), and climatic drivers (Castellano et al., 2015; Sokol et al., 2022).

Mineralogy may set an upper limit to MAOM formation depending on the type and amount of minerals in the clay or silt size fraction, their surface area, and their charge (Lützow et al., 2006; Xu et al., 2022). Silt and clay fractions may contribute equally to MAOM formation (Matus, 2021), but the relative rates at which C is sorbed to their surfaces may be different (Castellano et al., 2015). Differing rates, of soil surface sorption between clay and silt may control the contributions these size fractions make to overall MAOM formation. Practically, whether mineral surface saturation limits MAOM formation (Hassink and Whitmore, 1997) may depend on other factors, such as regional climate or sub-watershed-scale controls on plant productivity. Climate may impact MAOM formation through temperature, precipitation timing and amounts, and growing season length. For example, the rate at which microbial communities utilize plant C inputs and the rate of microbial turnover may be reduced in cold or dry conditions, slowing the transfer of C to MAOM pools and increasing the proportion of consumed C that gets respired (Herron et al., 2009; Crowther et al., 2015; Domeignoz-Horta et al., 2020). In ecosystems where growing season length is controlled by climatic constraints to plant-available water, microbial processing of C occurs in the absence of fresh plant inputs and the degree of microbial processing of litter and SOM is inversely related to growing season length (Hooker et al., 2008; Werth and Kuzyakov, 2010). At sub-watershed scales, primary productivity controls the amount and quality of plant inputs to soil – another important control on MAOM formation (Cotrufo et al., 2013; Sokol et al., 2022). Productivity can be highly spatially variable given land management legacies, subsurface hydrology, and nutrient availability. These three controls over MAOM formation – soil sorption, climate, and productivity – are explicit or implicit in existing frameworks of soil C formation such as MEMS (Cotrufo et al., 2013), In-N-Out (Cotrufo et al., 2021), and MIMICS (Wieder et al., 2014). Integrating controls over MAOM formation into Earth System Models improves soil C stock projections (e.g., Wieder et al., 2013; 2014). Methodologically, observing interactions among soil C sorption capacity, climate, and productivity on MAOM formation may be best approached using *in situ* C isotope tracer studies that track plant-derived C into MAOM pools (Pett-Ridge and Firestone, 2017; Fossum et al., 2022).

Montane meadows represent a unique model ecosystem to explore the interaction among climate, productivity, and mineralogy on MAOM formation. Because meadows are groundwater dependent ecosystems, they can be found across a range of climates (Germanoski and Miller, 2004; Weixelman et al., 2011; Balasubramanian et al., 2020). Meadows have large, dynamic soil C stocks (Norton et al., 2011; Hafner et al., 2012; Reed et al., 2021). Meadow C stocks are similar to other ecosystems with large soil C stocks: like grasslands (Bardgett et al., 2021), meadows have high mineral and soil C concentrations; like peatlands (Frolking et al., 2011), some meadows can have carbon concentrations >12%; like wetlands (Mitra et al., 2005), meadows experience inundated soils into the growing season. Unlike permanently inundated wetlands or grasslands, meadows typically have ephemeral, seasonal near-surface water tables (Weixelman et al., 2011) which support communities of shallow-rooted wetland obligate and facultative plants (Allen-Diaz, 1991). Soil C accumulation rates in meadows may equal or exceed 400 g C m^{-1} y^{-1} (Blackburn et al., 2021; Reed et al., 2021), on par with rates measured in wetlands and grasslands (480 and 375 g C m^{-2} y^{-1}, respectively; Saugier et al., 2001; Saunders et al., 2007). Despite seasonally shallow water tables, soil C accumulation in meadows is not dependent on reduced C losses associated with anoxic soil conditions, as in wetlands (Jia et al., 2020). Instead, net soil C change in meadows appears to be driven by the rate of belowground C inputs (Reed et al., 2021). Understanding of the relative influence of factors that control MAOM formation in meadows may help inform management and modeling of C stocks and fluxes in ecosystems with high soil carbon and mineral contents. To that end, we conducted an *in situ* ^{13}C isotope tracer experiment in montane meadows differing in productivity and climate regimes. We combined the ^{13}C labeling experiment with potential soil C sorption incubations to identify a hierarchy among plant productivity, climate, and soil relative sorption capacity as drivers of MAOM formation and microbial utilization of plant-derived C substrates.

Methods

Site description

We selected meadows in the California, USA Sierra Nevada and central Nevada, USA with two different climates based on the Koppen Climate Classification system (Kottek et al., 2006). We established plots in a cold semiarid climate (BSk) located in the Desatoya mountains of central Nevada, where the 30-year mean annual precipitation is 342 mm (Table 1). We also established plots in a warm summer humid continental climate (Dfb) located in the University of California Sagehen Creek Field Station in the Sierra Nevada mountains of California, which has a 30-year mean annual precipitation of 825 mm (Table 1). In addition to receiving less precipitation in the semiarid region, the watershed area contributing moisture to the semiarid region is 28 times smaller than the watershed found in the humid region. For simplicity, we refer to these climates as semiarid and humid, respectively.

Within each climate, we selected high and low productivity plots based on aboveground biomass at peak productivity and growing season length (calculated according to Yu et al. (2010); Table 1). Growing season length was calculated for all sites (humid high, humid low, semiarid high, semiarid low) using Sentinel 2 surface reflectance normalized difference vegetation index (NDVI) values at a 10 m resolution from 2018 to 2021. We first made linear interpolations between measurements taken approximately every two weeks and then using a three-day moving average values were smoothed. The smoothed NDVI values were standardized for each year and meadow by subtracting the minimum annual value and dividing that difference by the range in NDVI values. Using the standardized values, we classified the start of the growing season as the date that NDVI values surpassed 0.2 and the end of the growing season as the date that NDVI dropped below 0.6 as suggested by Yu et al. (2010).

^{13}C Pulse-labeled experiment

We added a ^{13}C spike to high and low productivity plots using 50 x 50 x 60 cm chambers constructed from Acrylite OP-3 with greater than 85% transmittance of photosynthetically active radiation (for full methods used see Reed et al., 2021). The label was added during peak productivity of humid and semiarid meadows in the spring of 2020. The labeling occurred in late May and early June for semiarid and humid meadows respectively. The spike was added as 200 mL of 99 atom% $^{13}CO_2$. To ensure the uptake of label by plants, chambers remained on the soil surface for two hours. Before removing each chamber, we collected a sample of gas from the head space to determine the amount of ^{13}C spike remaining at the end of the labeling period. The difference between the amount of label added and ^{13}C remaining in the chamber was used to estimate the amount of label assimilated (g 13C m^{-2}; Table 1). Each labeled plot was paired with a natural abundance plot that did not receive a ^{13}C spike to calculate enrichment relative to natural concentrations of ^{13}C in soils. In the humid meadows, we established three high productivity and three low productivity plots, each having a natural abundance replicate. In total there were 12 plots in the humid meadows. In the semiarid region, we established six sets of labeled and natural abundance plots in high productivity and low productivity meadows, making a total of 24 plots sampled in the semiarid meadows.

Plot sampling and size fractionation

Both natural abundance and labeled plots were sampled 24 h, one month, six months, and one year following the addition of the ^{13}C label. Samples were collected to a depth of 15 cm using a five cm-diameter slide-hammer (AMS Equipment Corp, American Falls, Idaho). To estimate the POM and MAOM fractions of soils, we separated soils using size fractionation according to Kettler et al. (2001) and Sanderman et al. (2011). Our experiment did not consider the incorporation of label into aggregates as the turnover of C occluded by aggregates is fast relative to the turnover of C protected by mineral complexation (Lavallee et al., 2020). Size fractionation has been shown to produce similar results to density fractionation (Poeplau et al., 2018; Lavallee et al., 2020). We added five grams of soil to 50 mL centrifuge tubes containing 20 mL of 3% sodium hexametaphosphate and placed the samples on a shaker table for 10 hours at 180 rpm to disperse soil particles. Following dispersal, we separated the POM fraction by shaking soils on a 63 µm sieve while rinsing with ~300 mL of deionized water. Particles smaller and larger than 63 µm were collected in separate tared beakers. The fraction of soils larger than 63 µm was considered to be the soil fraction dominated by POM while the soils < 63 µm were further split according to Lavallee et al. (2020) where particles ranging from 20 – 63 µm contained MAOM associated with the silt fraction and particles

< 20 µm contained MAOM associated with the clay fraction. Here after we refer to silt and clay sized fractions as silt MAOM and clay MAOM respectively. We separated the clay and silt MAOM by sedimentation, letting the solution containing particles < 63 µm sit for four hours allowing for the clay MAOM fraction (particles < 20 µm) held in the supernatant was decanted into a third tared beaker. Beakers were then dried to a constant mass at 105 °C and weighed to estimate the proportions of POM, clay and silt MAOM contained in each sample. We used the proportions of POM, clay, and silt MAOM to estimate soil texture. Gravimetric determination of proportions of POM, silt MAOM and clay MAOM produces similar estimates of the proportions of sand, silt, and clay measured using hydrometers (Kettler et al., 2001). We measured the δ^{13}C, and concentration of C, in each soil fraction at the Nevada Stable Isotope Laboratory using a Micromass Isoprime stable isotope ratio mass spectrometer (Elementar, Stockport, UK), equipped with a Eurovector elemental analyzer (Eurovector, Pavia, Italy).

The recovered label in soils (%) was calculated for POM, silt MAOM, or clay MAOM using equation 1 (Eq. 1). Recovered label is the ratio of ^{13}C assimilated during labeling ($^{13}C_{assim}$; g ^{13}C m^{-2}) and ^{13}C stock of soil fractions (g ^{13}C m^{-2}) times 100. The ^{13}C stock of each soil fraction was calculated in the numerator of Eq. 1. First, the mass of each size fraction (g of sand, silt, or clay m^{-2}) was the proportion of each size fraction found in bulk soils (*%Frac*) times the average rock-free, root-free bulk density of soils (*BD; g m^{-3}*). The BD was measured using six soil cores sampled from the high and low productivity meadows of each climate (Table 1). The mass of sand, silt, or clay (g m^{-3}) was multiplied by the concentration of C measured in each fraction ($\%C_{(POM,\, silt,\, clay)}$) and the depth of measurement *0.15* m to calculate the C stock (g C m^{-2}) held in POM, silt MAOM, or clay

MAOM (g C m^{-2}; data shown in Appendix B Table 2). The C stock for each soil fraction (g C m^{-2}) was multiplied by the atom % excess ^{13}C ($^{13}C_{natural} - {}^{13}C_{spiked}$) to calculate the amount of ^{13}C label held in POM, silt MAOM, or clay MAOM (g 13C m^{-2})

$$\frac{\%Frac * BD * \%C_{(POM,silt,clay)} * 0.15 * (13C_{natural} - 13C_{spike})}{13C_{assim.}} \quad \text{(Equation 1)}$$

Bulk soil recovery of ^{13}C was the sum of ^{13}C held in POM, silt MAOM, and clay MAOM (g 13C m^{-2}) divided by $^{13}C_{assim}$. Measurements comparing the C stock of bulk soils and fractionated soils revealed that the fractionation process may have resulted in the loss of 24% of soil C, on average. As a consequence, when summing the natural abundance of ^{13}C (the product of atom % ^{13}C and C stock) in POM, and MAOM pools, summed values were also 24% lower than natural abundance measured on bulk soils. Therefore, our estimates of percent label recovered in bulk soils may be an underestimate. However, the relative differences in ^{13}C allocation measured among sites are of greater importance than their absolute values. At each sampling date we measured field moisture by drying approximately 15 g of soils at 105 °C and converted the gravimetric water content to volumetric water content based on soil bulk density.

Due to the high variation in natural abundance of ^{13}C in soils, of 180 samples taken from 36 plots, the natural abundance of ^{13}C was higher than plots receiving the ^{13}C label in 52 samples, resulting in negative values for excess ^{13}C. Because our results are presented as percent label recovered, we interpreted negative values to indicate no allocation of ^{13}C to a fraction. We converted negative values to zero but retained the zeros in the analysis.

Sorption experiment

Soil sorption capacity potential represents the ability of soil to sorb dissolved organic carbon (DOC) onto mineral surfaces and is measured by adding a range of DOC concentrations to soil and measuring the quantity of DOC that is not recovered in solution. To compare the relative sorption potential of meadow soils from the four climate-productivity locations, we used a soil incubation similar to Feng et al. (2014). Sorption potential was measured on a composite of three randomly selected samples from each region collected on the day of soil labeling. Instead of using a single C substrate, which would bias sorption potential, we used a solution of sucrose, mannose, potassium citrate, cellobiose, pectin, and vanillic acid to more closely approximate the DOC found in soil rhizosphere solution (John Stark, personal communication; Appendix B Table 1). We mixed a stock solution (737 mg C L^{-1} in deionized water) which was diluted with deionized water to concentrations of 50, 100, 150, 200, 250, 300, 400, 500, 550 and 600, mg C L^{-1}. We mixed 100 mL of the diluted stock solutions with 0.25 grams of soil, while a set of soil-free solutions consisting of the ten concentrations served as a negative control. To account for water-soluble DOC released during incubation, we also included a positive control consisting of 0.25 g of soil added to 100 mL of deionized water. All solutions and controls were agitated using an orbital shaker (180 rpm) for 24 hours. Following incubation, solutions were filtered using Whatman GF/F filters (pre-combusted at 450 °C for four hours). Filtrate was acidified (2 mL of 2 N HCl) to remove inorganic C and the remaining DOC was measured using a total organic C analyzer (TOC-V, Shimadzu Scientific, Kyoto, Japan). Sorbed DOC (mg C g^{-1} soil) was calculated for each soil (n =40) according to equation 2 (Eq. 2), where the difference in C content from solutions of the negative controls ($Ctrl_{Neg}$; mg), the incubated soils ($Soil_i$; mg), and

C released from the positive controls (*Ctrl $_{Pos}$*; mg) was standardized by the mass of soil added, (*Soil mass*; g).

$$\frac{Ctrl_{Neg} - Soil_i - Ctrl_{Pos}}{Soil\ mass} \qquad \text{Equation 2}$$

Statistics

We performed all analyses in R (R Core Team, 2021). At each sampling date we used one tail t-tests to assess if the label recovered in each fraction was significantly different than zero ($\alpha = 0.05$). Where significant enrichment was not observed, we assume that the ^{13}C label recovered did not exceed natural abundance of ^{13}C. Except for soils sampled at 24 h, recovery of assimilated label in POM was never significantly different than zero. Therefore, we do not consider POM further in the analysis. A full list of δ13C values including those measured on POM can be found in Appendix B table 3.

Differences among plots were compared using mixed linear models that included a random intercept term to account for repeated measures of plots. Relative sorption potential was evaluated using linear models to assess the relationship between DOC added and DOC sorbed to mineral surfaces. The slopes of these linear models were used to show the relative sorption potential among bulk soils. Where significant linear relationships between the concentration and sorption of DOC occurred, we compared slopes among meadows or climates using an analysis of covariance (ANCOVA; Gotelli & Ellison 2004).

Results

The meadows in the humid climate had a higher proportion of clay, while meadows of the semiarid climate had a greater proportion of silt (Table 1). Despite these textural differences found between soils of humid and semiarid climates, sorption potential differed among meadows within the same parent materials ($p < 0.001$). In both humid and semiarid climates, sorption potential of low productivity plots was roughly ten times greater than sorption potential of soils in high productivity plots (Fig. 1). Across a range of DOC concentrations, soils of the low productivity plots located in the semiarid climate sorbed five times as much DOC as the low productivity plots in the humid climate ($p = 0.008$). There was not a significant relationship between DOC concentration and sorbed DOC in high productivity plots of humid or semiarid climates ($p = 0.09$ and $p = 0.09$ respectively). When comparing between either high or low productivity plots across climates, plots of the semiarid climate had a higher sorption potential than plots found in the humid climate ($p < 0.001$).

We measured similar amounts of 13C label recovery in bulk soil among meadow and climates at each sampling date (Fig. 2) despite different soil textures, climates, productivity, and total label assimilation rates (Table 2). Label recovery was less than 2% in silt and clay MAOM pools. However, general trends in ^{13}C label recovery in the MAOM fractions differed between high and low productivity plots. In general, low productivity plots rapidly allocated C to MAOM but failed to maintain it consistently; high productivity plots did not rapidly allocate C to MAOM but progressively gained MAOM. We measured significant ^{13}C label recovery 24 h after labeling in three of the four MAOM fraction-climate combinations in low productivity meadows: silt MAOM in the semiarid meadow and silt and clay MAOM in the humid climate ($p = 0.01$, $p = 0.009$, and $p = 0.04$ respectively). Though we recovered significant label in the silt and clay MAOM fractions six months after labeling in the humid low productivity meadow, we recovered no significant label in either silt or clay MAOM fractions one year after labeling in low productivity sites within either climate. In all low productivity silt and clay MAOM fractions, the average label recovery one year after labeling was lower than average label recovered after 24 h. By contrast, we did not measure significant ^{13}C label recovery 24 h after labeling in three of the four MAOM fraction-climate combinations in high productivity sites; silt MAOM at the semiarid meadow had significant label recovery at 24 h ($p = 0.05$). We recovered significant ^{13}C label recovery one year after labeling in three of the four MAOM fraction-climate combinations: clay MAOM in semiarid and humid meadows and silt MAOM in the semiarid meadow ($p = 0.05$, 0.02, 0.05, respectively). We did not recover significant label at any sampling date in the silt MAOM in the high productivity plot of the humid meadow ($p > 0.07$). In all high productivity silt and clay MAOM fractions, the average label recovered one year after labeling was higher than the average label recovered after 24 h. One year after labeling, high productivity plots in the semiarid meadow had 1.92 ± 0.93 % and 1.03 ± 0.47 % of the assimilated label in silt and clay MAOM, respectively, while high productivity plots in the humid meadow had 0.96 ± 0.17 % of the assimilated label in clay MAOM.

Discussion

Our *in situ* stable isotope approach allowed us to explore how interactions among productivity, potential sorption capacity, and climate influence allocation and retention of plant-assimilated CO_2 to mineral associated fractions in meadow soil. Our results highlight the interaction between plant primary productivity rates and mineral sorption capacity as proximate controls on the formation and retention of MAOM – and the relatively lesser influence of climate, which may be linked to MAOM formation via soil mineral sorption capacity. We demonstrate mechanisms of mineral associated soil C formation in meadow soils, which have large and dynamic soil C stocks (Morra et al.,in review; Norton et al., 2011; Reed et al., 2022) that make meadows C hotspots relative to their spatial extent (Norton et al., 2014; Reed et al., 2021)

Our results suggest high rates of plant productivity may discourage microbial destabilization of MAOM in both humid and semiarid climates (Fig. 3). Under low productivity, destabilization of MAOM by microbes can provide an important source of supplemental C for microbes (Hooker and Stark, 2012; Jilling et al., 2018). This supplemental C may be a less utilized resource in high productivity plots, where photosynthate supply is sustained later into the year (Table 1). Sustained photosynthesis may also provide a steady supply of labile C inputs to soil microbes, reducing decomposition of more complex substrates with low CUEs held in preexisting SOM. Loss of MAOM pools under low productivity may increase the sorption capacity of clay and silt MAOM fractions across climates. Despite a larger contribution of sorption capacity, low plant productivity may limit the contribution of mineral surfaces to MAOM formation.

The role mineral sorption capacity plays in MAOM formation decreases as mineral surfaces become coated in C (Hassink and Whitmore, 1997) and differed between low and high productivity plots (Fig. 1). Destabilization of MAOM in low productivity plots may help maintain surface sorption potential, while retention of MAOM in high productivity plots may contributes to a lower sorption potential (Fig. 1). The implications of differences in surface saturation on MAOM formation was proposed by Castellano et al. (2015) who developed a theoretical model to reconcile observations that high-quality (low C:N and lignin:N) plant litter inputs are not consistently incorporated into MAOM pools at greater efficiencies than low quality litters across soils. They found that the importance of C quality in MAOM formation, as suggested by the microbial efficiency microbial stabilization model (MEMS) (Cotrufo et al., 2013), become muted under conditions with low sorption potential. As a result, high quantities of C, independent of quality, may be required for MAOM formation in high productivity plots, while high quality C inputs which result in lower respiratory losses remain an important source of MAOM formation in low productivity plots. Therefore, productivity controls the contribution of mineral sorption capacity in bulk soils and may reduce the importance of substrate quality in MAOM formation.

Climate may control aspects of the sorption capacity of bulk soils and the relative contributions of silt and clay to MAOM formation. Silt may have a lower sorption capacity than clay (Stewart et al., 2007), as a result it should be expected that silt dominated soils would accumulate less C in MAOM than clay dominated soils as they approach saturation. The results of *in-situ* labeling and sorption potential incubation shows that meadows of humid ecosystems may be closer to saturation than meadows of semiarid ecosystems when comparing between high or low productivity plots. Therefore, in MAOM fractions farther from saturation, silt and clay fractions can have similar contributions to MAOM formation while the contribution of silt becomes diminished as soils approach saturation (Fig. 3).

Conclusions

This research shows that MAOM formation rates in ecosystems dominated by herbaceous vegetation are highly variable within climates and are the result of different inputs from plants. While frameworks and resulting models that incorporate primarily climate data and ecosystem type may sufficiently represent C cycling of pools with different turnover times at a global scale (Wieder et al., 2014; Cotrufo et al., 2021), understanding where soils can most effectively build MAOM to sequester atmospheric CO_2 may be most beneficial at scales relevant management. Our results show that efforts to model rates of MAOM formation at smaller spatial resolutions may be improved by considering the key role that productivity (within the context of climate conditions) plays in MAOM retention or destabilization, resulting in differing contributions from mineral sorption potential.

References

Allen-Diaz, B.H., 1991. Water Table and Plant Species Relationships in Sierra Nevada Meadows. American Midland Naturalist 126, 30. doi:10.2307/2426147

Balasubramanian, D., Zhou, W.J., Ji, H.L., Grace, J., Bai, X.L., Song, Q.H., Liu, Y.T., Sha, L.Q., Fei, X.H., Zhang, X., Zhao, J. Bin, Zhao, J.F., Tan, Z.H., Zhang, Y.P., 2020. Environmental and management controls of soil carbon storage in grasslands of southwestern China. Journal of Environmental Management 254, 109810. doi:10.1016/j.jenvman.2019.109810

Bardgett, R.D., Bullock, J.M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M., Durigan, G., L. Fry, E., Johnson, D., Lavallee, J.M., Le Provost, G., Luo, S., Png, K., Sankaran, M., Hou, X., Zhou, H., Ma, L., Ren, W., Li, X., Ding, Y., Li, Y., Shi, H., 2021. Combatting global grassland degradation. Nature Reviews Earth and Environment. doi:10.1038/s43017-021-00207-2

Blackburn, D.A., Oliphant, A.J., Davis, J.D., 2021. Carbon and Water Exchanges in a Mountain Meadow Ecosystem, Sierra Nevada, California. Wetlands 41. doi:10.1007/s13157-021-01437-2

Castellano, M.J., Mueller, K.E., Olk, D.C., Sawyer, J.E., Six, J., 2015. Integrating plant litter quality, soil organic matter stabilization, and the carbon saturation concept. Global Change Biology 21, 3200–3209. doi:10.1111/gcb.12982

Cotrufo, F., Lavallee, J., Zhang, Y., Hansen, P., Paustian, K., Schipanski, M., Wallenstein, M.D., 2021. In-N-Out : A hierarchical framework to understand and predict soil carbon storage and nitrogen recycling. Global Change Biology 27, 4465–4468. doi:10.1111/gcb.15782

Cotrufo, M.F., Ranalli, M.G., Haddix, M.L., Six, J., Lugato, E., 2019. Soil carbon storage informed by particulate and mineral-associated organic matter. Nature Geoscience 12, 989–994. doi:10.1038/s41561-019-0484-6

Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Denef, K., Paul, E., 2013. The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Global Change Biology 19, 988–995. doi:10.1111/GCB.12113

Crowther, T.W., Sokol, N.W., Oldfield, E.E., Maynard, D.S., Thomas, S.M., Bradford, M.A., 2015. Environmental stress response limits microbial necromass contributions to soil organic carbon. Soil Biology and Biochemistry 85, 153–161. doi:10.1016/j.soilbio.2015.03.002

Domeignoz-Horta, L.A., Pold, G., Liu, X.J.A., Frey, S.D., Melillo, J.M., DeAngelis, K.M., 2020. Microbial diversity drives carbon use efficiency in a model soil. Nature Communications 11, 1–10. doi:10.1038/s41467-020-17502-z

Feng, W., Plante, A.F., Aufdenkampe, A.K., Six, J., 2014. Soil organic matter stability in organo-mineral complexes as a function of increasing C loading. Soil Biology and Biochemistry 69, 398–405. doi:10.1016/j.soilbio.2013.11.024

Fossum, C., Estera-Molina, K.Y., Yuan, M., Herman, D.J., Chu-Jacoby, I., Nico, P.S., Morrison, K.D., Pett-Ridge, J., Firestone, M.K., 2022. Belowground allocation and dynamics of recently fixed plant carbon in a California annual grassland. Soil Biology and Biochemistry 165, 108519. doi:10.1016/j.soilbio.2021.108519

Frolking, S., Talbot, J., Jones, M.C., Treat, C.C., Kauffman, J.B., Tuittila, E.S., Roulet, N., 2011. Peatlands in the Earth’s 21st century climate system. Environmental Reviews 19, 371–396. doi:10.1139/a11-014

Germanoski, D., Miller, J.R., 2004. Great Basin Riparian Ecosystems—Ecology, Management, and Restoration. Island Press, Covelo.

Hafner, S., Unteregelsbacher, S., Seeber, E., Lena, B., Xu, X., Li, X., Guggenberger, G., Miehe, G., Kuzyakov, Y., 2012. Effect of grazing on carbon stocks and assimilate partitioning in a Tibetan montane pasture revealed by 13CO 2 pulse labeling. Global Change Biology 18, 528–538. doi:10.1111/j.1365-2486.2011.02557.x

Hassink, J., Whitmore, A.P., 1997. A Model of the Physical Protection of Organic Matter in Soils 131–139. doi:10.2136/sssaj1997.03615995006100010020x

Herron, P.M., Stark, J.M., Holt, C., Hooker, T., Cardon, Z.G., 2009. Microbial growth efficiencies across a soil moisture gradient assessed using 13C-acetic acid vapor and 15N-ammonia gas. Soil Biology and Biochemistry 41, 1262–1269. doi:10.1016/j.soilbio.2009.03.010

Hooker, T.D., Stark, J.M., 2012. Carbon Flow from Plant Detritus and Soil Organic Matter to Microbes-Linking Carbon and Nitrogen Cycling in Semiarid Soils. Soil Science Society of America Journal 76, 903–914. doi:10.2136/sssaj2011.0139

Hooker, T.D., Stark, J.M., Norton, U., Joshua Leffler, A., Peek, M., Ryel, R., 2008. Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA. Biogeochemistry 90, 291–308. doi:10.1007/s10533-008-9254-z

Jia, B., Niu, Z., Wu, Y., Kuzyakov, Y., Li, X.G., 2020. Waterlogging increases organic carbon decomposition in grassland soils. Soil Biology and Biochemistry 148, 107927. doi:10.1016/j.soilbio.2020.107927

Jilling, A., Keiluweit, M., Contosta, A.R., Frey, S., Schimel, J., Schnecker, J., Smith, R.G., Tiemann, L., Grandy, A.S., 2018. Minerals in the rhizosphere: overlooked mediators of soil nitrogen availability to plants and microbes. Biogeochemistry 139, 103–122. doi:10.1007/s10533-018-0459-5

Kettler, T.A., Doran, J.W., Gilbert, T.L., 2001. Simplified Method for Soil Particle-Size Determination to Accompany Soil-Quality Analyses. Soil Science Society of America Journal 65, 849–852. doi:10.2136/sssaj2001.653849x

Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R., Nico, P., 2015. Mineral Organic Associations: Formation, Properties, and Relevance in Soil Environments. Advances in Agronomy 130.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15, 259–263. doi:10.1127/0941-2948/2006/0130

Lavallee, J.M., Soong, J.L., Cotrufo, M.F., 2020. Conceptualizing soil organic matter into particulate and mineral-associated forms to address global change in the 21st century. Global Change Biology 26, 261–273. doi:10.1111/gcb.14859

Lützow, M. V., Kögel-Knabner, I., Ekschmitt, K., Matzner, E., Guggenberger, G., Marschner, B., Flessa, H., 2006. Stabilization of organic matter in temperate soils: Mechanisms and their relevance under different soil conditions - A review. European Journal of Soil Science 57, 426–445. doi:10.1111/j.1365-2389.2006.00809.x

Matus, F.J., 2021. Fine silt and clay content is the main factor defining maximal C and N accumulations in soils : a meta - analysis. Scientific Reports 1–17. doi:10.1038/s41598-021-84821-6

Mikutta, R., Turner, S., Schippers, A., Gentsc, N., Meyer-, S., Condron, L.M., Peltzer, D.A., Richardson, S.J., Eger, A., Hempel, G., Kaiser, K., Klotzbücher, T., Guggenberger, G., 2019. Microbial and abiotic controls on mineral-associated organic matter in soil profiles along an ecosystem gradient 1–9. doi:10.1038/s41598-019-46501-4

Mitra, S., Wassmann, R., Vlek, P.L.G., 2005. An appraisal of global wetland area and its organic carbon stock. Current Science 88, 25–35.

Morra, B., Richardson, W., Stringham, T.K., Sullivan, B., n.d. Carbon stocks and total belowground carbon fluxes are large, differ by plant community, and respond to weather and grazing in surface soils of semiarid montane meadows. Ecosystems.

Norton, J.B., Jungst, L.J., Norton, U., Olsen, H.R., Tate, K.W., Horwath, W.R., 2011. Soil Carbon and Nitrogen Storage in Upper Montane Riparian Meadows. Ecosystems 14, 1217–1231. doi:10.1007/s10021-011-9477-z

Norton, J.B., Olsen, H.R., Jungst, L.J., Legg, D.E., Horwath, W.R., 2014. Soil carbon and nitrogen storage in alluvial wet meadows of the Southern Sierra Nevada Mountains, USA. Journal of Soils and Sediments 14, 34–43. doi:10.1007/s11368-013-0797-9

Pett-Ridge, J., Firestone, M.K., 2017. Using stable isotopes to explore root-microbe-mineral interactions in soil. Rhizosphere 3, 244–253. doi:10.1016/j.rhisph.2017.04.016

Poeplau, C., Don, A., Six, J., Kaiser, M., Benbi, D., Chenu, C., Cotrufo, M.F., Derrien, D., Gioacchini, P., Grand, S., Gregorich, E., Griepentrog, M., Gunina, A., Haddix, M., Kuzyakov, Y., Kühnel, A., Macdonald, L.M., Soong, J., Trigalet, S., Vermeire, M.L., Rovira, P., van Wesemael, B., Wiesmeier, M., Yeasmin, S., Yevdokimov, I., Nieder, R., 2018. Isolating organic carbon fractions with varying turnover rates in temperate agricultural soils – A comprehensive method comparison. Soil Biology and Biochemistry 125, 10–26. doi:10.1016/j.soilbio.2018.06.025

R Core Team, 2021. R: A language and environment for statistical computing.

Reed, C., Berhe, A., Moreland, K., Wilcox, J., Sullivan, B., 2022. Restoring function: Positive responses of carbon and nitrogen to 20 years of hydrologic restoration in montane meadows. Ecological Applications 0–2. doi:10.1002/eap.2677

Reed, C., Merrill, A., Drew, M., Christman, B., Hutchinson, A., Keszey, L., Swanson, S., 2021. Montane Meadows: A Soil Carbon Sink or Source? Ecosystems. doi:10.1007/s10021-020-00572-x

Sanderman, J., Baldock, J., Hawke, B., Macdonald, L., Massis-puccini, A., Szarvas, S., 2011. National Soil Carbon Research programme : Field and laboratory methodologies 19.

Saugier, B., Roy, J., Mooney, H., 2001. Estimations of global terrestrial productivity: Converging toward a single number? Terrestrial Global Productivity.

Saunders, M.J., Jones, M.B., Kansiime, F., 2007. Carbon and water cycles in tropical papyrus wetlands. Wetlands Ecology and Management 15, 489–498. doi:10.1007/s11273-007-9051-9

Sokol, N.W., Whalen, E.D., Jilling, A., Kallenbach, C., Pett-Ridge, J., Georgiou, K., 2022. The Global Distribution, Formation, and Fate of Mineral-Associated Soil Organic Matter Under a Changing Climate – A Trait-Based Perspective. Functional Ecology 1–19. doi:10.1111/1365-2435.14040

Stewart, C.E., Paustian, K., Conant, R.T., Plante, A.F., Six, J., 2007. Soil carbon saturation: Concept, evidence and evaluation. Biogeochemistry 86, 19–31. doi:10.1007/s10533-007-9140-0

Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., Hendricks, D.M., 1997. Mineral control of soil organic carbon storage and turnover. Nature 389, 170–173. doi:10.1038/38260

Weixelman, D., Cooper, D., Hill, B., Berlow, E., Viers, J., Purdy, S., Merrill, A., Gross, S., 2011. A field key to meadow hydrogeomorphic types for the Sierra Nevada and Southern Cascade Ranges in California. Vallejo, CA.

Werth, M., Kuzyakov, Y., 2010. 13C fractionation at the root-microorganisms-soil interface: A review and outlook for partitioning studies. Soil Biology and Biochemistry 42, 1372–1384. doi:10.1016/j.soilbio.2010.04.009

Wieder, W.R., Bonan, G.B., Allison, S.D., 2013. Global soil carbon projections are improved by modelling microbial processes. Nature Climate Change 3, 909–912. doi:10.1038/nclimate1951

Wieder, W.R., Grandy, A.S., Kallenbach, C.M., Bonan, G.B., 2014. Integrating microbial physiology and physio-chemical principles in soils with the MIcrobial-MIneral Carbon Stabilization (MIMICS) model 3899–3917. doi:10.5194/bg-11-3899-2014

Xu, Y., Liu, K., Yao, S., Zhang, Y., Zhang, X., He, H., Feng, W., Ndzana, G.M., Chenu, C., Olk, D.C., Mao, J., Zhang, B., 2022. Formation efficiency of soil organic matter from plant litter is governed by clay mineral type more than plant litter quality. Geoderma 412, 115727. doi:10.1016/j.geoderma.2022.115727

Yu, H., Luedeling, E., Xu, J., 2010. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. Proceedings of the National Academy of Sciences of the United States of America 107, 22151–22156. doi:10.1073/pnas.1012490107

Tables:

	Semiarid High Productivity	**Semiarid Low Productivity**	**Humid High Productivity**	**Humid Low Productivity**
Average NDVI	0.19 ± 0.003 c	0.18 ± 0.004 d	0.33 ± 0.008 a	0.30 ± 0.006 b
Growing Season Length (days)	111 ± 2 c	96 ± 2 d	165 ± 3 a	127 ± 3 b
Bulk Density (g cm^{-3})	0.85 ± 0.05 ab	0.94 ± 0.09 a	0.65 ± 0.06 b	0.82 ± 0.05 ab
Shoot biomass (g m^{-2})	89.76 ± 21.28 a	49.13 ± 11.7 b	205.58 ± 28.47 c	76.55 ± 7.98 ab
Root biomass (g m^{-2})	715.50 ± 218.01 ab	867.60 ± 238.57 ab	1382.85 ± 175.86 a	439.68 ± 435.44 b
Assimilation rate (g C m^{-2} h^{-1})	338.89 ± 8.05 b	332.68 ± 91.28 b	756.62 ± 87.9 a	472.28 ± 17.75 b
Average volumetric water content	14.29 ± 1.22 b	12.19 ± 2.29 b	38.86 ± 8.91 a	10.41 ± 2.35 b
Percent Sand	28.34 ± 2.00 a	27.20 ± 1.78 a	29.88 ± 1.79 a	37.86 ± 0.48 b
Percent Silt	50.87 ± 3.50 b	50.41 ± 2.04 b	34.99 ± 3.50 a	32.84 ± 3.50 a
Percent Clay	20.78 ± 1.06 b	22.38 ± 1.03 b	35.12 ± 4.73 a	29.29 ± 1.97 a

	Semiarid	**Humid**
Dominant soil type	Ardic Argixerolls	Typic Cryaquolls
Annual precipitation (mm)	342	825
Average max temperature (°C)	13.2	14
Mean Temperature (°C)	5.9	6.2
Average min temperature (°C)	-1.4	-2
Average max VPD (hPa)	13.61	13.8
Average min VPD (hPa)	2.2	0.46
Watershed size (ha)	108	3063

Table 1.Productivity, climate, and soil characteristics of plots used in this study. NDVI is the average value from 2018 to 2021. Growing season length was calculated based off of the same NDVI data according to Yu et al. (2010). Bulk density was calculated using rock-free root-free soil mass. Average volumetric water content is the mean value measured throughout the experiment. Climate is based on 30-year average annual weather. Soil series (from the USDA taxonomic system) and climate are assumed to be the same for plots within the same climate. Percent POM, silt MAOM, and clay MAOM are the proportion of each fraction contained in bulk soil. Letters show differences among rows. Abbreviations: Normalized vegetation difference index (NDVI), Vapor pressure deficit (VPD)

Figures:

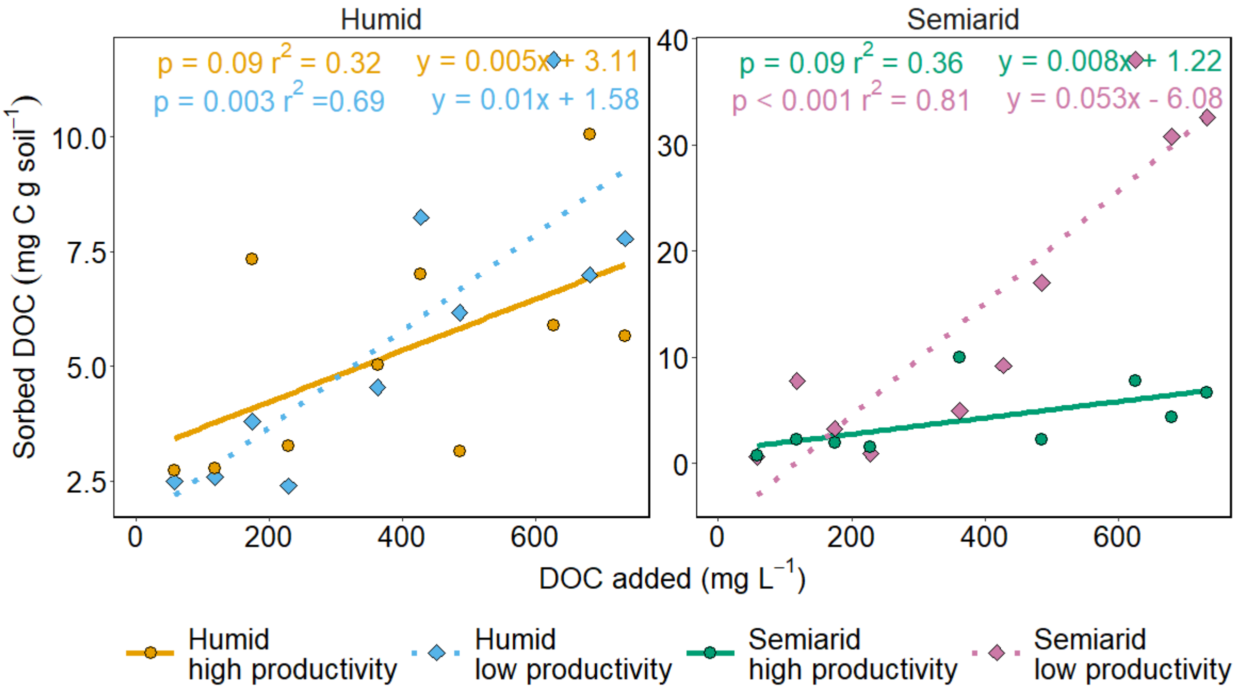

Figure 1**.** Soil C loadings of meadow soils incubated in solutions of increasing dissolved organic C concentration. High and low productivity plots within each climate are shown as solid or dashed lines respectively. Sorbed DOC is the result of formation of organo-mineral complexes following a 24-hour incubation of bulks soils collected at the start of the experiment.

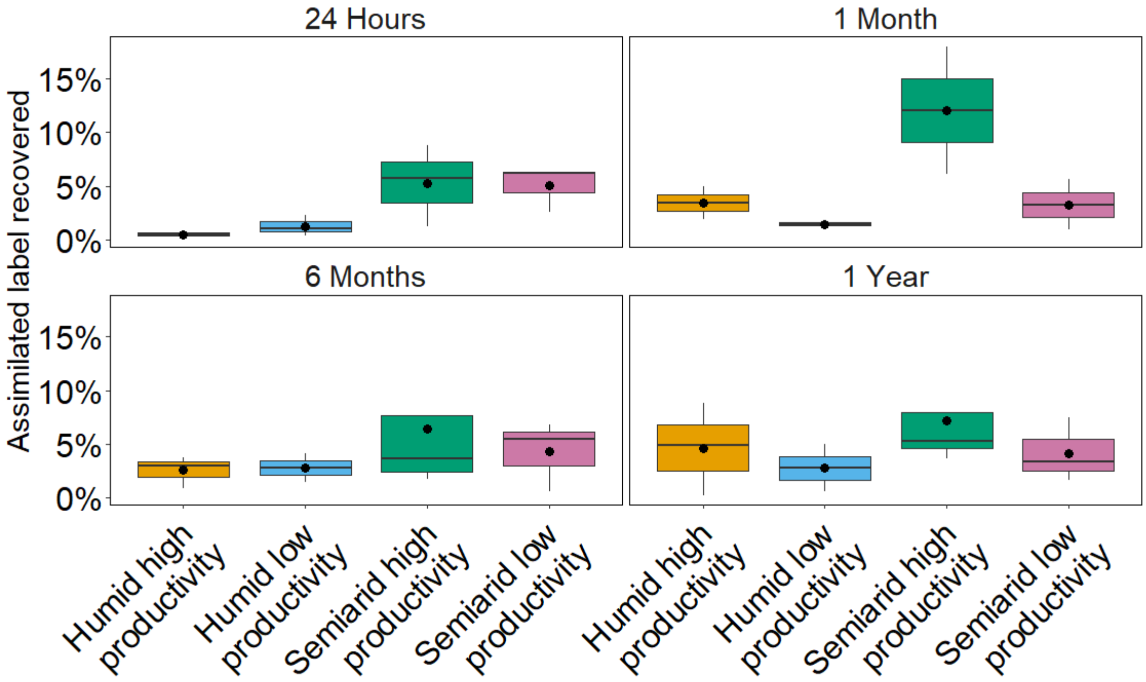

Figure 2. Assimilated label recovered in bulk soils at 24 hours, one month, six months, and one year after application of 13C label in high and low productivity meadows found in humid and semiarid ecosystems. We found no significant differences of bulk soil recovery of assimilated label among meadows at any time point. Points show the mean label recovery.

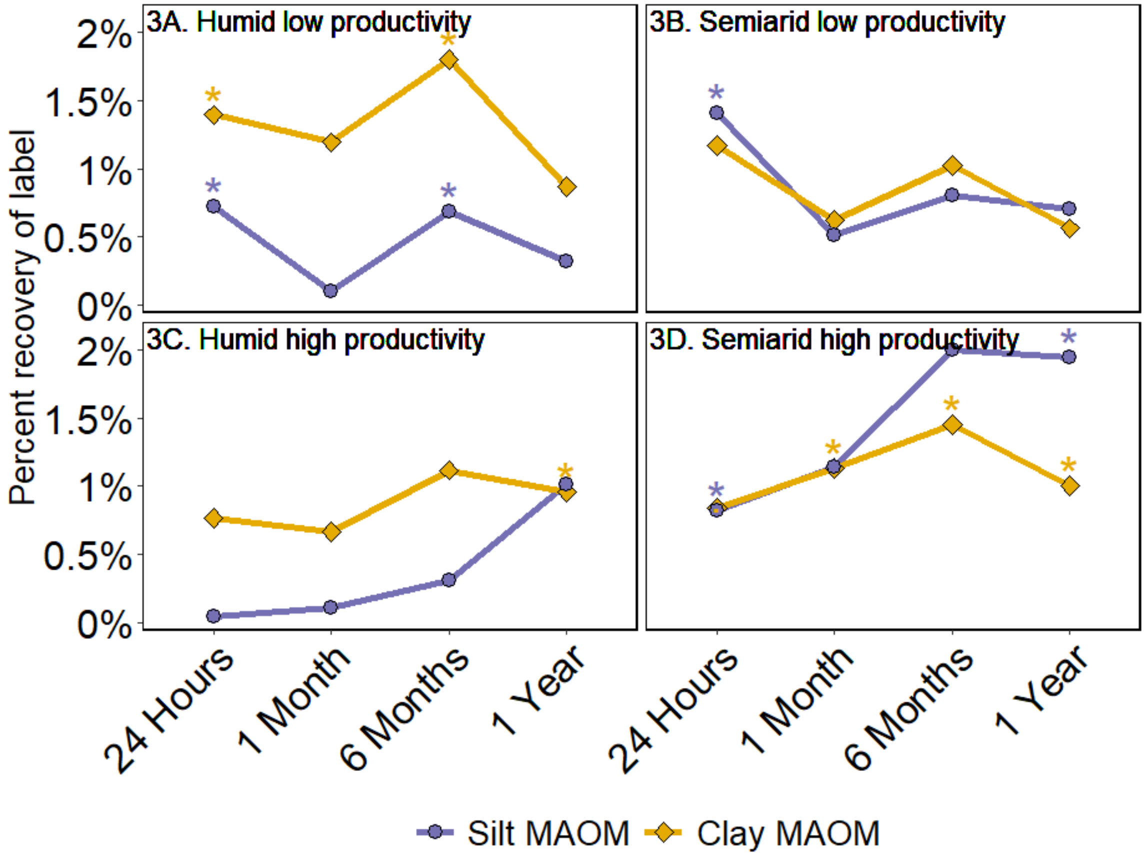

Figure 3. Percent of assimilated label in 3A. semiarid high productivity plots, 3B. humid high productivity plots, 3C semiarid low productivity plots, and 3D humid low productivity plots recovered at 24 hours, one month, six months, and one year in silt and clay, soil textures associated with silt mineral associated organic matter (silt MAOM), and clay mineral associated organic matter (clay MAOM) respectively. Stars indicate recovery of label that is significantly greater than zero ($p < 0.05$) using to a one-tail t test.

Chapter 3: Ecosystem carbon and nitrogen gains following 27 years of grazing management in a semiarid alluvial valley.

Authors: Brian Morra[1], Hondo Brisbin[2], Tamzen Stringham[2], Benjamin W. Sullivan[1,3]

[1] Department of Natural Resources & Environmental Science, The University of Nevada, Reno,

1664 N. Virginia St., Reno, NV 89557

[2] Department of Agriculture, Veterinary, and Rangeland Sciences, The University of Nevada, Reno, 1664 N. Virginia St., Reno, NV 89557

[3] The Global Water Center, The University of Nevada, Reno, 1664 N. Virginia St., Reno, NV 89557

Abstract

Soils in semiarid riparian ecosystems have large carbon (C) stocks that promote water and nutrient availability for productive plant communities consumed by grazing animals. Changes to riparian hydrologic conditions caused by channel incision result in different edaphic conditions and a greater abundance of less productive upland plant species that may be associated with lower soil C stocks. Can grazing management alone change riparian hydrologic conditions and increase ecosystem C stocks? Using riparian meadows alongside Maggie Creek in central Nevada, we show that 27 years of modified grazing practices can repair ecosystem processes and increase the C stocks. We compared C and nitrogen (N) stocks (of soils and plant biomass) on floodplains, terraces, and uplands of reaches where grazing was either modified or excluded to reaches where no changes to grazing practices were made. Grazing management allowed beaver to establish, increased sediment retention to reduce channel incision, and lengthening the growing season. These changes allowed C and N to accumulate on surfaces that extended from the stream channel to the surrounding hillslopes. A stoichiometric relationship between C and N shows carbon sequestration can reduce nutrient runoff to nearby waterways and may depend on nitrogen availability. Gains in ecosystem carbon ranged from 93-452 g C m^{-2} y^{-1} and were dominated by increases in soil C. Gains in soil C occurred across the full depth range measured (0-45 cm) and were comparable to those found in restored wetlands and meadows located in more humid ecosystems. Carbon gains exhibited substantial variability caused by microtopography, plant community composition, and subsurface processes. While grazing exclusion resulted in the largest gains in ecosystem C, managed grazing increased ecosystem C relative to reaches where

management wasn’t changed. We demonstrate that managed grazing that maintains ecosystem process is compatible with projects aimed at increasing soil carbon in semiarid riparian rangelands.

Introduction

Earth has 50 million km^2 of land managed for the production of food, fuels, or livestock (Klein Goldewijk et al., 2011). Adoption of management practices that increase carbon (C) storage in rangeland and cropland has the potential to sequester an additional 4-5 Gt of atmospheric carbon dioxide (CO_2) per year in soil organic matter (Paustian et al., 2019). In addition to climate benefits, C sequestration has the potential to generate revenue in developing voluntary C markets (Kreibich and Hermwille, 2021) and provide ecosystem services such as water storage and infiltration (Dominati et al., 2010; Ankenbauer and Loheide, 2017; Apfelbaum et al., 2022). Soil organic matter also contains substantial nitrogen (N), supporting plant productivity and reducing pollution of aquatic ecosystems. Consequently, soil C sequestration has the potential to increase soil N, benefitting terrestrial productivity and water quality. Soil C may be especially important in semiarid rangelands where plant productivity can be limited by water and nitrogen availability (Burke et al., 1997; Van Groenigen et al., 2017).

Soil C sequestration through management or restoration may be most impactful in ecosystems where potential C storage is greater than the current C stock (Paustian et al., 2019). One such location may include riparian and low-gradient meadow valleys in montane regions. In riparian meadows, water is supplied to floodplains adjacent to stream channels (Weixelman et al., 2011). A shallow water table during the growing season supports herbaceous plant communities that form dense root mats which allocate substantial C belowground (Reed et al., 2021). The condition of riparian meadows can be altered by disturbance to vegetation and soils which initiates a feedback loop resulting in channel incision (Trimble and Mendel, 1995), increased depth to groundwater, and loss of wetland meadow vegetation responsible for streambank stabilization (Darrouzet-Nardi et al., 2006). Meadow condition may alter C or N stocks and fluxes. For example, in the Sierra Nevada of California, USA, soil C and N stocks were lower in non-hydrologically functioning meadow conditions than in properly functioning meadows (Norton et al., 2011). Meadows that were net carbon sinks had a shallower depth to groundwater, soil bulk density, and greater aboveground plant and root biomass than meadows that were net carbon sources to the atmosphere (Reed et al., 2021).

Activities that restore riparian plant communities may be able to arrest and reverse the disturbance feedback by reducing channel erosion, increasing channel roughness, and capturing sediment to reverse incision (Beechie et al., 2010). Twenty years of meadow hydrologic restoration in the Sierra Nevada resulted in average sequestration rates of 3 g C kg soil^{-1} y^{-1} and 0.18 g N kg soil^{-1} y^{-1} (Reed et al., 2022). Soil C to N ratios did not change following restoration, indicating that soil C sequestration may occur at roughly the same rate as soil N sequestration. The surface soil was most responsive to C and N sequestration following restoration (Reed et al., 2022), probably because root turnover and exudation contribute the most C inputs to surface soil (Reed et al., 2021). In some cases, beaver (*Castor canadensis*) contribute to the restoration of channels and associated terrestrial vegetation by engineering dams that impound water and capture sediment to further reverse incision (Fairfax and Small, 2018; Nummi et al., 2018; Nash et al., 2021). Beaver dams can substantially increase the extent of wet riparian meadows (Hood and Larson, 2015). Hydrologic change associated with beaver have been shown to impact ecosystem C and N. Riparian areas containing beaver ponds hold 8 to 23% of the total ecosystem C in Rocky Mountain National Park, USA (Wohl, 2013).

Meadow restoration in semiarid ecosystems may represent an opportunity for C and N sequestration. Per unit area, semiarid meadows hold nearly three times as much C as their surrounding uplands, making their contribution to regional C stocks relatively greater than meadows in montane regions that receive more precipitation (Morra et al., in review). Additionally, semiarid meadows provide sources of forage, habitat, and late season water (Chambers et al., 2011). These resources often make meadows a focal point of grazing activities, which can contribute to the loss of meadow vegetation under heavy use (Trimble and Mendel, 1995; Bardgett et al., 2021). Similar to hydrologic restoration and beaver activity, modification of grazing can restore bankside vegetation (Green and Kauffman, 1995). In several semiarid watersheds in Nevada, USA, the regrowth of bankside vegetation following grazing modification has improved beaver habitat, supporting construction of beaver dams (Charnley, 2019). Grazing modification, subsequent bankside stabilization by plants, and development of beaver impoundments resulted in greater plant productivity and evapotranspiration in vegetation extending from the stream channel to the surrounding hill slopes of alluvial valleys in Nevada (Fairfax and Small, 2018).

We sought to quantify potential C and N sequestration following livestock grazing management and beaver activity in semiarid riparian ecosystems. We measured C and N stocks in beaver ponds and on floodplains, terraces, and uplands following 27 years of grazing management and in unmanaged baseline locations within the watershed to address the following questions and objectives:

1. How much do ecosystem C and N stocks in a riparian floodplain change in response to 27 years of grazing management and beaver activity in a semiarid region such as the Great Basin, USA?
2. How does the impact of livestock grazing management and beaver activity on C and N stocks vary laterally from the stream channel and vertically within the soil profile?
    a. We expected the largest C and N gains would occur in shallow soils adjacent to stream channels where impoundments of water by beaver have increased water availability to vegetation.
    b. We expected that gains in N would occur commensurately with gains in C.
3. Given the substantial temporal and spatial scale of the management actions in this study, we identified two additional objectives.
    a. Our first objective was to spatially extrapolate the unit-area stocks we measured across their respective geomorphic surfaces within the watershed to identify which surfaces have the greatest potential for C sequestration and what the range of variability might be for each surface.
    b. Our second objective was to use post-hoc tests to estimate how many years would have been required after management actions for significant

C sequestration to have occurred, where significant C gains occurred. These two objectives are designed to assist managers who may need to anticipate the possible impacts of actions taken on similar stream reaches of alluvial valleys in the region.

Methods

Site description

We worked in the Maggie Creek watershed in the Tuscarora Mountains in northeast Nevada, USA, a tributary of the Humboldt River. The 30-year average annual precipitation at Maggie Creek is 291 mm, which occurs mainly as winter snowfall; streamflow in Maggie Creek peaks after snowmelt in the spring (Kozlowski et al., 2016). The Maggie Creek watershed covers 254,150 acres and has been used for livestock grazing since the late 1800s (Horton, 2000). The United States Bureau of Land Management (BLM) manages 42% of the land, while 55% is privately owned. The remaining 3% are owned by the State of Nevada (Kozlowski et al., 2016). Nevada Gold (Formerly the Newmont Mining Corporation) operates an open pit mine near Maggie Creek. After increasing the pit depth in 1994, the mine began dewatering the surrounding riparian area. These actions required environmental mitigation of the reaches of Maggie Creek impacted by dewatering.

As part of this mitigation effort, the Maggie Creek Watershed Restoration Project (MCWRP) was implemented in 1994 by a partnership between the TS Ranch, owned by the Elko Land & Livestock Company (a subsidiary of Newmont), and the Elko (Nevada) BLM district. The goal of the MCWRP was to improve streams, riparian habitats, and watershed conditions in historically grazed riparian corridors by employing new grazing management or excluding grazing completely. Following a four-year rest period (1994-1998), grazing management consisted of short periods of use in the springtime (often a month or less) and fall use by cow-calf pairs. In the grazing exclusion pasture, fences were installed and consistent use by cattle ended in 1994. Implementation of the MCWRP allowed for the recovery of riparian vegetation and improved beaver habitat (ORC, 2017). Grazing changes increased the length of continuous stream from 38 km to 46 km between 2006 and 2010 (Jensen, 2011). Beavers, and the dams they constructed, further enhanced the restoration process, expanding the riparian area by as much as 250% in some stream reaches (ORC, 2017) (Fig. 1), though beaver did not successfully establish in all reaches. The recovery of stream channel function and the expansion of hydric vegetation along Maggie Creek has been reported through surface measurements by Kozlowski et al. (2016), and remotely sensed imagery contracted by Newmont (JBR, 2002; Jensen, 2011; ORC, 2017).

To measure the impact of changes in management on ecosystem C and N stocks, we made comparisons among three reaches within the MCWRP and a fourth reach on Maggie Creek where summer use by cattle continues (Fig. 1C). In two of the regions where grazing was excluded, two distinct reaches of beaver ponds formed. One reach was dominated by ephemeral beaver ponds which were smaller in size (30-40 m^2) and failed during years of high precipitation. The second reach was dominated by permanent beaver ponds, and created a continuous impounded reach (~1.5 ha) (Table 1). Pollock et al. (2014) observed similar patterns in beaver-built structures and found permanence required wide stream channels to dissipate stream energy. In the third reach, grazing was managed, but not excluded, and was associated with formation of ephemeral beaver ponds. We refer to these three reaches of Maggie Creek as “grazing excluded permanent pond,” “grazing excluded ephemeral pond,” and “managed grazing ephemeral pond.” The two grazing excluded reaches were located in the same pasture, roughly two kilometers apart while the managed grazing ephemeral pond reach was located in an adjacent pasture downstream. The fourth reach, located outside of the MCWRP, referred to as “unmanaged grazing”, was located 10 km downstream from the managed grazing reach. We used historical imagery and work by Evans (2009) to determine the unmanaged grazing reach is similar to the reaches within the MCWRP prior to grazing regime changes (Fig. 1).

To understand how changes in management affect surfaces extending laterally from the stream channel, we identified three geomorphic surfaces: floodplains that are actively being impacted by the surface flow of Maggie Creek, terraces that were previously influenced by surface flow, and upland areas that are outside of the influence of the stream channel, for each of the reaches. While uplands were likely not impacted by the stream channel, they were within the fences installed by the MCWRP and experienced the impact of changes to grazing management. When present, we also sampled accumulated sediment within beaver ponds. We were able to map the extent of all geomorphic surfaces within the reaches using satellite imagery (Google Earth, V 7.3.4.8642). The extent of floodplains, terraces, and upland areas were ground-truthed at the time of data collection in the field.

Soil and pond sediment sampling

We sampled to a depth of 45 cm at six locations on floodplains and terraces and three locations in the upland soils in the three reaches of the MCWRP. We sampled to this depth based on previous observations of homogeneity among soil C stocks of meadow soils deeper than 50 cm (Kasten, 2019; Reed et al., 2021). We chose to concentrate our sampling in the riparian corridor (floodplains and terraces) as management of these areas were the primary focus of the MCWRP. Additionally, cattle tend to concentrate in these areas which have accessible water and palatable forage. We expected upland areas would contain smaller C and N stocks and were less likely to experience change due to grazing management than the riparian corridor and sampled these areas at a lower spatial intensity. In unmanaged reaches outside of the MCWRP, soils and plant communities showed little difference among geomorphic surfaces. Therefore, we collected three samples on each geomorphic surface due to the deep channel incision that minimized the influence of the stream channel on geomorphic surfaces. Minimal channel influence was observed as spatial homogeneity of soils and plants in the unmanaged reach. All soil samples were collected in 15-cm increments using a five cm-diameter AMS slide-hammer (AMS Equipment Corp, American Falls, Idaho, USA).

To measure C and N stocks in accumulated sediment within ponds associated with managed grazing and the two excluded grazing reaches, we first estimated sediment volume within the ponds. To estimate volume, we measured the pond surface area using transect tapes, crossing the pond with a stand-up paddleboard when necessary. We then measured the depth of the sediment by repeatedly inserting a wooden rod to the sediment surface and then to the rocky substrate below the sediment in transects across the pond (perpendicular to the stream axis). We then sampled sediment for bulk density and C/N concentration by inserting a 5-cm diameter polyvinyl chloride (PVC) tube into the sediment. To retrieve the sample, we filled the remaining airspace in the tube with water and sealed the top using a 5-cm gripper plug (Oatey, Cleveland Ohio) to ensure the sample didn't slip back out of the PVC tube. We applied average depths of 20.6, 31.2, and 43.6 cm for ponds in the managed grazing ephemeral pond reach, the grazing exclusion ephemeral pond reach, and the grazing exclusion permanent pond reach respectively. The unmanaged reach outside of the MCWRP had no beaver activity. In reaches with ephemeral beaver dams, we multiplied the mean ponds size by the number of dams observed in satellite imagery (Google Earth, V 7.3.4.8642). The total impounded area in the grazing excluded permanent pond reach was estimated by drawing a polygon around the end points of the three transects used to estimate sediment depth.

We calculated soil C and N stocks (kg m^{-2}) as the product of C or N concentration in each sample (both soils and pond sediments), its bulk density, and the sampling depth. Bulk density was the rock-free, root-free mass of the soil dried at 105 °C. Roots and rocks were removed from soils by first passing them through a 2 mm sieve to capture the rocks. Roots were separated from the rocks by floatation and the supernatant was strained using a 0.5 mm sieve, air dried at 60 °C and weighed. We tested soils for the presence of inorganic C by adding several drops of 1M HCl which generates bubbles in the presence of carbonate minerals. Subsamples (~2 g) of rock free and root free soils that contained carbonate minerals were treated with 5 mL of 0.1 M HCl. After acidification, samples were shaken vigorously and spun in a centrifuge at 3000 rpm for five minutes. We tested the pH of the supernatant and added more HCl and repeated the shaking and centrifuging if the pH was above 6.3, assuming all the acid had been consumed. Once carbonates had been removed, the HCl supernatant was poured off and samples were rinsed 3 times using 20 mL of DI water by shaking and centrifuging the soil samples. We measured C and N concentration on each soil and sediment sample using a Costech 4010 Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA).

Plant C and N sampling

We quantified the C in herbaceous biomass by clipping vegetation in 0.89 m^2 hoops placed near each core location. Clipped vegetation was dried at 60 °C and weighed. We used estimates of C and N concentrations from herbaceous biomass in Nevada meadows of 0.35 g C g^{-1} and 0.02 g N g^{-1} biomass (Morra et al., in review). To estimate the C and N stocks of shrubs, we measured all shrubs within a 2.5-meter radius of soil cores and used species specific allometric equations to convert measurements of length, width, and height to estimates of shrub biomass (Appendix A Table 1, Reiner et al., 2010; United States Geological Survey, 2008). We assumed sagebrush tissue was 50% C and 0.9% N by weight based on measurements collected by Austreng et al. (2012) and Garcia-Moya & McKell (1969). Visual estimates of herbaceous species canopy cover were collected at each core location using 0.25 m^2 quadrats.

Estimates of C credits earned by management

We report the change in ecosystem C stocks between 1994 and 2021 (kg C m^{-2}) by making comparisons between unmanaged geomorphic surfaces (floodplains, terraces, and uplands) and their managed counterparts. We considered ecosystem carbon as the sum of root C, soil C, and the C contained in aboveground biomass. In geomorphic surfaces where change in ecosystem C stock was significantly different than zero, (see following section) we estimated the yearly change in ecosystem C stock by assuming a linear rate of change. We present the resulting mass eCO2 sequestered based on the area of geomorphic surface standardized by a 1-km stretch of valley length contained in a reach (Table 1). We recognize that interannual C stock change may not be linear from one year to the next, but linear models fit soil C increases in riparian meadow grasslands (Reed et al., 2022), abandoned agricultural fields (Knops and Bradley, 2009), and in fine textured soils of grasslands (Baer et al., 2010) over the two decades following restoration.

Statistics

This study sought to understand how management changes ecosystem C relative to unmanaged surfaces. Therefore, we calculated an effect size, which was the difference between values measured on a geomorphic surface of the MCWRP minus the corresponding values from surfaces of the unmanaged reach. Because ecosystem C is made up of aboveground pools split into two plant functional groups (shrubs and herbaceous vegetation) and two belowground pools (soil C and root C split by depth), effect sizes were calculated for each C pool individually. This includes changes in soil bulk density (g/cm^{-3}), soil C concentration (%C), root C stock ($kg\ m^{-2}$) soil C ($kg\ m^{-2}$), aboveground biomass C ($kg\ m^{-2}$), at each depth interval (0-15 cm, 15-30 cm, and 30-45 cm) of each geomorphic surface. We also calculated an effect size for changes in ecosystem C and N by summing C or N contained in roots and soils (0-45 cm) and aboveground biomass. We then calculated a 95% confidence interval assuming a one-tail t-distribution to show where changes were significantly different than zero. These same 95% confidence intervals are used to show a range of uncertainty presented in the results.

To compare the rates and evenness of gains in ecosystem C accumulation among surfaces where significant changes in ecosystem C stock occurred, we conducted a power analysis to estimate the amount of C gain required to create an observable change in ecosystem C stock. This estimate uses our sample size, variance, and an alpha equal to 0.05 (Schrumpf et al., 2011). We used two different levels of statistical power, 0.1 and 0.2, to show the uncertainty of our power analysis. We then used the estimates of mean annual gains in ecosystem C to calculate the number of years these management treatments would require to cause a minimum detectable difference in ecosystem C stocks relative to those measured in the unmanaged reach. We calculated coefficient of variance for ecosystem and soil C stocks to compare variance among fluvial surfaces.

We also made comparisons among ecosystem C stocks and soil C stocks of geomorphic surfaces by fitting linear mixed models. These models contained a random intercept term to account for unmeasured differences in meadows. Where differences were observed, we made pairwise comparisons using least squared means. The *p*-values of multiple pairwise comparisons were adjusted using Bonferroni corrections.

Results

Changes in C, N, roots, and bulk density by depth

The floodplains in the managed grazing ephemeral pond reach had similar C concentration, soil C stock, soil N stock, bulk density, and root C relative to the floodplains in the unmanaged reach (Fig. 2). In terrace soils, carbon stock increased by 1.41 ± 1.34 kg C m^{-2} and 1.41 ± 1.27 kg C m^{-2} in soils 0-15 cm and 15-30 cm respectively. Similarly, C concentration increased by 0.99% ± 0.86 and 0.97% ± 0.72 in soils 0-15 cm and 15-30 cm respectively. In upland soils of the managed grazing ephemeral pond reach, root C increased by 0.16 ± 0.10, and soil C and N stock increased by 1.49 ± 1.24 kg C m^{-2} and 0.18 ±0.13 kg N m^{-2} respectively at the middle depths of soils (15-30 cm) (Fig. 2). In the grazing excluded permanent pond reach, soil C concentration of 15-30 cm floodplain soils increased by 1.06% ± 0.63 (Fig. 3). Soil C stocks also increased by 3.55 ± 2.76 and 3.16 ± 2.74 kg C m^{-2} in the 15-30 cm and 30-45 cm depths. Root C increased at the 0-15, 15-30, and 30-45 cm depths by 1.11 ± 0.45, 1.23 ± 0.53, and 1.20 ± 0.46 kg C m^{-2} respectively. In the terrace soils of the grazing excluded permanent pond reach, bulk density of soils decreased by 0.39 ± 0.19 and 0.41 ± 0.34 in soils 0-15 and 15-30 cm respectively (Fig. 3). Percent C increased in soils 0-15 and 15-30 cm by 2.31% ± 1.17 and 1.41% ± 0.91 respectively. Similarly, soil C stocks increased by 2.64 ± 1.81 and 1.89 ± 1.72 kg C m^{-2} in soils 0-15 and 15-30 cm. In these soils, N stock only increased at the shallowest depth (0-15 cm) by 0.19 ± 0.16. Upland soils in this reach were unchanged relative the unmanaged reach (Fig. 3). In the grazing excluded ephemeral pond reach, floodplains were unchanged relative to their unmanaged counterparts (Fig. 4). In the terraces of this reach, bulk density decreased by 0.48 ± 0.23 and 0.51 ± 0.28 in 0-15 and 15-30 cm soils respectively. Soil C concentration also increased 2.62% ± 1.48, 1.77% ± 0.85, and 1.73% ± 1.29 in 0-15, 15-30, and 30-45 cm soils. Despite a decrease in bulk density, soil C increased by 2.24 ± 1.24 and 2.26 ± 1.61 kg C m^{-2} in 0-15 and 15-30 cm soils. In upland soils of the grazing excluded ephemeral pond reach, soil C concentration increased by 0.53% ± 0.49 in 0-15 cm soils and 0.42 ± 0.32 in 30-45 cm soils, root C increased by 0.09 ± 0.08 kg C m^{-2} in 15-30 cm soils, soil C stock increased by 0.78 ± 0.70 kg C m^{-2} in 0-15 cm soils, and N stock increased by 0.06 ±

0.05, 0.13 ± 0.12, and 0.12 ± 0.11, kg N m^{-2} in soils 0-15, 15-30, and 30-45 cm respectively (Fig. 4).

Components of ecosystem carbon

Ecosystem C stocks measured across all geomorphic surfaces and reaches were dominated by soil C (Fig. 5), which differed among reaches ($p < 0.001$), geomorphic surfaces ($p < 0.001$), and the interaction of geomorphic surfaces among reaches ($p < 0.001$; Supplementary Materials Table 1). Per unit area, the largest soil C stocks were in the floodplains of the grazing excluded permanent pond reach, where mean soil C stocks were 18.52 ± 1.86 kg C m^{-2} (supplementary materials Table 2). The next largest soil C stock (13.93 ± 1.32 kg C m^{-2}) was in the terraces of the grazing excluded ephemeral pond reach (supplementary materials Table 2). In the uplands, soil C ranged from 3.60 ± 0.81 kg C m^{-2} in the unmanaged grazing reach to 6.62 ± 1.29 kg C m^{-2} in the managed grazing ephemeral pond reach. However, upland soil C stocks were not significantly different among reaches (supplementary materials Table 2). Soil stocks were spatially variable, but the spatial variation differed among reach and management history (supplementary materials Table 2). After soil C, the next largest C pool was root C, which did not differ among geomorphic surfaces ($p = 0.33$) but differed by reach ($p = 0.004$) and the interaction of reach and geomorphic surface ($p = 0.001$) (supplementary materials Table 3). Aboveground herbaceous plant C increased in the terraces and uplands of the grazing excluded ephemeral pond reach and the terraces of the managed grazing ephemeral pond reach relative to corresponding surfaces in the unmanaged reach (Fig. 6A). Shrub C increased in the uplands of the grazing excluded permanent pond reach and the manage grazing ephemeral pond reach relative to corresponding surfaces in the unmanaged reach (Fig. 6B).

Changes in ecosystem carbon

There were five geomorphic surfaces where ecosystem C was significantly higher than the corresponding geomorphic surface within the unmanaged reach: terraces of the two grazing excluded reaches, floodplains of the grazing excluded permanent pond reach, and when considering only 0-30 cm soils, terraces and uplands of the managed grazing ephemeral pond reach (Fig. 7). Ecosystem C stocks were different among reaches ($p < 0.001$), geomorphic surfaces ($p < 0.001$), and the difference among geomorphic surfaces differed by reaches ($p < 0.001$) (supplementary materials Table 4). We consistently saw ecosystem C increases on terraces, where ecosystem C stock increased by 7.22 ± 5.57 and 5.68 ± 5.58 kg C m^{-2} in the grazing excluded ephemeral pond reach and the grazing excluded permanent pond reach, respectively, relative to the terraces found in the unmanaged reach (Fig. 7). When ecosystem C stocks were constrained to 0-30 cm soil depths, there was also an increase of 3.24 ± 2.02 C m^{-2} in ecosystem C on terraces in the managed grazing ephemeral pond reach relative to terraces in the unmanaged reach. The grazing excluded permanent pond reach was the only reach where ecosystem C increased on floodplains. Here, floodplains gained 12.19 ± 5.39 kg C m^{-2} of ecosystem C relative to floodplains in the unmanaged reach (Fig. 7) and the ecosystem C stock was 15.92 ± 1.99 kg C m^{-2}, the largest ecosystem C stock we measured (supplementary materials Table 5). Ecosystem C stock of ponds did not differ between permanent and ephemeral ponds within grazing excluded reaches where ecosystem C stocks were 5.3 ± 0.58 kg C m^{-2} and

5.0 ± 0.66 kg C m^{-2}, respectively (Fig. 7, supplementary materials Table 5). Both permanent and ephemeral ponds found in grazing excluded reaches contained more ecosystem C than the ponds in the managed grazing ephemeral pond reach (supplementary materials Table 5). We observed small increases in ecosystem C in the uplands of the grazing excluded ephemeral pond reach where ecosystem C increased by 2.67 ± 2.62 kg C m^{-2} relative to uplands of the unmanaged reach (Fig. 7). When omitting 30-45 cm soil depths, ecosystem C in the uplands of the managed grazing ephemeral pond reach increased by 2.43 ± 2.16 kg C m^{-2} relative to uplands in the unmanaged reach. We found no correlation between area impounded by beavers and ecosystem C stocks of ponds, floodplains, and terraces (supplementary materials Table 6). Ecosystem C showed similar patterns of variance as soil C (supplementary materials Fig. 1).

Potential sequestration from increases in ecosystem C

Mean annual gains in ecosystem C were similar among geomorphic surfaces, but when the annual gains in ecosystem C were multiplied by the area of a geomorphic surface occupying 1-km of valley length (Table 1), the amount of C sequestered by geomorphic surfaces ranged three orders of magnitude (Table 2). The largest spatially extrapolated mean C sequestration rate occurred on the terraces in the grazing excluded ephemeral pond reach, followed by uplands of the managed grazing ephemeral pond reach (Table 2). While ponds had similar increases in C stocks to terraces, they cover the least surface area and therefore sequester the least C annually of any geomorphic surface. Assuming a linear increase over the project period, significant changes in ecosystem gain may have been detectable within 5-13 years after the start of management (Table 2).

Changes in ecosystem nitrogen

Changes in ecosystem N were correlated with changes in ecosystem C (p = 0.005) (Fig. 9). Ecosystem N increased by ~0.03 kg for every kg increase in ecosystem C on most geomorphic surfaces (Fig. 9). The largest changes in ecosystem N, relative to the unmanaged grazing reach, occurred on the terraces of the two grazing excluded reaches (Table 3). The only surface in the managed grazing ephemeral pond reach where ecosystem N increased relative to unmanaged grazing was ponded areas. There was not a significant change in floodplain ecosystem N stocks among reaches. Based off the estimated annual increase in ecosystem N and the area of geomorphic surface held in 1-km of river valley within each reach (Table 1), across all geomorphic surfaces, annual gains in ecosystem N stocks range from 1- 21,832 g of N km^{-1} of valley length.

Discussion

In less than three decades, altered grazing management resulted in increased ecosystem C and N on geomorphic surfaces extending from the stream channel to the edge of the hillslopes surrounding Maggie Creek. Instead of consistently finding the largest gains in ecosystem C and N near the stream channel, we found gains in ecosystem C and N differed by the interaction of geomorphic surface, grazing season and duration, and beaver pond condition (permanent versus ephemeral). At Maggie Creek, grazing management led to gains in ecosystem C like those found in more humid ecosystems restored using physical manipulations to repair hydrologic function. The largest changes in ecosystem C occurred in shallow soils (0-15 cm), but on most geomorphic surfaces soil C increased to greater depths than measured in other restoration studies. Correlations between C and N gains suggests that increasing ecosystem C reduced N runoff to Maggie Creek and indicates C gains are reliant on N supply. We found high spatial variation in ecosystem C stocks, showing ecosystem C exhibits a diverse response to management within geomorphic surfaces in alluvial valleys.

Our results suggest C in semiarid riparian ecosystems may respond dynamically to management. Annual C gains in the MCWRP were much higher than those found in sagebrush-dominated ecosystems like those surrounding Maggie Creek. The annual ecosystem C gains we measured were an order of magnitude larger than net ecosystem exchange measurements from semiarid sagebrush steppe ecosystems in Wyoming, USA (Hunt et al., 2004). In fact, the accumulation of C in the MCWRP was similar to, or greater than, annual gains found in restored ecosystems located in more humid climates (Baer et al., 2002; Meyer et al., 2008). Relative to ecosystem C gains in restored wetlands in Nebraska, USA (0.22 and 0.26 kg C m^{-2} yr^{-1}; Meyer et al., 2008), terraces and ponds of both grazing excluded reaches were similar, and floodplains of the grazing excluded permanent pond reach in the MCWRP gained ecosystem C one and a half to two times faster (0.45 ± 0.20 kg C m^{-2} y^{-1}). Under managed grazing, annual gains in ecosystem C of ponds and terraces (0.10 and 0.11 kg C m^{-2} y^{-1} respectively), were similar to restored Minnesota, USA grasslands (83.3 g C m^{-2} yr^{-1}; Baer et al. 2002). Therefore, ecosystem C gains are of a similar magnitude, or greater than, those found in other wetland and grassland ecosystems located in more humid ecosystems.

We expected most soil C gains to be in shallow (0-15 cm) soil depths because prior research in other riparian ecosystems measured significant C gains in the top 15-20 cm and modest C gains below 20 cm. In a 22-year hydrologic restoration chronosequence, Reed et al. (2022) found soil C stocks increased by 232 g C m^{-2} y^{-1} in meadow soils (0-15 cm) of the Sierra Nevada mountains of California. Following 74 years of native plant restoration in old agricultural fields in Minnesota, soil C gains were not found below 20 cm (Knops and Bradley, 2009). Our results partially support this concept: across reaches and geomorphic surfaces, the greatest gains in soil C occurred in 0-15 cm depths (Fig. 2, Fig. 3, Fig. 4). Yet to our surprise, we measured significant soil C gains deeper in the soil profile in some areas of the MCWRP. Annual gains in soil C stocks ranged from 86 to 329 g C m^{-2} y^{-1} across reaches, showing similar soil C gains as those in the California Sierra Nevada, USA, but distributed to greater soil depths. We speculate that deeper soil C increases in this ecosystem may be due to deep rooting characteristics of semiarid vegetation (Fan et al., 2017) and downward percolation of dissolved organic C when bank-full height of the stream channel is exceeded (Mikutta et al., 2019). Carbon stored at greater depths might be more stable due to its isolation from microbial communities and other resources required for decomposition (Dynarski et al., 2020).

We anticipated that gains in ecosystem C would increase with proximity to the stream channel resulting in the largest gains in floodplains and smallest gains in uplands. This occurred where permanent ponds developed but not in the two reaches containing ephemeral ponds. We ascribe this outcome to dam failure, which can cause overbank flooding and floodplain scouring (Westbrook et al. 2011), limiting C gains in floodplains and allowing C gains in terraces away from the stream channel to exceed those in the channel. Conversely, the grazing excluded permanent pond reach contained the widest floodplains among reaches (Table 1). Reduced erosion provided by wide floodplains and permanent beaver ponds likely supported the large increases in root mass and soil C found in the grazing excluded permanent pond reach (Fig. 3). This result is consistent with our expectation that changes in root mass accompany gains in soil C. In addition to improved hydrology, changes to grazing likely improved plant productivity by allowing time for plant establishment and regrowth under managed grazing (Swanson et al., 2018) and reduced soil bulk density where grazing was excluded (Fig 3, Fig. 4). Reduced soil compaction can increase the thickness of soils, providing increased water storage and lengthening the growing season by as much as 35 days in meadows (Lowry and Loheide, 2010).

The large C gains following the implementation of the MCWRP were the result of modified grazing practices and subsequent beaver establishment. Understanding the mechanisms and implications of recovering ecosystem C may assist land managers anticipate the outcome of changes in grazing practices along similar stream reaches of alluvial valleys in the region.

Soil C gains were likely the result of a longer growing season leading to further primary productivity and belowground C allocation. Fairfax and Small (2018) found plant communities adjacent to the MCWRP had higher rates of evapotranspiration and longer growing season lengths where beaver had built ponds than reaches without beaver ponds. A longer growing season and greater soil water availability for plants in otherwise semiarid ecosystems likely extended the duration of plant contributions to soil C terraces and uplands that gained ecosystem C. Management may have initiated a feedback where a longer growing season increased soil C, which further lengthened the growing season by improving water infiltration and storage (Ankenbauer and Loheide, 2017). However, late season water can only increase growing days (and subsequent C inputs to soils) to a point, after which cold temperatures limit photosynthesis. Therefore, once water limitations are alleviated, further C gains may be tied to the amount of root mass plants can produce during the growing season. This relationship can be seen in the floodplains of the grazing excluded permanent pond reach and meadows of Nevada and California where changes in root mass preceded changes in soil C (Morra et al, in review; Reed et al., 2022).

Though mean ecosystem C gains were large, high spatial variability of ecosystems C gains demonstrate the inherently patchy nature of C responses to management. Ecosystem C stocks are inherently variable, even within a landscape. In alluvial valleys such as the one that surrounds Maggie Creek, frequent channel avulsion creates heterogeneity by leaving behind riparian plant communities which still have access to shallow groundwater as well as bands of well sorted soil particles from relict stream channels, which influence water and nutrient availability (Noy-Meir, 1973; Austin et al., 2004; Naiman et al., 2005). When compared to grass grown in an agricultural setting and grasslands globally (ecosystems studied for C sequestration potential), the riparian meadows found at Maggie Creek resulted in greater variation in ecosystem C stock. The coefficient of variance of change in ecosystem C at MCRWP (10% to 60%) was generally an order of magnitude higher than variance reported by Garten and Wullschleger (1999) for switch grass plantations. In a meta-analysis of grasslands globally, Schrumpf et al. (2011) also found lower coefficients of variance ranging from

12% to 29%. Spatial variability has direct management implications when an objective is C sequestration. In similar ecosystems, high sampling intensity and careful experimental design might improve estimates of ecosystem C change. Furthermore, managers should expect that restoration impacts in ecosystems with variable C stocks may require more time to observe than in ecosystems experiencing C gains with lower variation. We see this effect at MCWRP, where gains in ecosystem C were larger than in restored grasslands but both regions required approximately 10 years before changes in ecosystem C were significant Baer et al. (2002).

Grazing management increased ecosystem C stocks of geomorphic surfaces that were more than 500 m from the stream channel. The cross-valley influence of grazing management on ecosystem C stocks of Maggie Creek created the counterintuitive result that smaller unit area C gains found in uplands and terraces resulted in more C sequestration at the reach scale than in geomorphic surfaces constrained by hydrology (ponds and floodplains). Grazing management that includes the full valley width, or greater reach lengths, could be the most reliable way to sequester large amounts of C on terraces and uplands, especially when considering pond failure which resulted in limited C build up on floodplains of reaches with ephemeral ponds. While floodplains found in the grazing excluded permanent pond reach sequestered a large amount of C, the permanence of beaver dams is likely controlled by valley width rather than the exclusion of grazing (Pollock et al., 2014).

We found C:N ratios remained roughly constant across stream reaches and geomorphic surfaces, fitting our expectation that there is a stoichiometric relationship between C and N in plants and soils. In addition to sequestering C, grazing management in the MCWRP likely improved soil fertility and water quality of the adjacent waterway by accumulating N. Depending on expected yield, recommended N application to pastures from fertilizer ranges from 5 to 22 g m^{-2} (Koenig et al., 2002) which was similar to annual gains in the MCWRP, which ranged from 5 – 25 g m^{-2}. The correlation between C and N means the continued C gains facilitated by improved hydrology and grazing management may also rely on the availability of N. An example of a situation in which soil C gains depended on N availability comes from restored tailings dams in Ziaoquinlin, China (Wang et al. 2018). In the initial five-year period following restoration, gains in soil C and N occurred rapidly. Subsequent years showed smaller gains in soil C and no change in soil N. By contrast, linear soil C gains following 20 y of meadow restoration in the California Sierra Nevada were matched by commensurate gains in soil N. These results are a reminder that ecosystems need other resources than just water to sequester C at meaningful rates.

Conclusions

We show the positive impact grazing management can have on ecosystem function of riparian meadows in a semiarid climate. By allowing bankside vegetation to reestablish and beaver to colonize, improved hydrology following grazing management lengthened the growing season and increased ecosystem C and N stocks. While increased soil nutrients and water storage might be of interest to land users, voluntary C markets may also provide monetary incentives to change land management or fund restoration in the near future (Kreibich and Hermwille, 2021). The MCWRP includes 128 km of stream channel (JBR, 2002), meaning between 10,022 and 137,292 Mg of eCO_2 could be sequestered annually. At scales larger than Maggie Creek, the potential for grazing management to increase C storage may be of great importance in Nevada, where 63% of the land area is authorized for grazing by the BLM (BLM, 2022) and where there are an estimated 2526 km^2 of riparian area (Saito et al., 2020), representing a potentially substantial opportunity for C sequestration in the driest state in the USA. As a result of its aridity, the total area used for production of crops in Nevada is only 1117 km^2 (USDA, 2017a) making the large fluxes and large area occupied by riparian ecosystems of Nevada a potentially greater contributor to C sequestration than croplands. While we found the largest gains in ecosystem C in areas where grazing was excluded, managed grazing successfully increased ecosystem C of ponds, terraces, and uplands, showing C sequestration and grazing don’t have to be mutually exclusive. This was because managed grazing and grazing exclusion both help promote ecological recovery, leading to the recuperation of ecosystem C stocks. This is a unique example of how process based restoration, which has traditionally focused on aboveground characteristics (hydrology, plant communities, and habitat (Beechie et al., 2010)), can also improve conditions of the subsurface.

Works Cited

Ankenbauer, K.J., Loheide, S.P., 2017. The effects of soil organic matter on soil water retention and plant water use in a meadow of the Sierra Nevada, CA. Hydrol. Process. 31, 891–901. https://doi.org/10.1002/hyp.11070

Apfelbaum, S.I., Thompson, R., Wang, F., Mosier, S., Teague, R., Byck, P., 2022. Vegetation, water infiltration, and soil carbon response to Adaptive Multi-Paddock and Conventional grazing in Southeastern USA ranches. J. Environ. Manage. 308, 114576. https://doi.org/10.1016/j.jenvman.2022.114576

Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A., Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141, 221–235. https://doi.org/10.1007/s00442-004-1519-1

Austreng, A.C., 2012. The Carbon Budget Impact of Sagebrush Degradation. Masters Thesis 82.

Baer, S.G., Kitchen, D.J., Blair, J.M., Rice, C.W., 2002. Changes in ecosystem structure and function along a chronosequence of restored grasslands. Ecol. Appl. 12, 1688–1701. https://doi.org/10.1890/1051-0761(2002)012[1688:CIESAF]2.0.CO;2

Baer, S.G., Meyer, C.K., Bach, E.M., Klopf, R.P., Six, J., 2010. Contrasting ecosystem recovery on two soil textures: Implications for carbon mitigation and grassland conservation. Ecosphere 1, 1–22. https://doi.org/10.1890/ES10-00004.1

Bardgett, R.D., Bullock, J.M., Lavorel, S., Manning, P., Schaffner, U., Ostle, N., Chomel, M., Durigan, G., L. Fry, E., Johnson, D., Lavallee, J.M., Le Provost, G., Luo, S., Png, K., Sankaran, M., Hou, X., Zhou, H., Ma, L., Ren, W., Li, X., Ding, Y., Li, Y., Shi, H., 2021. Combatting global grassland degradation. Nat. Rev. Earth Environ. https://doi.org/10.1038/s43017-021-00207-2

Beechie, T.J., Sear, D.A., Olden, J.D., Pess, G.R., Buffington, J.M., Moir, H., Roni, P., Pollock, M.M., 2010. Process-based principles for restoring river ecosystems. Bioscience 60, 209–222. https://doi.org/10.1525/bio.2010.60.3.7

BLM, 2022. Nevada Rangeland Management and Grazing [WWW Document]. URL https://www.blm.gov/programs/natural-resources/rangeland-and-grazing/rangeland-health/nevada

Burke, I.C., Lauenroth, W.K., Parton, W.J., 1997. Regional and temporal variation in net primary production and nitrogen mineralization in grasslands. Ecology 78, 1330–1340. https://doi.org/10.1890/0012-9658(1997)078[1330:RATVIN]2.0.CO;2

Chambers, J.C., Chandra, S., Dudley, T., Germanoski, D., Jannusch, C.A., Jewett, D.G., Lord, M.L., Miller, J.R., Trowbridge, W., 2011. Geomorphology, hydrology, and ecology of Great Basin meadow complexes-implications for management and restoration, USDA Forest Service - General Technical Report RMRS-GTR. https://doi.org/10.2737/RMRS-GTR-258

Charnley, S., 2019. If you build it, they will come: Ranching, riparian revegetation, and beaver colonization in Elko County, Nevada. USDA For. Serv. - Res. Pap. PNW-RP 2019.

Darrouzet-Nardi, A., D'Antonio, C.M., Dawson, T.E., 2006. Depth of water acquisition by invading shrubs and resident herbs in a Sierra Nevada meadow. Plant Soil 285, 31–43. https://doi.org/10.1007/s11104-005-4453-z

Dominati, E., Patterson, M., Mackay, A., 2010. A framework for classifying and quantifying the natural capital and ecosystem services of soils. Ecol. Econ. 69, 1858–1868. https://doi.org/10.1016/j.ecolecon.2010.05.002

Dynarski, K.A., Bossio, D.A., Scow, K.M., 2020. Dynamic Stability of Soil Carbon: Reassessing the "Permanence" of Soil Carbon Sequestration. Front. Environ. Sci. 8. https://doi.org/10.3389/fenvs.2020.514701

Evans, C., 2009. 2006 Monitoring Summary and Evaluation of Biological Standards. Elko, Nevada.

Fairfax, E., Small, E.E., 2018. Using remote sensing to assess the impact of beaver damming on riparian evapotranspiration in an arid landscape. Ecohydrology 11, 1–15. https://doi.org/10.1002/eco.1993

Fan, Y., Miguez-Macho, G., Jobbágy, E.G., Jackson, R.B., Otero-Casal, C., 2017. Hydrologic regulation of plant rooting depth. Proc. Natl. Acad. Sci. U. S. A. 114, 10572–10577. https://doi.org/10.1073/pnas.1712381114

Garcia-Moya, E., McKell, C., 1969. Contribution of Shrubs to the Nitrogen Economy of a Desert-Wash Plant Community. Ecol. Soc. Am. 51, 81–88.

Garten, C.T., Wullschleger, S.D., 1999. Soil Carbon Inventories under a Bioenergy Crop (Switchgrass): Measurement Limitations. J. Environ. Qual. 28, 1359–1365. https://doi.org/10.2134/jeq1999.00472425002800040041x

Google Earth, n.d. Google Earth.

Green, D.M., Kauffman, J.B., 1995. Succession and livestock grazing in a northeastern Oregon riparian ecosystem. J. Range Manag. 48, 307–313. https://doi.org/10.2307/4002482

Hood, G.A., Larson, D.G., 2015. Ecological engineering and aquatic connectivity: A new perspective from beaver-modified wetlands. Freshw. Biol. 60, 198–208. https://doi.org/10.1111/fwb.12487

Horton, G., 2000. Humboldt River Chronology.

Hunt, E.R., Kelly, R.D., Smith, W.K., Fahnestock, J.T., Welker, J.M., Reiners, W.A., 2004. Estimation of Carbon Sequestration by Combining Remote Sensing and Net Ecosystem Exchange Data for Northern Mixed-Grass Prairie and Sagebrush – Steppe Ecosystems 33, 432–441. https://doi.org/10.1007/s00267-003-9151-0

JBR, 2002. South Operations Area Riparian Project 2001 Monitoring Results. Carlin, Nevada.

Jensen, S., 2011. Maggie Creek Watershed Restoration Project Remote Sensing Monitoring. Smithfield , UT.

Kasten, R., 2019. Above and belowground carbon stocks differ among meadow vegetation communities in the northern Sierra Nevada, California USA. University of Nevada, Reno.

Klein Goldewijk, K., Beusen, A., Van Drecht, G., De Vos, M., 2011. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. Glob. Ecol. Biogeogr. 20, 73–86. https://doi.org/10.1111/j.1466-8238.2010.00587.x

Knops, J.M.H., Bradley, K.L., 2009. Soil Carbon and Nitrogen Accumulation and Vertical Distribution across a 74-Year Chronosequence. Soil Sci. Soc. Am. J. 73, 2096–2104. https://doi.org/10.2136/sssaj2009.0058

Koenig, R., Nelson, M., Barnhill, J., Miner, D., 2002. Fertilizer Management for grass and grass-legueme mixtures. AF FG-03. Logan, UT.

Kozlowski, D.F., Hall, R.K., Swanson, S.R., Heggem, D.T., 2016. Linking Management and Riparian Physical Functions to Water Quality and Aquatic Habitat. J. Water Resour. Prot. 08, 797–815. https://doi.org/10.4236/jwarp.2016.88065

Kreibich, N., Hermwille, L., 2021. Caught in between: credibility and feasibility of the voluntary carbon market post-2020. Clim. Policy 21, 939–957. https://doi.org/10.1080/14693062.2021.1948384

Lowry, C.S., Loheide, S.P., 2010. Groundwater-dependent vegetation: Quantifying the groundwater subsidy. Water Resour. Res. 46, 1–8. https://doi.org/10.1029/2009WR008874

Meyer, C.K., Baer, S.G., Whiles, M.R., 2008. Ecosystem recovery across a chronosequence of restored wetlands in the Platte River valley. Ecosystems 11, 193–208. https://doi.org/10.1007/s10021-007-9115-y

Mikutta, R., Turner, S., Schippers, A., Gentsc, N., Meyer-, S., Condron, L.M., Peltzer, D.A., Richardson, S.J., Eger, A., Hempel, G., Kaiser, K., Klotzbücher, T., Guggenberger, G., 2019. Microbial and abiotic controls on mineral-associated organic matter in soil profiles along an ecosystem gradient 1–9. https://doi.org/10.1038/s41598-019-46501-4

Morra, B., Richardson, W., Stringham, T.K., Sullivan, B., in review. Carbon stocks and total belowground carbon fluxes are large, differ by plant community, and respond to weather and grazing in surface soils of semiarid montane meadows. Ecosystems.

Naiman, R., Decamps, H., McClain, M., 2005. Riparia: Ecology, Conservation, and Management of Streamside Communities (Aquatic Ecology), 1st ed. Elsevier Inc, Burlington MA.

Nash, C.S., Grant, G.E., Charnley, S., Dunham, jason B., Gosnell, H., Hausner, M.B., Pilliod, D.S., Taylor, J.D., 2021. Great Expectations: Deconstructing the Process Pathways Underlying Beaver-Related Restoration. Bioscience 71, 249–267. https://doi.org/10.1093/biosci/biaa165

Norton, J.B., Jungst, L.J., Norton, U., Olsen, H.R., Tate, K.W., Horwath, W.R., 2011. Soil Carbon and Nitrogen Storage in Upper Montane Riparian Meadows. Ecosystems 14, 1217–1231. https://doi.org/10.1007/s10021-011-9477-z

Noy-Meir, I., 1973. Desert Ecosystems: Environment and Producers. Annu. Rev. Ecol. Syst. 4, 25–51.

Nummi, P., Vehkaoja, M., Pumpanen, J., Ojala, A., 2018. Beavers affect carbon biogeochemistry: both short-term and long-term processes are involved. Mamm. Rev. 48, 298–311. https://doi.org/10.1111/mam.12134

ORC, 2017. Long Term Assesment of the Maggie Creek Riparian Area. Park City, Utah.

Paustian, K., Larson, E., Kent, J., Marx, E., Swan, A., 2019. Soil C Sequestration as a Biological Negative Emission Strategy. Front. Clim. 1, 1–11. https://doi.org/10.3389/fclim.2019.00008

Pollock, M.M., Beechie, T.J., Wheaton, J.M., Jordan, C.E., Bouwes, N., Weber, N., Volk, C., 2014. Using Beaver Dams to Restore Incised Stream Ecosystems. Bioscience 64, 279–290. https://doi.org/10.1093/biosci/biu036

Reed, C., Berhe, A., Moreland, K., Wilcox, J., Sullivan, B., 2022. Restoring function: Positive responses of carbon and nitrogen to 20 years of hydrologic restoration in montane meadows. Ecol. Appl. 0–2. https://doi.org/10.1002/eap.2677

Reed, C., Merrill, A., Drew, M., Christman, B., Hutchinson, A., Keszey, L., Swanson, S., 2021. Montane Meadows: A Soil Carbon Sink or Source? Ecosystems. https://doi.org/10.1007/s10021-020-00572-x

Reiner, A., Tausch, R., Walker, R., 2010. Estimation procedures for understory biomass and fuel loads in sagebrush steppe invaded by woodlands. West. North Am. Nat.

Saito, L., Byer, S., Badik, K., McGwire, K., Provencher, L., Minor, B., 2020. Mapping indicators of groundwater dependent ecosystems in Nevada : Important resources for a water-limited state. J. Nevada Water Resour. Assoc. 48–72. https://doi.org/10.22542/jnwra/2020/1/3

Schrumpf, M., Schulze, E.D., Kaiser, K., Schumacher, J., 2011. How accurately can soil organic carbon stocks and stock changes be quantified by soil inventories? Biogeosciences 8, 1193–1212. https://doi.org/10.5194/bg-8-1193-2011

Swanson, S., Schultz, B., Novak-Echenique, P., Dyer, K., McCuin, G., Linebaugh, J., Perryman, B., Tueller, P., Jenkins, R., Scherrer, B., Vogel, T., Voth, D., Freese, M., Shane, R., McGowan, K., 2018. Nevada Rangeland Monitoring Handbook. University of Nevada Cooperative Extension Special Publication.

Trimble, S.W., Mendel, A.C., 1995. The cow as a geomorphic agent — A critical review. Biogeomorphology, Terr. Freshw. Syst. 13, 233–253. https://doi.org/10.1016/b978-0-444-81867-6.50019-8

United States Geological Survey, n.d. Post-Fire Treatment Impacts on Fine Fuels in Westside Sierra Nevada Forests [WWW Document]. URL https://web.archive.org/web/20161231121745/https://www.werc.usgs.gov/OLDsited%0Aata/fire/seki/finefuels/chna.html%0A (accessed 12.31.16).

USDA, 2017. Total and Per Farm Overview, 2017 and change since 2012.

Van Groenigen, J.W., Van Kessel, C., Hungate, B.A., Oenema, O., Powlson, D.S., Van Groenigen, K.J., 2017. Sequestering Soil Organic Carbon: A Nitrogen Dilemma. Environ. Sci. Technol. 51, 4738–4739. https://doi.org/10.1021/acs.est.7b01427

Weixelman, D., Cooper, D., Hill, B., Berlow, E., Viers, J., Purdy, S., Merrill, A., Gross, S., 2011. A field key to meadow hydrogeomorphic types for the Sierra Nevada and Southern Cascade Ranges in California. Vallejo, CA.

Westbrook, C., Cooper, D., Baker, W., 2011. Beaver Assited River Valley Foration. River Res. Appl. 27, 132–133. https://doi.org/10.1002/rra

Wohl, E., 2013. Landscape-scale carbon storage associated with beaver dams. Geophys. Res. Lett. 40, 3631–3636. https://doi.org/10.1002/grl.50710

Tables:

Stream reach	Latitude, Longitude	Upland area (ha km^{-1})	Terrace area (ha km^{-1})	Floodplain area (ha km^{-1})	Pond area (ha km^{-1})	Upland soil type	Terrace soil type	Floodplain soil type	Dominant upland species	Dominant terrace species	Dominant floodplain species
Grazing exclusion ephemeral ponds	40.91°, -116.17°	42.3	44.2	6.2	0.2	Xeric Haplocambids	Aquandic Endoaquolls	Alluvial Land	*Elymus elymoides, Artemisia tridentata*	*Leymus triticoides, Artemisia tridentata*	*Carex pellita*
Grazing exclusion permanent ponds	40.89°, -116.184°	30.2	17.5	8.3	2.8	Xeric Haplocambids	Aquandic Endoaquolls	Alluvial Land	*Achnatherum speciosum, Artemisia tridentata*	*Muhlenbergia richardsonis, Artemisia tridentata*	*Carex pellita*
Managed grazing	40.86°, -116.21°	66.3	24.5	4.8	0.04	Xeric Haplocambids	Aquandic Endoaquolls	Vertic Halaquepts	*Distichlis spicata, Artemisia tridentata*	*Leymus triticoides, Artemisia tridentata*	*Symphyotrichum ascendens*
Year-round grazing	40.77°, -116.134°	45.7	27.3	2.3	0	Xeric Haplocambids	Aquandic Endoaquolls	Aquandic Endoaquolls	*Elymus elymoides, Artemisia tridentata*	*Iva axillaris, Artemisia tridentata*	*Conyza canadensis*

Table 1. Areas of geomorphic surfaces contained in a 1-km stretch of valley for each reach. Soil descriptions were collected from USDA, NRCS Web Soil Survey. Dominant plant species is the herbaceous plant species with the highest mean percent cover measured at coring locations

Reach	Surface	Depth (cm)	Mean Annual Change kg C m^{-2}	Annual C credits per km of valley (Mg eCO_2 km^{-1} yr^{-1})	Years to create significant change
Grazing excluded permanent ponds	Terrace	0-45	0.21 ± 0.2	2.4-268.0	6 – 13
Grazing excluded permanent ponds	Floodplain	0-45	0.35 ± 0.21	76.8-198.1	6 – 12
Grazing excluded permanent ponds	Ponds	0-45	0.20 ± 0.06	13.6-26.3	–
Grazing excluded ephemeral ponds	Upland	0-45	0.1 ± 0.01	3.3-303.5	6 – 12
Grazing excluded ephemeral ponds	Terrace	0-45	0.27 ± 0.21	98.9-767.4	5 – 11
Grazing excluded ephemeral ponds	Ponds	0-45	0.19 ± 0.05	1-1.7	–
Managed grazing	Uplands	0-30	0.09 ± 0.08	37.5-412.9	10 – 12
Managed grazing	Terrace	0-30	0.10 ± 0.01	40.7-175.2	6 – 13
Managed grazing	Ponds	0-45	0.10 ± 0.03	0.06-0.2	–

Table 2. Annual change in ecosystem C and the resulting generation of C credits (Mg eCO_2 km^{-1} yr^{-1}) normalized to 1-km of valley length. Ranges come from the 95% confidence interval of the difference between mean ecosystem C stock of a geomorphic surface from a reach within the MCWRP and the mean ecosystem C stock of its corresponding geomorphic surface outside of the MCWRP. Years to change represents the time required to surpass an effect size threshold generated by power analysis given our sample size, sample variance, alpha of 0.05, and statistical power ranging from 0.1 to 0.2.

Reach	Surface	Depth (cm)	Mean Annual Change (g N m^{-2})	Annual accumulation (g N yr^{-1} km^{-1})
Grazing excluded permanent ponds	Ponds	0-45	5.56 – 14.44	231.13 – 600.11
Grazing excluded ephemeral ponds	Ponds	0-45	3.37 – 19.59	10.30 – 59.62
Managed grazing	Ponds	0-45	1.86 – 8.52	1.06 – 4.88
Grazing excluded permanent ponds	Terraces	0-45	2.97 – 27.41	780.8 – 7,205.93
Grazing excluded ephemeral ponds	Terraces	0-45	9.26 – 32.96	6,133.8 – 21,832.52
Grazing excluded ephemeral ponds	Uplands	0-45	5.18 – 32.96	3289.3 – 11,760.33

Table 3. Annual gains in ecosystem N for geomorphic surfaces and accumulation of N on the landscape normalized as g of N accumulated per 1-km valley length. Values are only shown where significant increases in ecosystem N were observed relative to unmanaged counterparts according to a one-tailed t test.

Figures

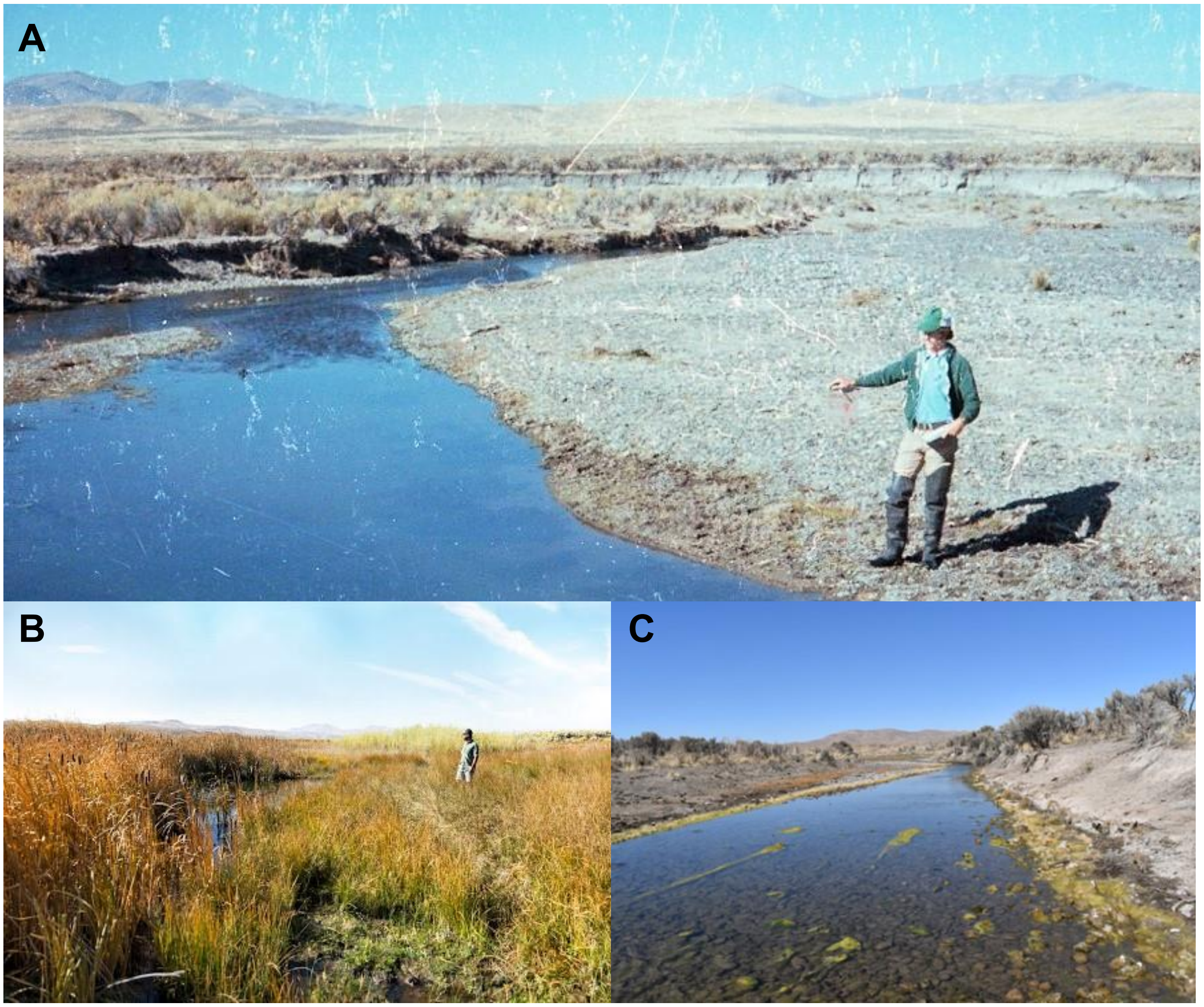

Figure 1. Photo point comparison of three floodplains in Maggie Creek. Photo A shows the condition of floodplains in 1980 before grazing exclusion. Photo B shows the same floodplain after 27 years of grazing exclusion. Photo C shows the present condition of floodplains still experiencing summer season grazing. Historical photo provided by Carol Evans, United States Bureau of Land Management. Present-day photos in panel B and C were taken during a site visit by B. Morra.

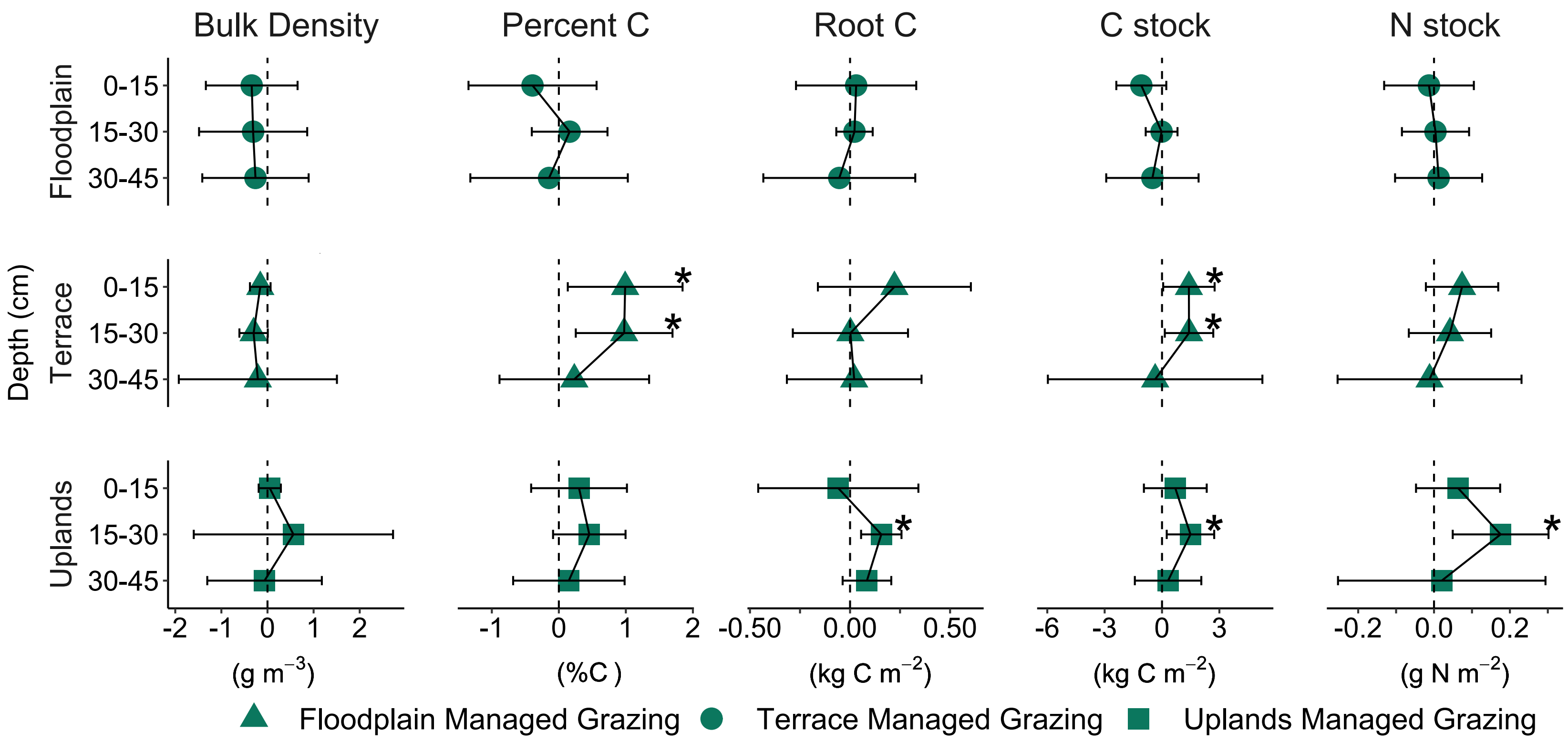

Figure 2. Change in the soil of the managed grazing ephemeral pond reach relative to unmanaged grazing. Values greater than zero show an increase relative to unmanaged grazing. Error bars are the 95% confidence interval of a one tail t-distribution. An asterisk indicates changes that are different than zero.

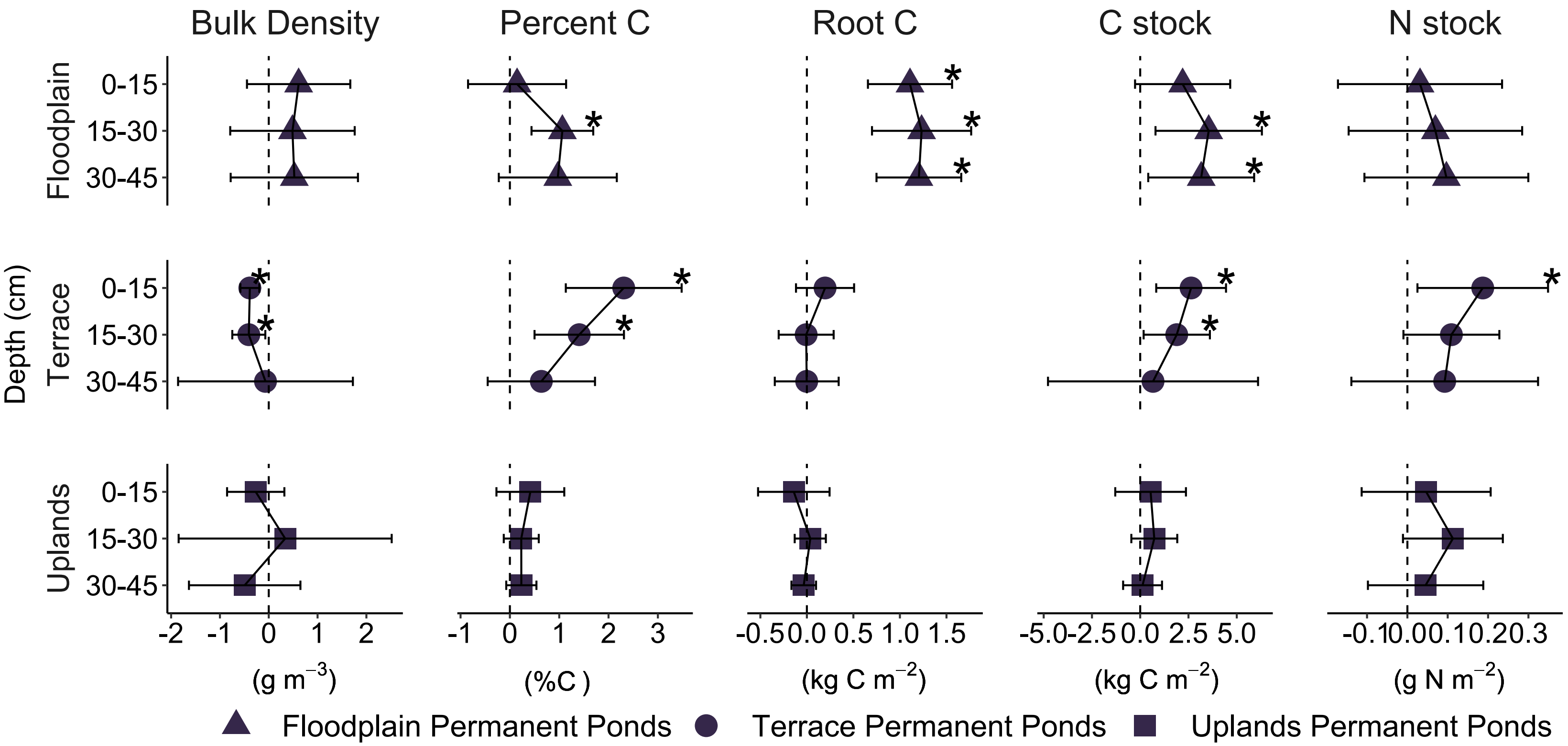

Figure 3. Change in the soil of grazing excluded permanent pond reach relative to unmanaged grazing. Values greater than zero show an increase relative to unmanaged grazing. Error bars are the 95% confidence interval of a one tail t-distribution. An asterisk indicates changes that are different than zero.

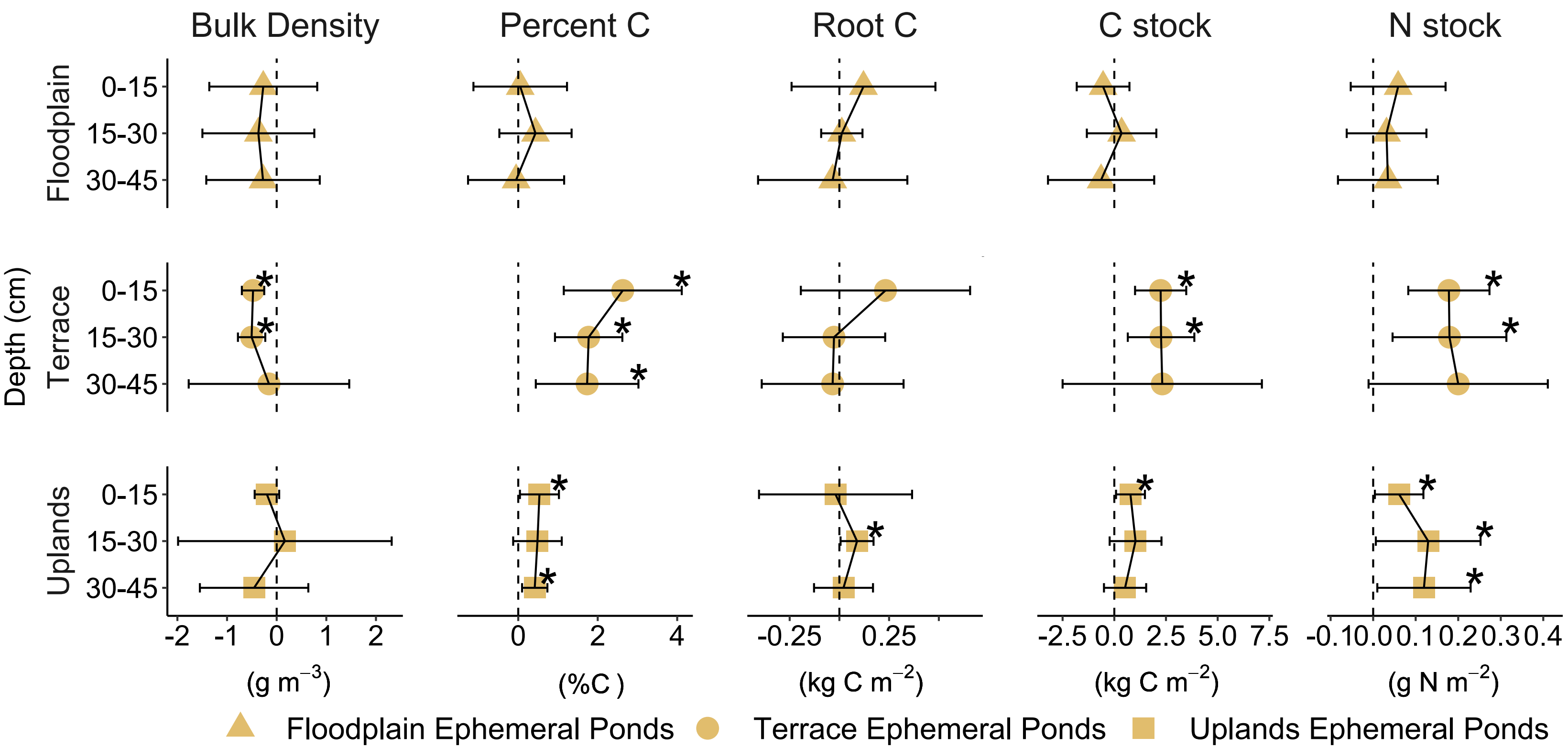

Figure 4. Changes in soil of the grazing excluded ephemeral pond reach, relative to unmanaged grazing. Values greater than zero show an increase relative to unmanaged grazing. Error bars are the 95% confidence interval of a one tail t-distribution. An asterisk indicates changes that are different than zero

.

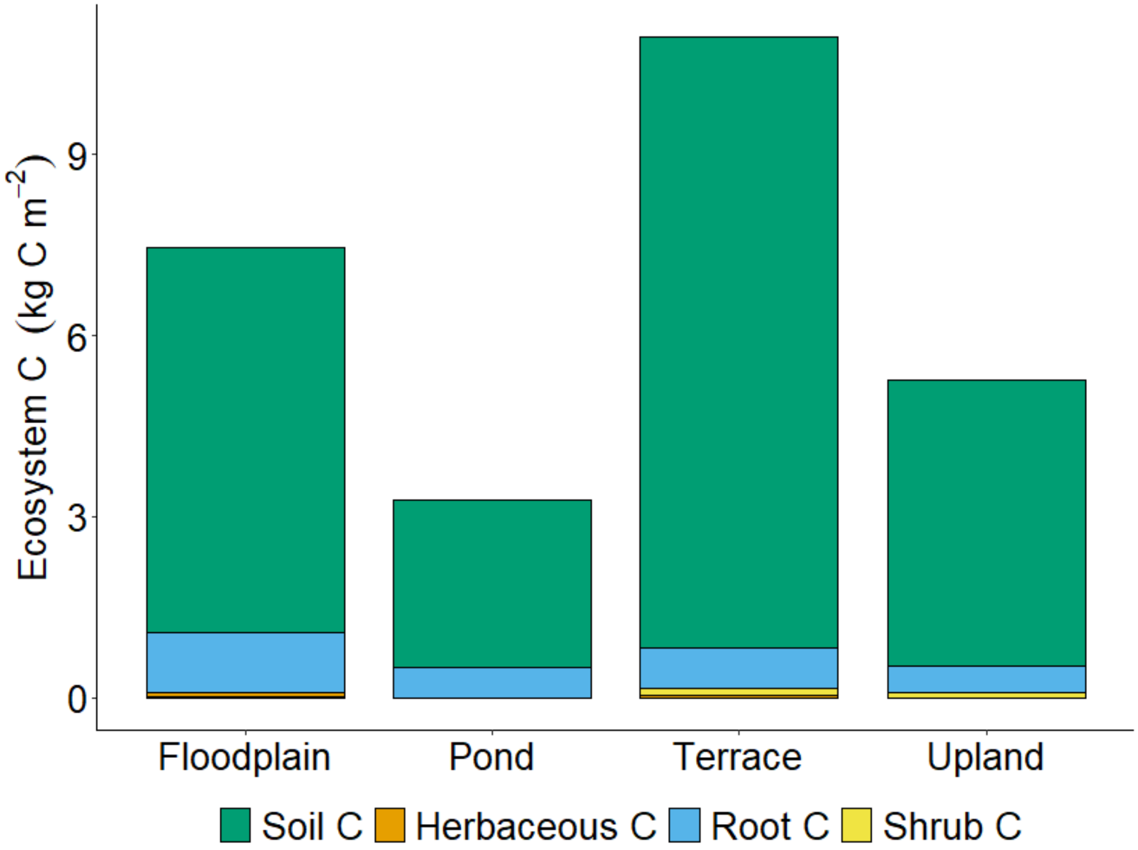

Figure 5. Ecosystem C stock is the sum of four components: aboveground shrub, aboveground herbaceous vegetation, root, and soil C stock found on floodplains, ponds, terraces, and upland areas calculated as the mean across all reaches. Root and soil C stocks are in the 0-45 cm mineral soil depth.

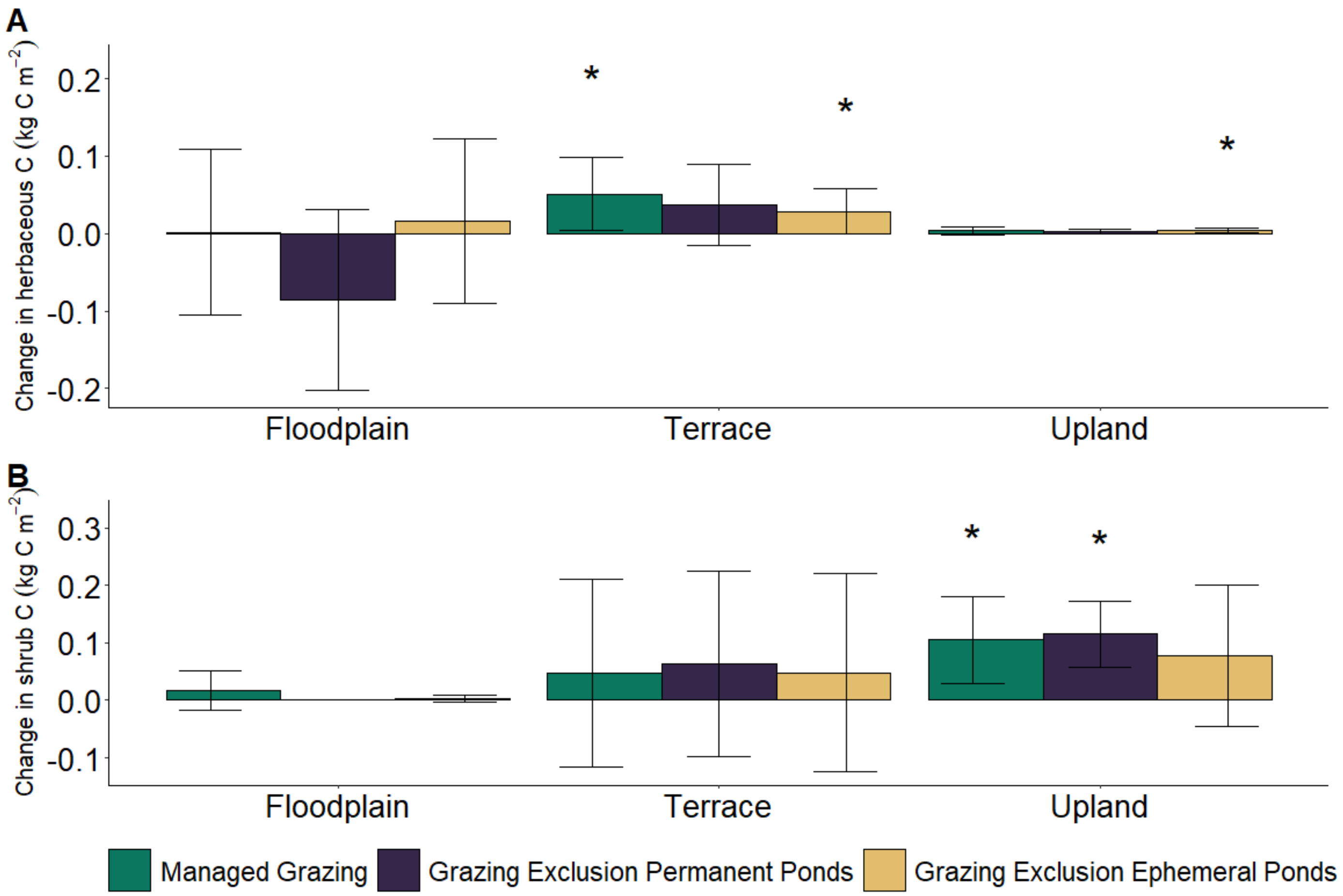

Figure 6. Changes in aboveground C stocks in herbaceous plants (5A) and shrubs (5B) of the managed grazing ephemeral pond reach, grazing excluded ephemeral pond reach, and the grazing excluded permanent pond reach relative to corresponding surfaces in unmanaged reaches. Error bars are the 95% confidence interval and stars indicate changes that are significantly different than zero.

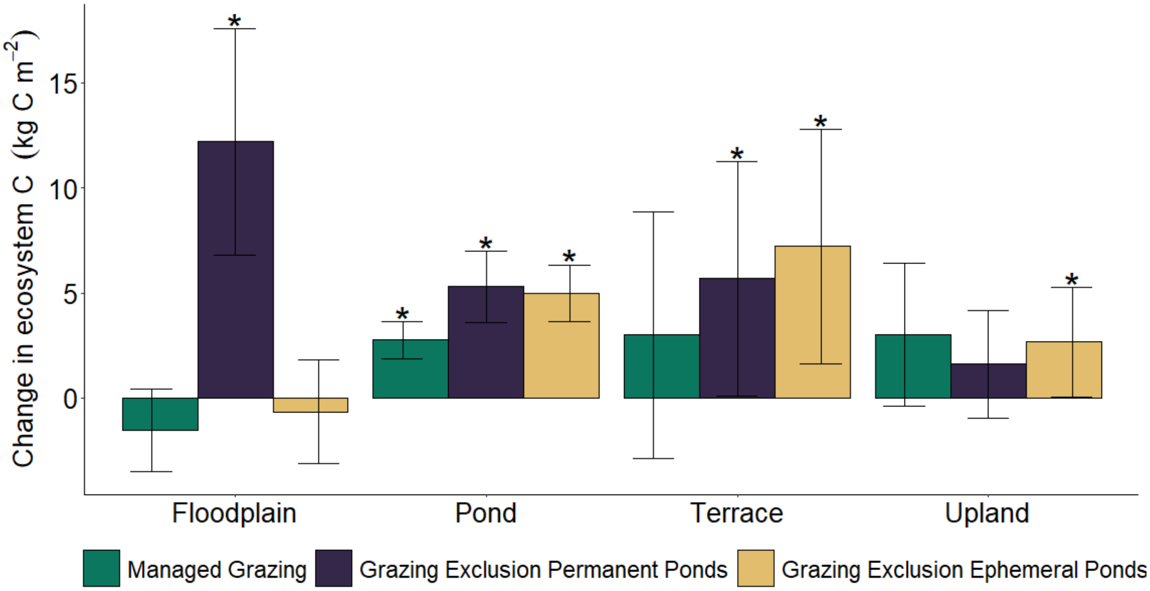

Figure 7. Change in ecosystem C stocks of the managed grazing ephemeral pond reach, grazing excluded ephemeral pond reach, and the grazing excluded permanent pond reach relative to corresponding geomorphic surfaces in the unmanaged reach. Results are shown for the full depth (0-45). Error bars are the 95% confidence interval and stars indicate changes that are significantly different than zero according to a one-tail t-test.

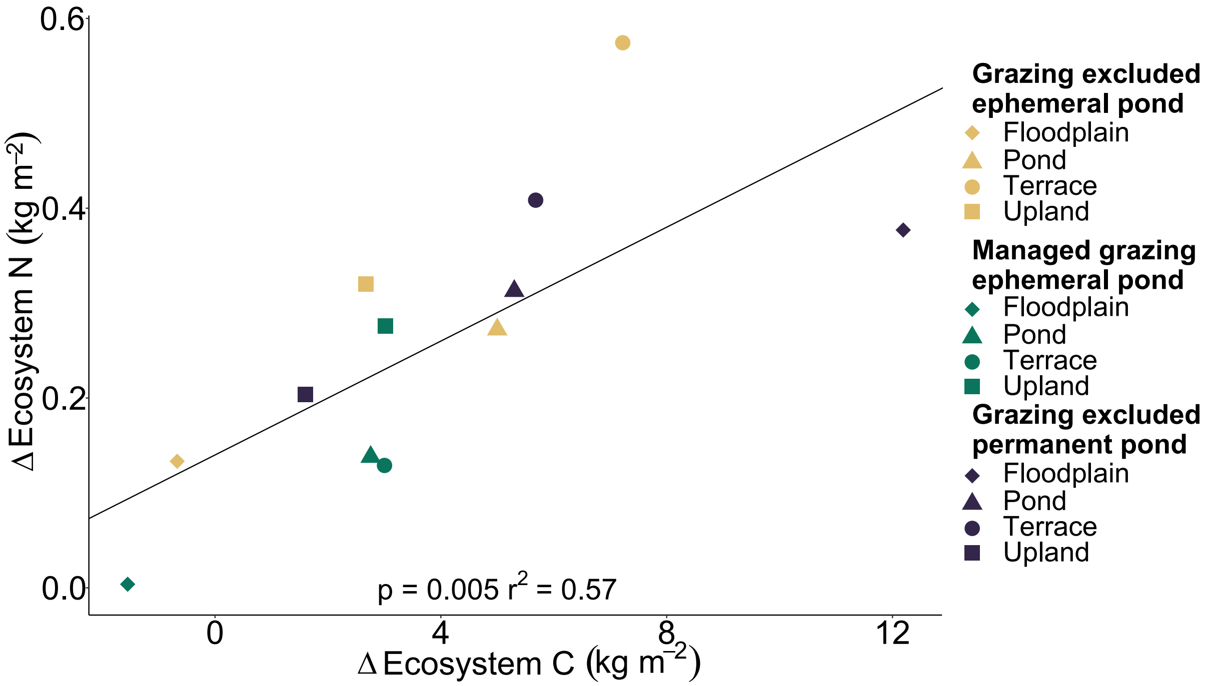

Figure 8. Change in ecosystem N plotted against change in ecosystem C (soils 0-45 cm). Line is the result of a linear model plotting change in ecosystem N as a function of change in ecosystem C.

Conclusion

My dissertation explored some of the conditions that may be associated with maintaining or gaining soil C in meadows of semiarid ecosystems. Maintaining a C stock requires an understanding of the inputs that generate a stock and the factors which build stable soil C. By incorporating grazing as a factor contributing to, or detracting from, soil C fluxes in Chapters 1 and 3, this work demonstrates that C stocks of semiarid meadows are sensitive to grazing but can support it in some conditions. For example, in Maggie Creek, grazing changes led to significant increases in soil C - even when grazing resumed. Therefore, grazing and soil C sequestration in these ecosystems do not have to be mutually exclusive. I hope to close this document by contextualizing the “unseen C flux” occurring in meadows to show that manipulation of soil C in Nevada meadows may occur more easily than other ecosystems where voluntary C markets have traditionally focused. Croplands, for example, are frequently used to generate C credits due to their homogeneity and long history of C cycle research dating back to the 1800’s (Gorham, 1991). However, in Nevada, meadows may be an important location for C sequestration, creating economic incentives to restore or conserve meadow soil C stock. Nevada meadows are an important C sink due to their prevalence, productivity, and response to grazing management. In Nevada, the land area occupied by meadows and riparian areas is estimated to be between 2000-3000 km^2 (Saito et al., 2020), roughly the same as the land area occupied by croplands (2700 km^2; USDA, 2017).

In addition to occupying a relatively high proportion of Nevada, I found that, per unit area, the soils of Nevada meadows hold as much as three times the amount of C as their surrounding upland ecosystems. In Chapter 1, I show that the C stocks of Nevada meadows are likely derived from high rates of plant productivity, given the high rates of plant allocation to soil that occurred in the wet 2019 growing season. These results were similar to findings by Reed et al., (2021) and Schwieger et al. (2021) for California meadows. Across years, plant communities, and grazing intensities there was a consistent contribution of antecedent root mass to soil C stocks. This chapter also showed that grazing management was effective in maintaining belowground C inputs relative to no management during years of reduced precipitation. Taken together, Chapter 1 shows that grazing management may be an important tool to maintain soil C stocks in meadows due to its impact on inputs. In Nevada, a state where 61% of the lands are permitted for grazing (BLM, 2022), implementation of management designed to use meadows as C sinks may be able to incorporate large areas of meadows.

The importance of inputs were explored in greater detail in Chapter 2, where I compared the formation of mineral associated organic matter (MAOM) in regions of meadows with high and low inputs between two climates. This work shows that the contribution of surface sorption potential in MAOM formation is limited by C inputs to soils across climates. Furthermore, under low productivity, MAOM may be an important source of C for soil heterotrophs. Here I measured sorption potential of bulk soils standardized by soil mass. In some cases, soil minerals can impact the sorption potential of soils due to different surface areas and charges associated with mineralogy (Adhikari and Yang, 2015.; Xu et al., 2022). In other studies, mineralogy has a limited contribution to MAOM formation, but is linked to differences in MAOM retention (Sanderman et al., 2014). Other research has shown that the chemistry of dissolved organic C has a greater impact on MAOM formation than soil properties (Sokol et al., 2019). While understanding the mechanisms behind MAOM formation is a rapidly developing field filled with many unknowns, my work indicates that a fraction of MAOM in meadows may be rapidly lost following disturbances to meadows that reduce their inputs.

How much can restoration of inputs help rebuild C stocks of meadows that were depleted following disturbance? Chapter 3 shows that grazing management, which resulted in the establishment of beaver (Castor canadensis) populations (Jensen, 2011) and likely increased primary productivity (Fairfax and Small, 2018), was effective at increasing ecosystem C stocks in riparian meadows adjacent to Maggie Creek. This is a unique example of how mitigation or elimination of disturbances, process-based restoration, allows for ecosystems to recover from perturbations caused by grazing and create changes in the subsurface. Process-based restoration, which has traditionally focused on aboveground characteristics (Beechie et al., 2010), increased soil C stocks by 80 to 303 g C m^{-2} annually at Maggie Creek. Compared to croplands, gains in ecosystem C occurring at Maggie Creek were large and required less effort to achieve. For example, techniques commonly employed to sequester C in croplands, such as planting cover crops and changing tillage sequester between 30 to 97 g C m^{-2} yr^{-1} and 10 to 29 g C m^{-2} yr^{-1} respectively (Paustian et al., 2019). Under these management schemes, gains in soil C may cease or be lost without continued management (Amundson and Biardeau, 2018).

This work highlights the size of C stocks and fluxes of semiarid meadows and the extent to which grazing management restores C stocks of degraded meadows. However, applying this work to management aimed at increasing soil C may be improved through the use of common language and methodology used to categorize meadow regions that are characterized by different plant communities, C stocks, and fluxes. For example, to account for the heterogeneity of meadows, I broadly classified meadow regions by plant functional groups in Chapter 1, by normalized difference vegetation index (NDVI) in Chapter 2, and geomorphic surfaces in Chapter 3. Although these three measurements were distinct, they may capture similar vegetative patterns in meadows. Plant functional groups in meadows are a community of individual species that have established based on their dependance on, or tolerance of shallow ground water (Allen-Diaz, 1991). In Chapter 1, I referred to these plant groups as wetland, mesic, or edge plant communities (based on classifications derived by Richardson et al., (2021) in the same sites). In Chapter 2, more productive regions of the meadows were associated with greater aboveground biomass, and a longer growing season, possibly as a result of greater groundwater availability. In Chapter 3, I used geomorphic surfaces to capture different depths to groundwater in the soils of riparian meadows. This is because increased elevation above the stream channel likely decreased the availability of groundwater. As a result, the geomorphic surfaces measured, floodplains, terraces, and uplands, were dominated by wet, mesic and edge plant communities respectively. However, within terraces the impact of microtopography on groundwater availability could be seen in abandoned stream channels. Abandoned stream channels created low points dominated by wetland plant communities. In locations several feet away at slightly higher elevations, wetland plant communities were replaced by mesic and edge plant communities. A common tool to define meadow regions may therefore rely on both elevation above the water table and surface plant communities. One method to do this across large areas would rely on the combination of high-resolution digital elevation models and remote sensed greenness indices, calibrated to distinguish between herbaceous and shrub dominated regions. Further uncertainty may come from measurements of bulk density, an issue that complicates measurements of soils in all ecosystems. In meadows, annual shrink swell from soil moisture and changes in soil density following changes in soil C complicate measurements of soil C stock. Adopting practices like measuring bulk density using equivalent soil masses (Wendt and Hauser, 2013) and standardizing the time of soil sampling to periods where soils are driest may be important for capturing reproducible measurements of meadow soil C stock. I have shown that soil C and moisture in meadows can be highly dynamic, making standardizations such as these particularly important for measuring soil C stocks of meadows.

References

Adhikari, D., Yang, Y., 2015. Selective stabilization of aliphatic organic carbon by iron oxide. Nature Publishing Group 1–7. doi:10.1038/srep11214

Allen-Diaz, B.H., 1991. Water Table and Plant Species Relationships in Sierra Nevada Meadows. American Midland Naturalist 126, 30. doi:10.2307/2426147

Amundson, R., Biardeau, L., 2018. Soil carbon sequestration is an elusive climate mitigation tool. Proceedings of the National Academy of Sciences of the United States of America 115, 11652–11656. doi:10.1073/pnas.1815901115

Beechie, T.J., Sear, D.A., Olden, J.D., Pess, G.R., Buffington, J.M., Moir, H., Roni, P., Pollock, M.M., 2010. Process-based principles for restoring river ecosystems. BioScience 60, 209–222. doi:10.1525/bio.2010.60.3.7

BLM, 2022. NEVADA RANGELAND MANAGEMENT AND GRAZING [WWW Document]. URL https://www.blm.gov/programs/natural-resources/rangeland-and-grazing/rangeland-health/nevada

Fairfax, E., Small, E.E., 2018. Using remote sensing to assess the impact of beaver damming on riparian evapotranspiration in an arid landscape. Ecohydrology 11, 1–15. doi:10.1002/eco.1993

Gorham, E., 1991. Biogeochemistry: Its origens and development. Biogeochemistry 199–239.

Jensen, S., 2011. Maggie Creek Watershed Restoration Project Remote Sensing Monitoring. Smithfield , UT.

Paustian, K., Larson, E., Kent, J., Marx, E., Swan, A., 2019. Soil C Sequestration as a Biological Negative Emission Strategy. Frontiers in Climate 1, 1–11. doi:10.3389/fclim.2019.00008

Reed, C., Merrill, A., Drew, M., Christman, B., Hutchinson, A., Keszey, L., Swanson, S., 2021. Montane Meadows: A Soil Carbon Sink or Source? Ecosystems. doi:10.1007/s10021-020-00572-x

Richardson, W., Stringham, T.K., Lieurance, W., Snyder, K.A., 2021. Changes in meadow phenology in response to grazing management at multiple scales of measurement. Remote Sensing 13. doi:10.3390/rs13204028

Saito, L., Byer, S., Badik, K., McGwire, K., Provencher, L., Minor, B., 2020. Mapping indicators of groundwater dependent ecosystems in Nevada : Important resources for a water-limited state. Journal of Nevada Water Resources Association 48–72. doi:10.22542/jnwra/2020/1/3

Sanderman, J., Maddern, T., Baldock, J., 2014. Similar composition but differential stability of mineral retained organic matter across four classes of clay minerals 409–424. doi:10.1007/s10533-014-0009-8

Schwieger, S., Kreyling, J., Couwenberg, J., Smiljanić, M., Weigel, R., Wilmking, M., Blume-Werry, G., 2021. Wetter is better: rewetting of minerotrophic peatlands increases plant production and moves them towards carbon sinks. Ecosystems. doi:10.1007/s10021-020-00570-z

Sokol, N.W., Kuebbing, S.E., Karlsen-Ayala, E., Bradford, M.A., 2019. Evidence for the primacy of living root inputs, not root or shoot litter, in forming soil organic carbon. New Phytologist 221, 233–246. doi:10.1111/nph.15361

USDA, 2017. Census of Agriculture State data.

Wendt, J., Hauser, S., 2013. An equivalent soil mass procedure for monitoring soil. doi:10.1111/ejss.12002

Xu, Y., Liu, K., Yao, S., Zhang, Y., Zhang, X., He, H., Feng, W., Ndzana, G.M., Chenu, C., Olk, D.C., Mao, J., Zhang, B., 2022. Formation efficiency of soil organic matter from plant litter is governed by clay mineral type more than plant litter quality. Geoderma 412, 115727. doi:10.1016/j.geoderma.2022.115727

Appendix A Supporting information for chapter 1

Methods

Soil sampling and depth stratification

Each of the three replicated plots were sampled from 0-15 cm, while two of the replicates were sampled to 0-30 cm and one location was sampled to a depth of 0-45 cm. The cores taken from deeper depths, 15-30 (n=2) and 30-45 (n=1) were used to estimate 0-45 cm soil C stocks for areas that were only sampled to shallow depths. We staggered our sampling intensity by depth because previous meadow research has shown the surface soil to be the most responsive to C change, whereas the top 45 cm often contains most of the total soil C stock and the 15-45 cm depths are often less variable than the 0-15 cm depth (Kasten, 2019; Reed et al., 2021, 2022).

Soil moisture and temperature

We measured soil moisture using time domain reflectometry (TDR; FieldScout 100, Spectrum Technologies, Aurora, IL, USA) and soil temperature using analog thermometers at each plot (n = 63 per sampling event). We refer to these measurements as high spatial resolution soil moisture and temperature data. Soil moisture and temperature were also measured at the plant community level (n = 21) every two hours using capacitive soil moisture probes (5TM soil moisture probe, Meter Group, Pullman, WA, USA) connected to a data logger (EM50, Meter Group). We refer to these measurements as high temporal resolution soil moisture and temperature data.

Interpolation of daily values for high spatial resolution data

We interpolated daily values for high spatial resolution data in two steps. The high temporal resolution data were detrended by subtracting the slope of a least means squared regression from the dates bracketed by high spatial resolution data. Then, the detrended data were added to daily values that were linearly interpolated between high spatial resolution data. Combining the data in this way allowed us to capture precipitation events reflected in the high temporal resolution data and soil moisture trends that differed among plant communities of a meadow reflected in the high spatial resolution data.

Variables used in stepwise linear model

Days of vegetative growth were measured by Richardson and others (2021) according to Gu and others (2009) using a threshold method to calculate upturn and recession dates of each plant community from Green Chromatic Coordinate (GCC) data collected by near surface cameras (phenocams). Soil drought days were defined as days with a VWC less than 11% based on Xu and others (2021). Soil drying rate was calculated as the change from maximum VWC to minimum VWC divided by the number of days that VWC decreased occurred over.

Soil greenhouse gas fluxes

Using vented static chambers, we collected headspace gas concentrations after 0, 15, and 30 minutes. Gas samples were stored in evacuated Exetainers (Labco, Lampeter, Wales, UK) and were analyzed on a gas chromatograph (GC-2014; Shimadzu Scientific Instruments, Columbia, MD, USA) equipped with a flame ionization detector, methanizer, and electron capture device. Using the ideal gas law to convert gas concentrations to moles of gas measured per unit area, we calculated fluxes (µmol or nmol m^{-2} sec^{-1}, depending on the gas) based on a linear change with time. Fluxes of CH_4 and N_2O were expressed as CO_2 equivalents which considers the 30 and 200 times higher radiative forcing capacity of these two gases. We estimated growing season GHG fluxes by summing daily values interpolated between sample dates assuming linear rates of change.

Plant Community	Description
Wet	Nebraska sedge (*Carex nebrascensis*), arctic rush (*Juncus arcticus*), and a mixture of facultative wet forbs (e.g., *Montia chamissoi, Veronica americana*).
Mesic	The mesic plant community contained Douglas' sedge, arctic rush, and a mixture of meadow forbs (e.g., *Chorispora tenella, Symphyotrichum ascendens*)
Edge	edge plant community featured an overstory of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) and an understory of primarily Douglas' sedge (*Carex douglasii*).

Table A1. Description of mesic, wet, and edge plant communities defined by Richardson et al. 2021. These plant communities were defined based on plant's degree of dependence on shallow water tables and were used to stratify sampling.

Study	Plant community	Upland soil C stock kg C m^{-2}	Root C stock kg C m^{-2}	Upland biomass kg C m^{-2}	Notes
Rau et al. (2011)	Phase 1 PJ	4.8	0.18	---	
	Phase 3 PJ	5.2	0.54	---	0-45 cm Sagebrush STEP sites
Fusco et al. (2019)	PJ	---	---	2.75	
	Sagebrush	---	---	0.36	
Austreng (2012)	Cheatgrass	2.97	0.297	0.78	0-48cm South E., Idaho
	Bunchgrass	3.75	0.594	0.13	
	Sagebrush	5.08	0.837	0.42	
Hooker et al. (2008)	Cheatgrass	3.42	0.14	0.12	Vernon, Utah
	Crested wheatgrass	3.26	0.16	0.13	
	Sagebrush	3.11	0.22	0.7	
			---	---	
Norton et al. (2004)	Cheatgrass	4.46	---	---	Central & Northern Utah, and South Idaho
	Bunchgrass	6.06			Cheatgrass 0-34cm bunchgrass 0-40cm
Morra (unpublished)	Sagebrush	4.74	0.449	0.078	Soils 0-45 cm Near Elko NV.

Table A2. List of values from a literature review of C stocks found in upland ecosystems of the Great Basin. Depths are 0-45 cm unless otherwise stated. Full citations are included on the last page of this document.

	Sum of squares	Mean Squared	DF	DenDF	F value	Pr(>F)
Treatment	4.09	2.05	2.00	189.00	0.44	0.65
Year	99.01	99.01	1.00	189.00	21.14	0.00
Plant	5.35	2.68	2.00	189.00	0.57	0.57
Treatment * Year	0.81	0.41	2.00	189.00	0.09	0.92
Treatment * Plant	6.03	1.51	4.00	189.00	0.32	0.86
Year * Plant	4.89	2.45	2.00	189.00	0.52	0.59
Treatment * Plant * Year	6.95	1.74	4.00	189.00	0.37	0.83

Table A3 Results of analysis of variance test to evaluate the main effects and interactions of grazing treatment, vegetation community, and year on TBCF from 2019 to 2021 in the 0-45 cm profile. This was used to compare the differences among lines fit using mixed linear models that featured a random intercept term to account for non-independence of repeatedly sampled plots.

Plant community	Variable 1	Variable 2	Variable 3	Variable 4	Variable 5	Variable 6	Variable 7	Variable 8	AIC	R^2	p-val
All plants	Peak Biomass ***	Mean Soil Temp	Spring VWC	Mean VWC	Growing Days	Spring Soil Temp	% Drought Days	Drying Rate	221.23	0.10	0.01
All plants	Peak Biomass ***	Mean Soil Temp	Spring VWC	Mean VWC	Growing Days	Spring Soil Temp	% Drought Days		219.25	0.10	0.01
All plants	Peak Biomass ***	Mean Soil Temp	Spring VWC	Mean VWC	Growing Days	Spring Soil Temp			217.27	0.10	>0.01
All plants	Peak Biomass ***	Mean Soil Temp	Spring VWC	Mean VWC	Growing Days				215.28	0.10	>0.01
All plants	Peak Biomass ***	Mean Soil Temp	Spring VWC	Mean VWC					213.22	0.10	>0.01
All plants	Peak Biomass ***	Mean Soil Temp	Spring VWC						211.34	0.10	>0.01
All plants	Peak Biomass ***	Mean Soil Temp							209.87	0.10	>0.01
Mesic	Spring VWC	Growing Days *	Drying Rate	Mean VWC	Spring Soil Temp	% Drought Days	Mean Soil Temp	Peak Biomass	60.99	0.14	0.39
Mesic	Spring VWC *	Growing Days *	Drying Rate	Mean VWC	Spring Soil Temp	% Drought Days	Mean Soil Temp		58.99	0.14	0.29
Mesic	Spring VWC *	Growing Days *	Drying Rate	Mean VWC	Spring Soil Temp	% Drought Days			56.99	0.14	0.20
Mesic	Spring VWC *	Growing Days *	Drying Rate	Mean VWC	Spring Soil Temp				55.06	0.14	0.12
Mesic	Spring VWC *	Growing Days *	Drying Rate	Mean VWC					53.75	0.13	0.09
Mesic	Spring VWC *	Growing Days *	Drying Rate						52.45	0.12	0.06
Mesic	Spring VWC *	Growing Days *							51.29	0.11	0.03
Wet	Peak Biomass	Mean Soil Temp	Growing Days	Spring VWC	Spring Soil Temp	Drying Rate	% Drought Days	Mean VWC	97.48	0.24	0.05
Wet	Peak Biomass	Mean Soil Temp	Growing Days	Spring VWC	Spring Soil Temp	Drying Rate	% Drought Days		95.48	0.24	0.03
Wet	Peak Biomass	Mean Soil Temp	Growing Days	Spring VWC	Spring Soil Temp	Drying Rate			93.58	0.23	0.01
Wet	Peak Biomass	Mean Soil Temp	Growing Days	Spring VWC	Spring Soil Temp				91.90	0.23	>0.01
Wet	Peak Biomass	Mean Soil Temp **	Growing Days	Spring VWC					90.72	0.22	>0.01
Wet	Peak Biomass	Mean Soil Temp **	Growing Days						89.18	0.21	>0.01
Edge	Peak Biomass	Mean VWC	Spring VWC	% Drought Days	Mean Soil Temp	Growing Days	Spring Soil Temp	Drying Rate	62.00	0.14	0.37
Edge	Peak Biomass	Mean VWC	Spring VWC	% Drought Days	Mean Soil Temp	Growing Days	Spring Soil Temp		60.00	0.14	0.27

Edge	Peak Biomass	Mean VWC	Spring VWC	% Drought Days	Mean Soil Temp	Growing Days	58.01	0.14	0.18
Edge	Peak Biomass	Mean VWC	Spring VWC	% Drought Days	Mean Soil Temp		56.01	0.14	0.11
Edge	Peak Biomass	Mean VWC	Spring VWC	% Drought Days			54.04	0.14	0.06
Edge	Peak Biomass	Mean VWC	Spring VWC				52.23	0.14	0.03
Edge	Peak Biomass	Mean VWC *					50.83	0.13	0.02

Table A4. Models returned by the stepwise linear model selection process. Results are shown for drivers of all plants, edge, mesic, and wet plant communities. Results are ranked by Akaike information criterion (AIC) with the most parsimonious models listed at the bottom of each table. Stars indicate significance ‘*’= $p < 0.05$, ‘**’= $p < 0.01$, ‘***’= $p < 0.00$

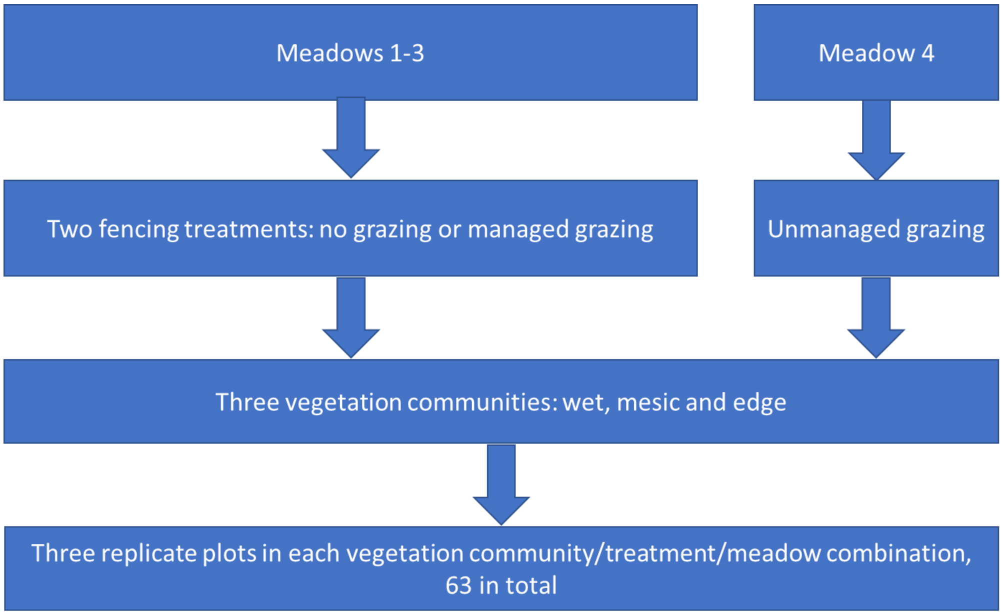

Figure A1. Hierarchy of the experimental design. Three of the meadows had fences installed to split them into grazing exclusion or managed grazing pairs while a fourth meadow was treated as an unmanipulated control. Within each grazing treatment, three plant communities were delineated. Each plant community contained three replicated plots where TBCF was measured (63 plots total).

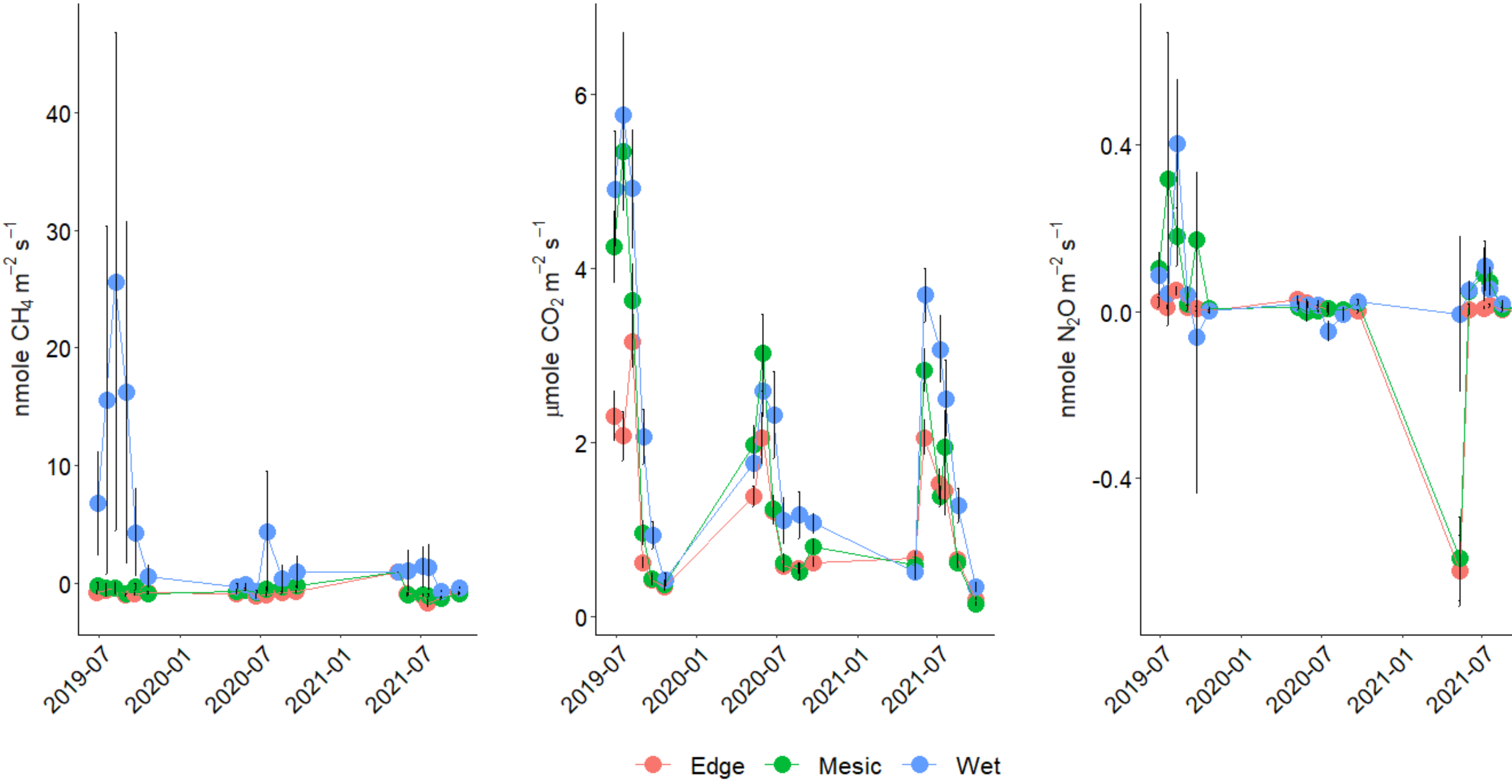

Figure A2. Average growing season trace gas fluxes measured at roughly three-week intervals. Error bars are the standard error of the mean flux across meadow and grazing intensity for each plant community.

References

Austreng, A. C. (2012). The Carbon Budget Impact of Sagebrush Degradation. *Masters Thesis*, (May), 82. Retrieved from http://scholarworks.boisestate.edu/cgi/viewcontent.cgi?article=1269&context=td

Fusco, E. J., Rau, B. M., Falkowski, M., Filippelli, S., & Bradley, B. A. (2019). Accounting for aboveground carbon storage in shrubland and woodland ecosystems in the Great Basin. *Ecosphere*, *10*(8). https://doi.org/10.1002/ecs2.2821

Hooker, T. D., Stark, J. M., Norton, U., Joshua Leffler, A., Peek, M., & Ryel, R. (2008). Distribution of ecosystem C and N within contrasting vegetation types in a semiarid rangeland in the Great Basin, USA. *Biogeochemistry*, *90*(3), 291–308. https://doi.org/10.1007/s10533-008-9254-z

Kasten, R., 2019. Above and belowground carbon stocks differ among meadow vegetation communities in the northern Sierra Nevada, California USA. University of Nevada, Reno.

Norton, J. B., Monaco, T. A., Norton, J. M., Johnson, D. A., & Jones, T. A. (2004). Soil morphology and organic matter dynamics under cheatgrass and sagebrush-steppe plant communities. Journal of Arid Environments, 57(4), 445–466. https://doi.org/10.1016/S0140-1963(03)00104-6

Rau, B. M., Johnson, D. W., Blank, R. R., Tausch, R. J., Roundy, B. A., Miller, R. F., et al. (2011). Woodland expansion's influence on belowground carbon and nitrogen in the Great Basin U.S. *Journal of Arid Environments*, *75*(9), 827–835. https://doi.org/10.1016/J.JARIDENV.2011.04.005

Reed, C., Merrill, A., Drew, M., Christman, B., Hutchinson, A., Keszey, L., Swanson, S., 2021. Montane Meadows: A Soil Carbon Sink or Source? Ecosystems. doi:10.1007/s10021-020-00572-x

Reed, C., Berhe, A., Moreland, K., Wilcox, J., Sullivan1, B., n.d. Restoring function: positive responses of carbon and nitrogen to 20 years of hydrologic restoration in montane meadows.

Appendix B. Supporting information for chapter 2

	mols (g L^{-1})	mols C (g C L^{-1})
Sucrose	1.79	0.75
Mannose	1.85	0.74
Potassium citrate	3.33	0.74
Cellobiose	5.28	1.11
Pectin	5.45	2.02
Vanillic acid	2.61	1.49

Table B1. Concentrations of compounds used to approximate DOC chemistry of rhizosphere soil solution. Recipe was provided by John Stark (personal communication).

Meadow	**Fraction**	**C stock (g C m^{-2})**
Humid high	POM	1438.1 ± 344.48
Humid high	Silt MAOM	1647.51 ± 197.18
Humid high	Clay MAOM	1678.34 ± 132.56
Humid low	POM	603.47 ± 121.14
Humid low	Silt MAOM	878.64 ± 91.66
Humid low	Clay MAOM	1202.94 ± 93.22
Semiarid high	POM	700.16 ± 73.9
Semiarid high	Silt MAOM	931.73 ± 53.83
Semiarid high	Clay MAOM	987.23 ± 44.68
Semiarid Low	POM	822.39 ± 91.89
Semiarid Low	Silt MAOM	1050.11 ± 57.96
Semiarid Low	Clay MAOM	1362.23 ± 33.98

Table B2. Mean carbon stock measured across all sample dates (24 h, one month, six months, and one year) held in the particulate organic matter fraction (POM), silt mineral associated organic matter fraction (Silt MAOM), and clay mineral associated organic matter fraction (Clay MAOM). Error is the standard error of the mean.

Order	Prod	Climate	Fraction	δ ^{13}C spike	δ ^{13}C natural abundance
24 Hours	High	Humid	Clay	-25.45 ± 0.12	-25.51 ± 0.18
24 Hours	High	Humid	POM	-26.74 ± 0.04	-26.48 ± 0.13
24 Hours	High	Humid	Silt	-26.29 ± 0.05	-26.12 ± 0.15
24 Hours	High	Semiarid	Clay	-23.66 ± 0.27	-23.8 ± 0.22
24 Hours	High	Semiarid	POM	-25.29 ± 0.47	-26.22 ± 0.47
24 Hours	High	Semiarid	Silt	-24.03 ± 0.48	-24.16 ± 0.38
24 Hours	Low	Humid	Clay	-25.59 ± 0.18	-25.99 ± 0.23
24 Hours	Low	Humid	POM	-27.45 ± 0.38	-27.28 ± 0.23
24 Hours	Low	Humid	Silt	-26.32 ± 0.23	-26.71 ± 0.25
24 Hours	Low	Semiarid	Clay	-23.67 ± 0.12	-23.7 ± 0.29
24 Hours	Low	Semiarid	POM	-26.04 ± 0.27	-26.1 ± 0.66
24 Hours	Low	Semiarid	Silt	-23.95 ± 0.18	-24.02 ± 0.48
1 Month	High	Humid	Clay	-25.49 ± 0.2	-25.61 ± 0.14
1 Month	High	Humid	POM	-26.33 ± 0.1	-26.57 ± 0.18
1 Month	High	Humid	Silt	-26.14 ± 0.11	-26.12 ± 0.13
1 Month	High	Semiarid	Clay	-23.73 ± 0.23	-23.93 ± 0.13
1 Month	High	Semiarid	POM	-25.73 ± 0.56	-26.41 ± 0.38
1 Month	High	Semiarid	Silt	-24.3 ± 0.39	-24.48 ± 0.28
1 Month	Low	Humid	Clay	-25.66 ± 0.14	-26 ± 0.14
1 Month	Low	Humid	POM	-27.24 ± 0.17	-27.02 ± 0.15
1 Month	Low	Humid	Silt	-26.4 ± 0.03	-26.41 ± 0.15
1 Month	Low	Semiarid	Clay	-23.97 ± 0.15	-23.93 ± 0.14
1 Month	Low	Semiarid	POM	-26.65 ± 0.17	-26.57 ± 0.46
1 Month	Low	Semiarid	Silt	-24.53 ± 0.24	-24.33 ± 0.32
6 Months	High	Humid	Clay	-25.43 ± 0.12	-25.67 ± 0.1
6 Months	High	Humid	POM	-26.34 ± 0.02	-26.55 ± 0.15
6 Months	High	Humid	Silt	-26.13 ± 0.12	-26.19 ± 0.09
6 Months	High	Semiarid	Clay	-23.6 ± 0.29	-23.89 ± 0.22
6 Months	High	Semiarid	POM	-25.12 ± 0.71	-26.02 ± 0.57
6 Months	High	Semiarid	Silt	-23.8 ± 0.52	-24.19 ± 0.36
6 Months	Low	Humid	Clay	-25.46 ± 0.24	-26.07 ± 0.36
6 Months	Low	Humid	POM	-26.74 ± 0.27	-27.11 ± 0.47
6 Months	Low	Humid	Silt	-26.26 ± 0.29	-26.52 ± 0.3
6 Months	Low	Semiarid	Clay	-23.73 ± 0.09	-23.85 ± 0.13
6 Months	Low	Semiarid	POM	-25.78 ± 0.49	-26.54 ± 0.2
6 Months	Low	Semiarid	Silt	-24.1 ± 0.18	-24.14 ± 0.16
1 Year	High	Humid	Clay	-25.33 ± 0.2	-25.63 ± 0.15
1 Year	High	Humid	POM	-25.95 ± 0.15	-26.3 ± 0.11
1 Year	High	Humid	Silt	-25.91 ± 0.16	-26.09 ± 0.04
1 Year	High	Semiarid	Clay	-23.56 ± 0.27	-23.84 ± 0.14
1 Year	High	Semiarid	POM	-24.98 ± 0.63	-26.15 ± 0.3
1 Year	High	Semiarid	Silt	-23.72 ± 0.51	-24.08 ± 0.24
1 Year	Low	Humid	Clay	-25.57 ± 0.28	-25.85 ± 0.36
1 Year	Low	Humid	POM	-26.9 ± 0.2	-27.17 ± 0.38
1 Year	Low	Humid	Silt	-26.29 ± 0.22	-26.4 ± 0.39
1 Year	Low	Semiarid	Clay	-23.73 ± 0.15	-23.84 ± 0.24
1 Year	Low	Semiarid	POM	-25.79 ± 0.28	-26.28 ± 0.43
1 Year	Low	Semiarid	Silt	-24.02 ± 0.19	-24.18 ± 0.29

Table B4. Mean (± the standard error) delta ^{13}C of POM, Clay MAOM, Silt MAOM fractions of high and low productivity plots located in humid or semiarid climates. Mean values are shown for plots spiked with 99 atom% ^{13}C or plots that were not spike, which represent natural abundance of ^{13}C. Values are shown for the four dates of sampling occurring at 24 hours, one month, six months, and one year. Error is the standard error of the mean

Appendix C Supporting information for chapter 3

	Df	Sum	Sq	Mean	Pr(>F)
Reach	3	278.8	92.92	17.514	4.57E-08
Surface	3	491	163.68	30.851	9.36E-12
Reach:Surface	9	231.5	25.73	4.849	9.21E-05
Residuals	54	286.5	5.31		

Table C1. Results of mixed linear models comparing fixed effects of reach (Unmanaged grazing, managed grazing, grazing excluded ephemeral pond, and grazing excluded permanent pond) on soil C content of geomorphic surfaces (ponds, floodplains, terraces, and uplands).

Surface	Reach	Mean	Standard error	Coefficient of variation	Letter
Floodplain	Grazing excluded ephemeral ponds	4.88	1.17	0.59	a
Floodplain	Unmanaged grazing	5.71	0.36	0.11	a
Floodplain	Managed grazing	4.1	0.95	0.57	a
Floodplain	Grazing excluded permanent ponds	14.61	2.07	0.24	b
Pond	Grazing excluded ephemeral ponds	4.05	0.65	0.39	a
Pond	Unmanaged grazing	0	0	NA	b
Pond	Managed grazing	2.37	0.39	0.4	c
Pond	Grazing excluded permanent ponds	4.72	0.45	0.16	a
Terrace	Grazing excluded ephemeral ponds	12.79	1.35	0.26	a
Terrace	Unmanaged grazing	5.97	2.06	0.6	b
Terrace	Managed grazing	8.43	0.75	0.22	ab
Terrace	Grazing excluded permanent ponds	11.16	1.4	0.31	ab
Uplands	Grazing excluded ephemeral ponds	5.52	0.74	0.23	a
Uplands	Unmanaged grazing	3.18	0.7	0.38	a
Uplands	Managed grazing	5.69	1.16	0.35	a
Uplands	Grazing excluded permanent ponds	4.57	0.81	0.31	a

Table C2. Results of post hoc tests from mixed linear models comparing fixed effects of reach (Unmanaged grazing, managed grazing, grazing excluded ephemeral pond, and grazing excluded permanent pond) on soil C content of geomorphic surfaces (ponds, floodplains, terraces, and uplands). Letters are used to show differences among fluvial surfaces.

	Df	Sum sq	Mean Sq	F	Pr(>F)
Reach	3	7.03	2.3432	20.136	6.89E-09
Surface	3	3.13	1.0434	8.967	6.45E-05
Reach:Surface	9	26.137	2.9041	24.956	3.24E-16
Residuals	54	6.284	0.1164		

Table C3. Results of mixed linear models comparing fixed effects of reach (Unmanaged grazing, managed grazing, grazing excluded ephemeral pond, and grazing excluded permanent pond) on root C content of geomorphic surfaces (ponds, floodplains, terraces, and uplands).

Statistics

	Df	Sum sq	Mean sq	F value	Pr(>F)
Reach	3	384.6	128.19	23.222	8.70E-10
Surface	3	576.4	192.15	34.808	1.17E-12
Reach:Surface	9	366.6	40.73	7.378	6.35E-07
Residuals	54	298.1	5.52		

Table C4. Results of mixed linear models comparing fixed effects of reach (Unmanaged grazing, managed grazing, grazing excluded ephemeral pond, and grazing excluded permanent pond) on ecosystem C content of geomorphic surfaces (ponds, floodplains, terraces, and uplands).

Surface	Reach	Mean	Standard error	Coefficient of variation	letters
Floodplain	Grazing excluded ephemeral ponds	5.67	1.22	0.53	a
Floodplain	Unmanaged grazing	6.34	0.19	0.05	a
Floodplain	Managed grazing	4.79	0.98	0.5	a
Floodplain	Grazing excluded permanent ponds	18.53	1.86	0.17	b
Pond	Grazing excluded ephemeral ponds	5	0.66	0.33	a
Pond	Unmanaged grazing	0	0	NA	b
Pond	Managed grazing	2.76	0.43	0.38	c
Pond	Grazing excluded permanent ponds	5.3	0.58	0.19	a
Terrace	Grazing excluded ephemeral ponds	13.93	1.32	0.23	a
Terrace	Unmanaged grazing	6.71	2.15	0.56	b
Terrace	Managed grazing	9.71	0.71	0.18	ab
Terrace	Grazing excluded permanent ponds	12.39	1.46	0.29	a
Uplands	Grazing excluded ephemeral ponds	6.27	0.91	0.25	a
Uplands	Unmanaged grazing	3.6	0.81	0.39	a
Uplands	Managed grazing	6.62	1.29	0.34	a
Uplands	Grazing excluded permanent ponds	5.21	0.9	0.3	a

Table C5. Results of post hoc tests from mixed linear models comparing fixed effects of reach (Unmanaged grazing, managed grazing, grazing excluded ephemeral pond, and grazing excluded permanent pond) on ecosystem C content of geomorphic surfaces (ponds, floodplains, terraces, and uplands). Letters are used to show differences among fluvial surfaces.

	Df	Sum sq	Mean sq	F value	Pr(>F)
Reach	3	1.627	0.5424	16.67	8.66E-08
Surface	3	3.648	1.2161	37.37	3.28E-13
Reach:Surface	9	0.498	0.0553	1.7	0.112
Residuals	54	1.757	0.0325		

Table C6. Results of post hoc tests from mixed linear models comparing fixed effects of reach (Unmanaged grazing, managed grazing, grazing excluded ephemeral pond, and grazing excluded permanent pond) on ecosystem N content of geomorphic surfaces (ponds, floodplains, terraces, and uplands).

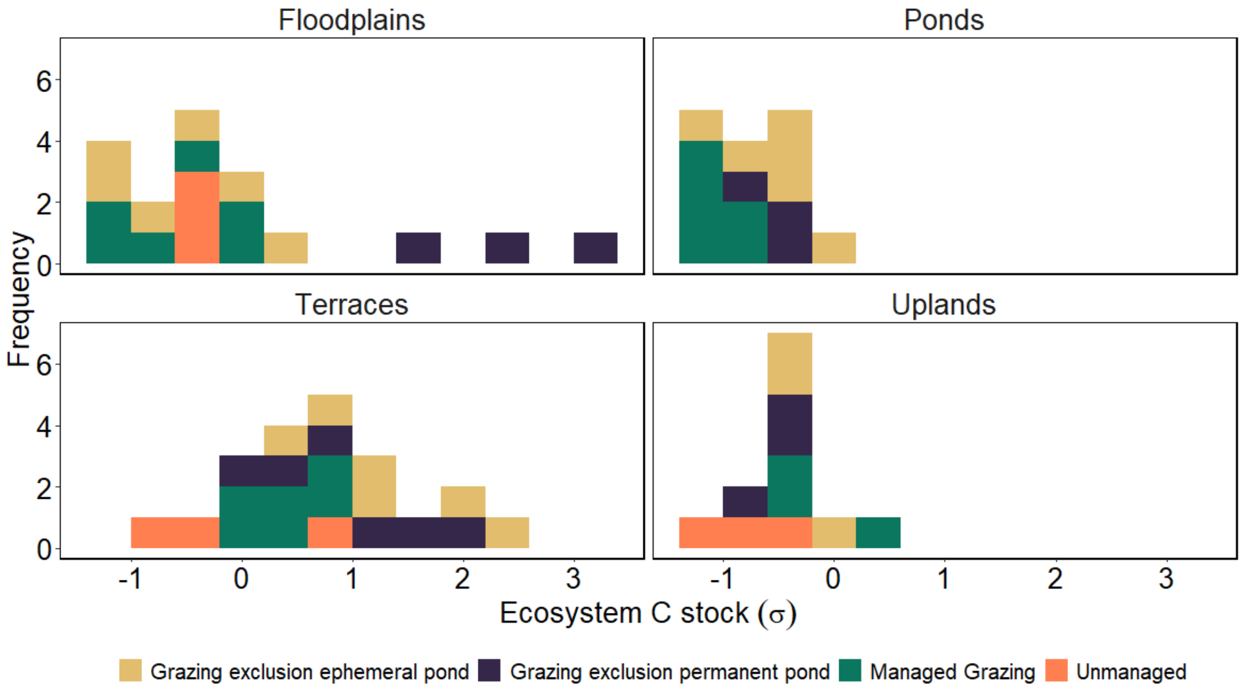

Figure 1C. Frequency distribution of ecosystem C stocks found on geomorphic surfaces of Maggie Creek. Values have been scaled to units of standard deviation of the mean ecosystem C found at Maggie Creek.