Above and belowground carbon stocks differ among meadow vegetation communities in the northern Sierra Nevada, California USA

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by

Ryan Kasten

Dr. Benjamin W. Sullivan/Thesis Advisor

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We recommend that the thesis prepared under our supervision by

RYAN KASTEN

Entitled

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be accepted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

Benjamin Sullivan, Ph.D., Advisor

Sarah Bisbing, Ph.D., Committee Member

Paul Verburg, Ph.D., Committee Member

Peter Weisberg, Ph.D., Committee Member

Adam Csank, Ph.D., Graduate School Representative

David W. Zeh, Ph.D., Dean, Graduate School

August, 2019
Abstract

While they cover a relatively small geographic area, montane meadows are hotspots of soil carbon (C) and are characterized by diverse vegetation communities. Estimates of C stocks in meadows could be improved by linking vegetation communities to above- and belowground C stocks. Here, we explored the spatial distribution of above- and belowground C stocks associated with different vegetation communities from the center of a meadow to the forest edge in eight montane meadows in the Sierra Nevada mountains of California, USA. We found significant differences in belowground C stocks among vegetation communities within most meadows. Meadows that were adjacent to *Pinus jeffreyi* forest showed strong associations between belowground C stocks and vegetation communities, but meadows that were adjacent to mixed conifer forest did not. Belowground C stocks represented the dominant fraction of the total ecosystem C stock in all meadows. The presence of shrubs and establishing trees in meadows generally corresponded with lower belowground and total C stocks. The increase in aboveground C in communities with shrubs or establishing trees did not offset the decrease in belowground C relative to herbaceous plant communities. Though meadows are hydrologically dynamic ecosystems, vegetation communities exhibit strong controls over the quantity and location of C stocks within the ecosystem that may be identified by the composition of the surrounding forest. Our data provide a reference point for future efforts to manage C stocks in Sierra Nevada meadows.
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Preface

This thesis is formatted for submission to an academic journal. I plan to submit the work to *Plant and Soil*. When submitted, the research will include coauthors. Therefore, throughout the thesis I use the pronouns “we” and “our,” instead of “I” and “my.”
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Introduction

Soils contain more carbon (C) than the atmosphere and terrestrial vegetation combined (Schlesinger and Bernhardt 2013). Quantifying the amount of soil C within ecosystems is critical for estimates and management of C sequestration at landscape scales. In the Sierra Nevada mountains of California, USA, montane meadows represent a small fraction of the regional land area (2%, UC Davis Center for Watershed Sciences and USDA Forest Service Pacific Southwest Region 2017) but are a disproportionately large fraction of the regional C reservoir (31%, Norton et al. 2011). Per unit area, meadow C stocks (15-40 kg C m\(^{-2}\), Reed et al. in prep) are similar to those in estuarine and palustrine wetlands and peatlands in the western United States (~20 kg C m\(^{-2}\), Nahlik and Fennessy 2016).

Meadows are not uniform ecosystems, however. Meadow ecosystems are composed of diverse and productive vegetation communities that depend on spatially and temporally dynamic hydrologic conditions (Allen-Diaz 1991, Loheide et al. 2009, Lowry et al. 2011, McIlroy and Allen-Diaz 2012). Meadows in the Sierra Nevada have a long history of anthropogenic land use, such as road, rail, and trail construction, mining, and grazing, that has disrupted hydrology and vegetation by creating incised stream channels (Ratliff 1985; Hunsaker et al. 2015). Currently, meadows in the Sierra Nevada range are being restored to improve hydrologic function and ecosystem services (Drew et al. 2016). In relatively undisturbed meadows or meadows that have been restored, community composition and ecosystem functions are maintained by a shallow groundwater table (Murray et al. 2003, Loheide et al. 2009). In areas where groundwater is shallow, obligate
and facultative wetland plants are often dominant (McIlroy and Allen-Diaz 2012). A gradient of vegetation communities may be present between the center of the meadow and the surrounding forest and depending on the hydrologic conditions within the meadow. For example, if one were to walk from the center of a meadow to the surrounding forest edge, herbaceous vegetation dominated by sedges, rushes, grasses, and forbs typically gives way to upland vegetation like shrubs and newly establishing trees (Darrouzet-Nardi et al. 2006, Loheide and Gorelick 2007, Norton et al. 2011).

Vegetation communities and productivity are strongly associated with soil C stocks (Post et al. 1982, Jobbágy and Jackson 2000). In grassland ecosystems, establishment of woody vegetation resulted in soil C losses that were greater than the aboveground C gained by woody plant establishment (Jackson et al. 2002). Reductions in vegetation diversity may also result in lower soil carbon stocks (e.g., Fornara and Tilman 2008, Lange et al. 2015, Chen et al. 2018). Such changes in vegetation composition may be related to climatic shifts, changing disturbance regimes, or even millennial changes in edaphic properties. Given the importance, and vulnerability, of hydrologic characteristics for vegetation in meadows, it is a logical next step to determine if soil C stocks change with meadow vegetation community characteristics. In Sierra Nevada meadows, landscape position, degree of meadow degradation, and soil moisture were associated with differences in soil C stocks (Norton et al. 2011, Norton et al. 2014). However, it is uncertain whether C stocks have strong relationships with vegetation community characteristics in meadows, where the influence of dynamic hydrology on biogeochemical cycling may mask relationships with vegetation.
Belowground C stocks are an important, and often overlooked, component of total ecosystem C in many ecosystems. Current legislation in California requires that the state reduce or offset annual greenhouse gas emissions by 182.9 Tg CO\textsubscript{2} equivalent by 2030 (California Global Warming Solutions Act, 2006). Achieving such reductions may require management actions designed to retain and sequester belowground C stocks, an approach being pursued internationally (Soussana et al. 2019). Identifying associations between vegetation communities and C stocks may improve our ability to spatially estimate and manage belowground C in the region. In this study, we sampled above- and belowground C stocks in vegetation communities distributed from the center of meadows to forest edges in eight northern Sierra Nevada meadows to test two hypotheses. We hypothesized that there would be lower belowground C stocks in woody vegetation communities in the meadow, where species diversity may be relatively lower, than herbaceous vegetation communities in the meadow. We also hypothesized that increases in aboveground C stocks would be offset by decreases in belowground C between woody and herbaceous vegetation communities in meadows.
Methods

Site Description

We addressed our hypotheses by measuring vegetation composition and C stocks in eight northern Sierra Nevada meadows with a range of elevations, geomorphological characteristics, watershed sizes and climates (Table 1). The sites spanned a range of elevation (1582-2067 m), 30-y mean annual temperature (5.8-7.6 °C; 1981-2010), and 30-y mean annual precipitation (57-123 cm; 1981-2010, PRISM Climate Group 2010). Following the methodology of Petersky and Harpold (2018), we used Google Earth Engine to estimate the average annual snow-covered days (MODIS 16-d 500 m Normalized Differential Snow Index) for each site between September 1st, 2009 and May 15th, 2019. Average snow-covered days varied between 57 and 162 d y⁻¹ (Table 1). We used the approach used by (Yu et al. 2010) in Tibetan meadows to estimate average annual growing season length for each site between January 1st, 1998 and December 31st, 2018. Briefly, we calculated a normalized difference vegetation index (NDVI) ratio (defined as the minimum NDVI divided by the range of maximum minus minimum NDVI at a site) using Landsat imagery in Google Earth Engine. Growing season start began when the NDVI ratio crossed above 0.2; growing season end date occurred when the NDVI ratio fell below 0.6. Mean growing season lengths for the period were 62-117 d (Table 1). Most sites in the region are hydrologically degraded (Hunsaker et al. 2015) or have undergone restoration in the last several decades; the eight meadows here represent a range of restoration conditions associated with meadows in the region (Table 1). All sites have been grazed, though grazing practices and intensities likely varied over time and among meadows. Unlike the other meadows where anthropogenic change of meadow
hydrology resulted in the lowering of the water table through stream incision or re-routing, Van Norden was dammed into a shallow lake between 1916 and 1976 (Donner Summit Historical Society 2016). Of the other seven meadows, six had experienced some sort of hydrologic restoration of the stream channel in the last 20 y designed to raise the groundwater level.

**Vegetation Characterization**

In each meadow, we initially visually identified plant communities and ecotones that represented the vast majority of the vegetation present between the meadow center and the forest edge adjacent to the meadow. For simplicity, we describe them as wet meadow, grass/forb, shrub/grass, shrub, tree establishment or forest edge vegetation communities. Not all vegetation communities were present in all meadows. We then quantitatively assessed the vegetation in each community present per meadow. In each vegetation zone at each site, we established six plots located 15 m distant from each other (20 m apart in vegetation communities with trees), typically with 3 plots located on two adjacent transects 15 m apart (again, 20 m apart in vegetation communities with trees). Halfway between the two rows of three plots, we placed 1-m² quadrats in which we measured percent cover of herbaceous species. All herbaceous plants were identified to genus and species when possible. In all six plots, 1.5 m radius plots extending from the plot center of all six plots per vegetation community, we measured shrub species composition and density, calculated as the number of individuals per m². We measured tree species composition and basal area, based on diameter at breast height (DBH, 1.5 m), in a 10-m radius from plot center plots at all six plots within each vegetation community.
We do not assume that the vegetation communities we measured are at steady state. For example, in tree establishment zones, three lines of evidence demonstrate that trees are new to the vegetation community: no evidence of stumps or dead trees in the area, the small stature and diameter of the trees present, and a comparison of current satellite imagery with past aerial photographs (SI Figure 1). We were able to find aerial images taken between 1952 and 1987 for all meadows but Perazzo; more recent imagery was available from Google Earth. This comparison of imagery demonstrated that the trees in the tree establishment zones were not present in prior decades. We sampled vegetation communities regardless of their trajectory of change in response to hydrologic disturbance, restoration condition, or surrounding forest management.

**Carbon Quantification**

We measured above- and belowground C stocks at each of the six plots within each of the dominant plant communities identified above that occurred in the eight meadows. At a minimum, three 0-15-cm, two 15-30-cm, and one 30-45-cm soil cores were collected from each plant community. From each core, we sieved the fine soil fraction (<2 mm) and carefully extracted root biomass by hand and by floating roots. Soil bulk density was measured as the mass of fine soil in each core volume; rocks were excluded. Fine soil C concentration was measured with an elemental analyzer (ECS 4010, Costech Analytical Technologies Inc., Valencia, CA). Root biomass was separated from the soil by first picking out roots and then floating roots in water. We then oven dried the roots and used a correction factor of 0.37 developed in some of the same meadows to convert root dry mass to root C concentration (Reed et al. in prep). We did not estimate coarse roots. In vegetation communities with trees, coarse roots are usually estimated...
with a single scalar based on aboveground biomass for all species (e.g., Bisbing et al. 2010 using equations from Cairns et al. 1997). While such a scalar may be appropriate for large scale analyses, here, we are exploring how C stocks change over fine-spatial scales within sites with different climates, forest tree species composition, disturbance histories, and hydrology. A single relationship between aboveground biomass and coarse root biomass may not hold in this situation. Further, such an allometric model is not available, to our knowledge, for the shrub species present in these meadows, preventing the comparison of tree and shrub coarse root C stocks. We acknowledge that we do not include fine roots and soil C below 45 cm, but most C in the solum is located in the top 0.5 m in these meadows (Reed et al. in prep).

We sampled aboveground herbaceous biomass by clipping vegetation to within 1 cm of the soil surface within a single 25-cm$^2$ quadrat at each of the six plots in each vegetation community. When present, we collected forest litter (including humus) to mineral soil within the same 25-cm$^2$ quadrat per plot. Herbaceous biomass and forest litter were dried to a constant mass at 60 $^\circ$C and converted to C stock using correction factors of 0.43 and 0.48, respectively developed in similar meadows and forests of the Sierra Nevada region (Reed et al. in prep; Obrist et al. 2009).

Where shrubs occurred, we measured the shrub height, longest and shortest shrub diameters, and shrub species within a 1.5-m radius plot. We applied species-specific allometric equations (SI Table 1, Reiner et al. 2010; United States Geological Survey 2008) to estimate aboveground biomass of shrubs based on shrub volume. We then converted aboveground shrub biomass to aboveground shrub C using a correction factor (0.48; Jagodzinski et al. 2012) to calculate C content.
In vegetation communities where trees occurred in the eight meadow sites, individual trees were measured within six 10 m radius plots. We measured diameter at breast height (DBH) and species of each tree, including saplings. We estimated the whole tree biomass of each tree we sampled using published allometric equations that converted the measured DBH or BA for individual trees (SI Table 1, Jenkins et al. 2003). We converted tree biomass to tree C using a correction factor of 0.48 (Kaye et al. 2005).

Data Analysis

In order to confirm that our sampling captured distinct plant communities within each meadow, we estimated cover of grasses, rushes, sedges, and forbs, the Shannon diversity index (H) and species richness for herbaceous plants, the density of shrubs, and basal area of tree stems. We estimated aboveground C stocks as the sum of herbaceous, litter, shrub, and tree C stocks. Belowground C stocks were estimated as the sum of soil and root C stocks. All C stocks were scaled to kg C m$^{-2}$ for comparison with other studies.

We tested differences in above- and belowground C stocks among vegetation communities within meadows using the non-parametric Kruskal Wallis test with a Bonferroni correction ($\alpha = 0.003$). To test differences between above- and belowground stocks within meadows, we used a Pairwise Wilcoxon Rank Sum Test with a Bonferroni correction ($\alpha = 0.004$). We explored relationships among C stocks and plant community characteristics using Spearman correlation on mean values of C stocks, species diversity, and species richness, for each vegetation community. To analyze the net difference in C stocks between herbaceous and woody vegetation within meadows, we calculated the aboveground C increase associated with woody plants as the difference between the
woody community and the herbaceous community; we calculated the belowground net C decrease associated with woody plants as the difference between the herbaceous community and the woody community. The net C difference between herbaceous and woody sites was calculated as the difference between the aboveground C gain and the belowground C loss. We excluded the forest edge from this analysis, and considered wet meadow and grass/forb to be herbaceous communities and shrub/grass, shrub, and tree establishment communities to be woody. We used a two-tailed, one-sample Wilcoxon t-test to determine if the net C change between herbaceous and woody communities among sites was significantly different from zero. We used 1-way analysis of variance (ANOVA) to test if MAP, MAT, growing season length, and the duration of snow-covered days were statistically different between meadows of different forest communities. All statistical tests were performed using R v. 3.5.3 (R Core Team, 2019); when statistical tests were not Bonferroni corrected, we designated an a priori $\alpha = 0.05$. 
Results

Vegetation composition differed among the six potential communities within the eight meadows in this study (Table 2). Wet meadow communities were dominant in grasses, rushes, and sedges. Grass/forb and shrub/grass communities had higher coverage of forbs than meadow transects. Forb coverage was generally lowest in shrub and tree establishment communities, but was higher in forest transects than in the shrub and tree establishment transects. Species diversity and richness decreased from meadow center to forest edge in five of the eight meadows: Davies, Goodrich, Kyburz, McReynolds, and Upper Clark’s. In Dotta, diversity and richness peaked in the shrub/grass and shrub communities. In Perazzo, species richness was lowest in the wet meadow and similar in the grass/forb, shrub/grass, tree establishment, and forest edge communities. In Van Norden, there were no herbaceous plants in the tree establishment zone and diversity and richness were similar in the meadow as the forest edge (Table 2).

We identified two different forest communities adjacent to the meadows in this study. Five of the eight meadows (Davies, Dotta, Kyburz, McReynolds, and Upper Clarks) had adjacent forests that were dominated by Pinus jeffreyi (Jeffrey pine) forest (>95% of trees were Jeffrey pine). The forest adjacent to the other three meadows (Goodrich, Perazzo, Van Norden) included Abies concolor (white fir), Pinus contorta (lodgepole pine) and Jeffrey pine (hereafter, we refer to these species in the adjacent forest as “mixed conifer” in the forest edge communities). Mean annual precipitation (MAP) was significantly higher in meadows surrounded by mixed conifer forest than Jeffrey pine forest (F = 7.977, P = 0.030), but mean annual temperature, mean growing
season length, and mean snow-covered days were not different between meadows with the two adjacent forest communities.

In all eight meadows, the largest belowground C stock in any vegetation community was higher than the largest aboveground C stock in any vegetation community, per unit area (Figure 1). Aboveground C stocks were a negligible fraction of total C except in the tree expansion and forest edge communities (Figure 1). Aboveground C stocks increased from meadow to forest communities. We observed significant differences in aboveground C stocks among communities at all sites (P < 0.003 with Bonferroni correction); with the exception of McReynolds (P = 0.011 was greater than the Bonferroni corrected α = 0.003).

Belowground C stocks significantly differed among vegetation communities within sites at six of eight sites (P < 0.003 with Bonferroni correction) with the exceptions of Davies and Van Norden (P = 0.005, P = 0.262, respectively, which were greater than the Bonferroni corrected α = 0.003). We identified two different patterns of belowground C stock change among vegetation communities: one in meadows surrounded by Jeffrey pine forest, and another in meadows surrounded by mixed conifer forest. In meadow sites surrounded by Jeffrey pine forest, C stocks followed a similar pattern among vegetation communities: belowground C stocks were highest in the meadow and grass/forb communities, lowest in the shrub and tree expansion communities, and intermediate in the forest edge (Figure 1). By contrast, belowground C stocks were highest in the forest communities in sites surrounded by mixed conifer forest. In Perazzo, the only mixed conifer-adjacent meadow that had shrubs (Table 2), belowground C stocks were lower in communities with shrubs and establishing trees than
either the meadow or forest transects. Similarly, in Goodrich, belowground C stocks were lower in the tree establishment transect than in the meadow and forest. However, as noted above, belowground C was not significantly different among communities in Van Norden. Because of the different patterns in belowground C stocks and MAP between Jeffrey pine and mixed conifer forest, we further explored relationships between C stocks and vegetation communities between these two groups.

Excluding forest communities, belowground C stocks in the Jeffrey pine-adjacent meadows were lower in woody vegetation communities (grass/shrub, shrub, tree establishment communities) than in herbaceous vegetation communities (meadow, grass/forb communities) and the increase in aboveground C stocks in the woody communities relative to the herbaceous communities did not offset the belowground difference. Consequently, the total ecosystem C was significantly lower in woody communities than in herbaceous communities in Jeffrey pine-adjacent meadows (t = -3.357, P = 0.028; Figure 2A). In the mixed conifer-adjacent meadows, the net C difference between aboveground and belowground C stock change between the herbaceous and woody sites (again, excluding the forest edge) was not significantly different from zero (Figure 2B). Goodrich and Perazzo meadows had lower total C stocks in woody than herbaceous plots, but this pattern was offset by Van Norden, where there was little difference in belowground C stocks between meadow and tree expansion communities and dense stands of lodgepole pine (Pinus contorta) resulted in greater aboveground C stocks in the tree expansion community than the meadow community.

We identified numerous significant relationships among C stocks and vegetation characteristics (diversity and richness) in sites surrounded by Jeffrey pine forest, but not
in sites surrounded by mixed conifer forest (Figure 3). In Jeffrey pine-adjacent sites, soil C was positively correlated to root C, herbaceous C, aboveground tree C, and plant richness, \(r = 0.7, 0.63, 0.66, \text{ and } 0.54; p < 0.001, 0.001, 0.038, \text{ and } 0.003, \text{ respectively}\) and was negatively related to shrub C stocks \(r = -0.46; p = 0.041\). Root C stocks were positively correlated with herbaceous and tree C stocks, plant richness \(r = 0.53, 0.66, 0.46; p = 0.005, 0.038, \text{ and } 0.013 \text{ respectively}\), and were negatively related to shrub C \(r = -0.49; p = 0.028\). Herbaceous C stocks were positively correlated with plant diversity and richness \(r = 0.43 \text{ and } 0.6, p = 0.03 \text{ and } 0.001 \text{ respectively}\) and negatively correlated with shrub C stocks \(r = -0.73; p < 0.001\). Tree C stocks were positively related to litter C stocks \(0.93; p = 0.003\). However, there was only one significant belowground relationship relevant to our study in mixed conifer-adjacent meadows: Root and herbaceous C stocks were positively correlated \(r = 0.65; p = 0.043\).
Discussion

Meadow ecosystems in mountain regions have hydrologically responsive, productive, and diverse vegetation, and it has long been recognized that meadow hydrology and plant communities have implications for downstream water supplies and grazing (Dwire et al. 2006; Allen-Diaz 1991, Lowry et al. 2011, Loheide et al. 2009). More recently, scientific, economic, and socio-political interest has turned to the characteristics, fluxes, and ecosystem services of C in meadow ecosystems because of a recognition that meadows may represent an opportunity to manage for C sequestration (e.g., Genxu et al. 2002, Norton et al. 2011, 2014, Blankinship and Hart 2014, Ankenbauer and Loheide 2016, Drew et al. 2016, Arnold et al. 2014, 2015). In order for meadow C stocks to be better understood with regards to their role in moderating regional C budgets, water retention, and nutrient fluxes, it is necessary to identify the spatial patterns of C stocks within the ecosystem.

**Belowground C stocks in meadows usually differ by vegetation community**

Our results clearly show that C stocks within meadows vary by vegetation community. The results are largely consistent with our first hypothesis that belowground C stocks would be lower in woody vegetation communities (shrub and tree establishment communities, excluding forest edge communities) than in herbaceous vegetation communities (such as the wet meadow and grass-forb communities): seven of the eight meadows had less belowground C in woody than herbaceous communities. Only Van Norden meadow had no difference in belowground C between the woody and herbaceous communities. Van Norden has a different site history than the other meadow sites (Table 1): it was dammed for 60 years. During the spring it filled with water and during the
summer the water was released for electricity generation, resulting in an ephemeral reservoir of fluctuating depth (Donner Summit Historical Society 2016). The tree establishment transects were on or near the high-water mark (SI Figure 1). The different belowground C stock pattern in the tree establishment community may be related to this land use history.

When considering the adjacent forest edge communities, our first hypothesis was still largely supported in meadow sites surrounded by Jeffrey pine forest, in that belowground C stocks were still higher in the herbaceous communities than the forest edge. Yet this was not the case in meadow sites surrounded by mixed conifer forest. Belowground C stocks in the mixed conifer forest edge were equivalent to or higher than belowground C stocks in the center of the adjacent meadow. The difference in forest composition may reflect climatic and hydrologic differences that may manifest in different C stocks at the forest edge. Though we did not see significant differences between the forest communities in the length of the snow-covered season or the length of the growing season, it is likely that the mixed conifer species are indicative of wetter, cooler conditions than those of Jeffrey pine forest. Wetter conditions were apparent in the significant difference in MAP between the Jeffrey pine and mixed conifer sites, but may also depend on meadow topography and the presence of groundwater flow or ephemeral springs into the forest soil near the base of the hillsides surrounding the meadow sites. For example, at Goodrich, which is not a particularly high elevation site and is in an area of northern California that typically has Jeffrey pine-dominant forest communities, we observed springs running out of the base of the surrounding hillside into the meadow in the early growing season that may support the presence of these wetter forest species.
Wetter soils in the mixed conifer forest surrounding the meadow may have supported the development and retention of higher belowground C stocks in all vegetation communities, unlike the Jeffrey pine dominated forest sites.

The stronger relationships among C stocks and vegetation characteristics in drier meadows surrounded by Jeffrey pine forest than in wetter meadows surrounded by mixed conifer meadow forest may result from larger hydrologic gradients in Jeffrey pine sites between the relatively wet meadow center and the drier surrounding environment. These strong relationships in Jeffrey pine adjacent forest likely reflect processes that reinforce the difference in C stocks among vegetation communities within a meadow. It is well established that herbaceous vegetation communities have high rates of C allocation belowground (De Deyn et al. 2008), and that soil C stocks and biogeochemical processes are often higher in high diversity plant communities than low diversity plant communities (Fornara and Tilman 2008, Lange et al. 2015, Chen et al. 2018). The presence of shrubs is likely to reduce herbaceous production, reflected in our data by lower cover and diversity of herbaceous plants, thereby reducing belowground C allocation. Shrubs in Sierra Nevada meadows (and herbaceous species growing in shrub-dominated communities) are able to acquire water from deeper in the soil profile than many of the herbaceous species present in the meadow (Darrouzet-Nardi et al. 2006). This different belowground resource acquisition strategy may also reflect drier soil conditions that could reduce productivity rates and further reduce belowground C allocation rates beyond those associated with species changes alone. Root C turnover or root exudation may be important C sources in meadow communities, and the change in belowground productivity and allocation between herbaceous wet meadow communities and dry shrub
communities are likely responsible for the difference we observed between these communities.

The reinforcing feedbacks among C stocks and vegetation characteristics in Jeffrey pine-adjacent meadows were less apparent in meadows that were adjacent to mixed conifer forest. The only relevant reinforcing feedback was between herbaceous C stocks and root C stocks, but unlike in the Jeffrey-pine adjacent meadows, we found no correlation between root C or herbaceous C and soil C in these sites. Soil C stocks in mixed-conifer adjacent meadows may be less responsive to present vegetation communities than Jeffrey pine adjacent meadows or may be sustained by high rates of productivity by trees. Mixed-conifer Sierra Nevada forests can be highly productive (Campbell et al. 2009), which may help explain why forest belowground C stocks were similar to or higher than in meadow vegetation communities. High rates of forest productivity at mixed conifer meadow sites may sustain belowground C stocks similar to those in meadow ecosystems. We note that the belowground C stocks we report in mixed conifer forest may not represent other, more upland Sierra Nevada forests with similar species. High rates of productivity and soil C accumulation may be caused by a confluence of factors, including the proximity of the forest to the meadow and the potential influence of meadow hydrology on forest productivity.

*Differences between aboveground and belowground C stocks in woody and herbaceous species*

Using repeat remote imagery (SI Figure 1), we were able to observe the relatively recent establishment of trees in our tree-establishment communities during the last several decades, though shrub extent did not appear to be as dynamic. The presence of
shrubs in meadows is related to depth to groundwater (Darrouzet-Nardi et al. 2006) and may reflect microtopography, subsurface restrictive features that prevent water storage, or historic meadow degradation. The establishment of woody species in grassland ecosystems has been shown to reduce total ecosystem C stocks in some cases (Jackson et al. 2002) and increase total ecosystem C stocks in other cases (McKinley and Blair 2008), though overall the effects of woody plant establishment may be positive (Barger et al. 2011). Where total ecosystem C stocks were lower in woody than herbaceous communities, higher aboveground C stocks in woody communities relative to herbaceous communities were offset by even lower belowground C stocks in woody plant communities than herbaceous communities (Jackson et al. 2002). Jackson et al. (2002) demonstrated that this phenomenon was strongest at the wetter end of a precipitation gradient that extended from 200-1,200 mm y\(^{-1}\). Given that our sites were on the wet end of the MAP spectrum of grassland/woody plant establishment identified by Jackson et al. (2002) and that meadows experience additional water inputs from the surrounding watersheds, this observation led us to our second hypothesis - that meadows would see a similar phenomenon. Our hypothesis was largely supported: higher aboveground C stocks in woody plant communities were offset by lower belowground C stocks than herbaceous communities in seven of the eight meadows, regardless of surrounding forest composition. The only meadow where shrubs or establishing trees resulted in a net increase in total ecosystem C stocks relative to the meadow or grass-forb communities was in Van Norden meadow, where there was no difference in belowground C stocks between community types and dense lodgepole pine saplings nearly doubled the total
ecosystem C stock. As noted above, this may be due to the unique management history of this site.

In all sites except Van Norden, aboveground shrub C and establishing tree C was a small fraction of total ecosystem C stocks, and lower belowground C stocks in woody communities than herbaceous communities were not offset by an increase in aboveground C. However, we cannot definitively conclude that the establishment of trees and shrubs reduces the soil C stock. Rather, woody plants may have been able to establish in relatively dry areas of the meadow already had lower C stocks. Further, it is not clear that tree establishment, in the long term, is necessarily detrimental for ecosystem C stocks. In most meadows, the largest total ecosystem C stocks were in the forest edge on the boundary of the meadow. If tree establishment ultimately yields productive forest communities, belowground C stocks may increase and total ecosystem C stocks may be higher. However, as has been noted elsewhere (e.g., Barger et al. 2011), this shift of C stocks aboveground creates C stock vulnerabilities to disturbance that may make C stocks more ephemeral over long time scales.

Implications for meadow C management

As policy and management efforts increasingly include C sequestration as an objective (e.g., Soussana et al. 2019), management of belowground C in meadow ecosystems may be an important means of achieving these goals. In the Sierra Nevada, meadow hydrologic restoration typically consists of efforts to fill or otherwise block flow of incised stream channels and return groundwater closer to the soil surface (Loheide et al. 2009). Presently, it is an open question whether hydrologic restoration is a potential opportunity to maintain large belowground C stocks and increase belowground C stocks
that may have declined over decades of hydrologic degradation (Drew et al. 2016). Our results have several implications for the management of meadow C stocks. As noted by others (Norton et al. 2011, 2014), per unit area, belowground meadow C stocks can be as large, or larger, than aboveground C stocks in the surrounding forest. Aboveground C stocks in meadows are a small fraction of the belowground C stock – even where shrubs are present. Yet, belowground meadow C stocks are usually as variable as the vegetation communities within a meadow. No matter the mechanisms that create these associations between belowground C stocks and vegetation communities, the feedbacks between plant communities and soil C we described above may persist in the first decades after meadow restoration efforts designed to raise the groundwater level. For example, Upper Clarks was the meadow that had the most elapsed time since restoration of any of the sites (~15 years). While it is possible that meadow restoration altered the belowground C stock in the wet meadow community, differences in belowground C were still apparent among vegetation communities. Therefore, management efforts should prioritize the retention of the large belowground C stocks within the wetter vegetation communities in the meadow and, where appropriate for other non-C-based management objectives, consider ways to increase C stocks by shifting dry vegetation communities to wetter ones. While such management efforts may involve meadow hydrologic restoration efforts, the strong relationships among C stocks and vegetation communities we observed suggest that changes in C stocks may occur over time periods that exceed two decades.
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Tables

Table 1: Meadow site characteristics. MAP: mean annual precipitation; MAT: mean annual temperature; GS: Growing season; SD: standard deviation

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<thead>
<tr>
<th>Site</th>
<th>Elevation (m)</th>
<th>Latitude &amp; Longitude</th>
<th>Restoration state (Year)</th>
<th>Adjacent forest community</th>
<th>Soil Classification (Vegetation community)</th>
<th>Watershed size (ha)</th>
<th>GS length (d ± SD)</th>
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Table 2: Mean vegetation characteristics (± standard error) among vegetation communities and meadows. BA: basal area.

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<th>Rushes (%) cover</th>
<th>Sedges (%) cover</th>
<th>Forbs (%) cover</th>
<th>Shannon Diversity(H)</th>
<th>Richness (stems m⁻²)</th>
<th>Shrubs (m² ha⁻¹)</th>
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Figures

Figure 1: Carbon (C) stocks in different components of the ecosystem across vegetation communities within meadows. Values show means (n=6) of each C stock per vegetation community. Shrub, herbaceous, and litter carbon stocks are generally too small to be seen at scale.
Figure 2: Mean aboveground carbon (C) increase (calculated as the difference between the mean of shrub and tree establishment aboveground C stocks and the mean of meadow and grass-forb aboveground C stocks), mean belowground C decrease (calculated as the difference between mean meadow and grass-forb belowground C stocks and the mean of shrub and tree establishment belowground C stocks) and the net change in total ecosystem C stocks between woody plants and herbaceous plant communities in meadows surrounded by Jeffrey pine forest (panel A) and mixed conifer forest (panel B). Each meadow is shown individually (left panels); the distribution of net change in total ecosystem C stocks were significantly different from zero in Jeffrey pine forest but were not significantly different from zero in mixed conifer forest (right panel).
Figure 3: Spearman correlations between carbon (C) stocks and vegetation characteristics (diversity, richness, basal area) in meadows surrounded by Jeffrey pine (*Pinus jeffreyi*) forest and meadows surrounded by mixed conifer forest. The size of the circle represents the strength of the significance, color represents a gradient of correlation coefficients (r), and non-significant relationships are not shown. There was only one shrub C value (Perazzo) in mixed-conifer dominated sites, preventing any correlation analysis (indicated by NA).
Supplementary Information

SI Table 1: Allometric equations for all woody plant species identified in this study. DBH: diameter at breast height

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<td></td>
<td></td>
</tr>
<tr>
<td><em>Pinus jeffreyi</em> &amp;</td>
<td>DBH: 2.54-86.36 in</td>
<td>$e^{(-1.9976+0<em>Dia1+2.952</em>ln(Dia1))}$</td>
<td>megagrams</td>
<td>Dia1 = Diameter in cm</td>
<td>Brown 1978; Means et al. 1994;</td>
</tr>
<tr>
<td><em>ponderosa</em></td>
<td>(crowns)</td>
<td>$+e^{(0.268+0<em>Dia2+2.074</em>ln(Dia2))}$</td>
<td></td>
<td>Dia2 = Diameter in inches</td>
<td>Jenkins et al. 2004</td>
</tr>
<tr>
<td></td>
<td>DBH: 22.4-133.1 cm</td>
<td>$+e^{(3.7398+0<em>Dia2+2.8376</em>ln(Dia2))}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(stems)</td>
<td>$\times 0.000453592$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pinus contorta</em></td>
<td>DBH: 0-10.0 cm</td>
<td>$(-1.5 + 0.215X) + (-0.50 + 0.030X) + (-0.14 + 0.025X)$</td>
<td>kilograms</td>
<td>$X = Basal Area \ (cm^2)$</td>
<td>Pearson et al. 1984; Jenkins et al. 2004</td>
</tr>
<tr>
<td></td>
<td>10.1-19.9 cm</td>
<td>$(-4.3 + 0.305X) + (-0.50 + 0.039X) + (-0.14 + 0.025X)$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Abies concolor</em></td>
<td>DBH: 20.0-60.0 cm</td>
<td>$(4.3 + 0.305X) + (-0.50 + 0.039X) + (10.3 + 0.016X)$</td>
<td>grams</td>
<td>$X = DBH$ in (cm)</td>
<td>Westman 1987; Jenkins et al. 2004</td>
</tr>
<tr>
<td></td>
<td>7-98 cm</td>
<td>$e^{(4.36982+0<em>X+2.5043</em>ln(X))}$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Juniperus spp.</em></td>
<td>DBH: 3.0-112.0 cm</td>
<td>$e^{(-0.86896+0<em>X+1.652882</em>ln(X))}$</td>
<td>kilograms</td>
<td>$X = DBH$ in (cm)</td>
<td>Chojnacky and Moisen 1993; Jenkins et al. 2004</td>
</tr>
<tr>
<td><strong>Shrubs</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Artemisia spp.</em></td>
<td>All</td>
<td>$0.0136 \ (X^{0.1850})$</td>
<td>grams</td>
<td>$X = Diameter 1 \times Diameter 2 \times Height \times (3.14159/6)$</td>
<td>Reiner et al. 2010</td>
</tr>
<tr>
<td><em>Purshia tridentata</em></td>
<td>All</td>
<td>$e^{(-5.290 + 2.604 \times ln(X))}$</td>
<td>grams</td>
<td>$X = crown diameter$ (cm)</td>
<td>USGS 2008</td>
</tr>
<tr>
<td><em>Ericameria nauseosa</em></td>
<td>All</td>
<td>$e^{(-3.871 + 2.263 \times ln(X))}$</td>
<td>grams</td>
<td>$X = crown diameter$ (cm)</td>
<td>USGS 2008</td>
</tr>
</tbody>
</table>
SI Figure 1: Historical aerial photography of meadow sites (left column) and current satellite imagery (right column) of seven of eight meadow sites in our study (Perazzo was photographed during winter with snow on ground, so we excluded it). The approximate vegetation community locations are shown in white boxes.
Davies

1987

2018
Dotta

1968

2014
Goodrich

1954

2017

Tree establishment

Meadow

Forest