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UNIVERSITY OF CALIFORNIA, MERCED

Assessing Soil Drying and Rewetting Effects on Greenhouse Gas Emissions Across Contrasting Montane Meadows

A Thesis submitted in partial satisfaction of the requirements
for the degree of Master of Science

in

Environmental Systems

by

Susan M. Soltau

Committee in charge:

Professor Stephen C. Hart, Chair
Professor Asmeret Asefaw Berhe
Assistant Professor Benjamin Sullivan

2019

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The Thesis of Susan Marie Soltau is approved, and it is acceptable in quality and form for publication on microfilm and electronically

Asmeret Asefaw Berhe, Ph.D.

Benjamin Sullivan, Ph.D.

Stephen C. Hart, Ph.D.
Committee Chair

University of California, Merced

2019

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CURRICULUM VITAE

2816 Van Tuyl Pl. Modesto, CA 95356
209-202-7224
ssoltau@ucmerced.edu

Education

2016–2019- University of California, Merced

- M.S. Environmental Systems
- Cumulative GPA: 3.3

2009-2014- University of California, Merced

- B.S. Ecological and Evolutionary Biology
- Honors: Dean's List

Research Experience

2016-2018 –Graduate Level Researcher for the Sierra Nevada Research Institute (SNRI), University of California, Merced - *Supervisor: Stephen C. Hart, PhD*

- Coordination with Caltrout and Sierra Foothill Conservancy in GHG emission capture and monitoring project(s) within montane meadow systems in the Mariposa and East Tulare County regions

2012-2013– Research Assistant for the Sierra Nevada Research Institute (SNRI), University of California, Merced - *Supervisor: Andrea Joyce, PhD*

- Partial participation in the etymological behavioral analysis and genetic differentiation for West Nile vector modeling with local corn leaf hopper (*Dalbulus maidis*) and mosquito hybrid (*Culex pipien Culex quinquefasciatus*) species

Presentations

Soltau, S.M., Dove, N.C., Hart, S.C. (Oral) Assessing the Birch Effect within Contrasting Montane Meadows in the Sierra Nevada, SSSA International Soils Meeting – San Diego, CA January 8, 2019

Awards and Fellowships

2018 ES Professional Development Fellowship ($1000)
2018 ES Travel Fellowship ($1000)
2017 Bobcat Travel Fellowship ($1600)
2017 ES Bobcat Fellowship ($1500)

Teaching Experience

2016-18 – Teaching Assistant, School of Natural Sciences, University of California Merced

- 2 semesters teaching ESS 010: Environment in Crisis
- 1 semester teaching BIO 001: Introduction to Biology
- 1 semester teaching ESS/BIO 148: Fundamentals of Ecology

Research Skills

Techniques

- Terrestrial Gas Emission Capture and Analysis
    - In situ gas sampling via static field chambers
- Soil Microbial Biomass Extraction
    - Chloroform fumigation on freshly saturated soil samples
    - K_2SO_4 extraction and filtration
    - Running a Shimadzu TOC-Vcsh with TNM-1 Total Nitrogen Measuring Unit
    - Running a Lachat AE Flow-Injection Autoanalyzer for nitrate and ammonium
- Extracellular Enzymatic Activity
    - Soil slurry method using BAG fluorescence standard for BG, NAG, and AP activity detection
    - Running a Tecan Trading AG Infinite 200 Pro Fluorimeter
- General Soil Meta-Biochemical Analyses
    - Obtaining physical textural data using the "feel test" and the hydrometer method preceded by organic matter removal via 30% hydrogen peroxide
    - Taking in situ soil moisture measurements using a FieldScout TDR meter
- Using a Bruker FTIR spectrometer to differentiate SOM
- Proper Sampling, Preparation, and Archiving of soil samples
- Miscellaneous Biological Analyses
    - Separating and Purifying DNA and RNA samples from assorted mammalian tissues
    - Dissection and compound light microscopy
    - Basic familiarity with the cell staining processes involved with various bacterium

Computer applications

- R – Statistics ▪ Microsoft Excel ▪ Microsoft Word ▪ Microsoft PowerPoint ▪ Adobe Photoshop ▪ Adobe Illustrator

Other Training:

2017-Summer Soils Institute, Colorado State University Fort Collins (2-week course)

- Gained general technical knowledge on in field and in lab collection and analytical methodologies for physical, biological, and chemical soil factors
- Graduate coursework: Fundamentals of Terrestrial Ecology, Statistical Analyses for Environmental Data, and Biogeochemical Factors of Soil Organic Matter

ABSTRACT

Title: Assessing Soil Drying and Rewetting Effects on Greenhouse Gas Emissions Across Contrasting Montane Meadows
Student: Susan Marie Soltau
Degree: Master of Science, Environmental Systems
School: University of California, Merced
Committee Chair: Stephen C. Hart

In pristine montane meadows, soils can sequester more carbon (C) per year than soils from tropical forests. However, many of these meadows have been degraded from overgrazing by domestic livestock, road construction, and other human disturbances, altering their hydrology, and resulting in more frequent soil drying and rewetting (DRW) cycles. Such increased frequency of DRW cycles could lead to reduction in soil C and nitrogen (N) pools via the "Birch Effect," a frequently observed phenomenon where an increase in soil organic matter decomposition (SOM) occurs immediately following the rewetting of dried soils. Using laboratory incubations, we evaluated the potential impact of increased fluctuations in soil water content on greenhouse gas emissions (CO_2, N_2O, CH_4), microbial C and N, salt-extractable organic C and N, rates of net N transformations, potential exoenzyme activities, organic matter functional composition, and reduction-oxidation active metals across two pairs of meadows (undegraded-degraded and restored-unrestored) in the Sierra Nevada, California, USA, with different degrees of degradation. Replicate air-dry soil samples (0-15 cm depth) were subjected to five different water treatments over a 91-d period (including a seven-day preincubation): no water addition (air-dry control), maintained at field capacity, maintained at saturation, maintained at saturation for one-week pre-incubation, allowed to dry for three weeks and then rewetted to saturation (4 cycles), and maintained at saturation for one-week pre-incubation, allowed to dry for one week and then rewetted to saturation (12 cycles). We found that cumulative net CO_2 emission was not increased under the two DRW treatments compared to the continuously saturated condition for any of the four soils assessed. Surprisingly, cumulative net CO_2 emissions were either greater or similar under continuously saturated soil moisture conditions compared to soils maintained at field capacity. Only for the degraded soil was cumulative net N_2O emissions higher under DRW treatments (4 cycle only) than under continuously saturated conditions. There were no significant differences in net CH_4 emissions across all five treatments for any soil. While there was an immediate increase in net CO_2 and N_2O (but not CH_4) emissions following the rewetting of dried soils analogous of the Birch effect (especially in the 4 cycle treatment), there were only relatively minor changes in other soil biochemical processes and pools compared to the consistently saturated soils. Overall, our results were largely consistent with field measurements that suggest the observed decreases in C storage in degraded Sierran meadow soils are due to reductions in C inputs rather than increases in C outputs.

1. INTRODUCTION

In their undisturbed state, montane meadows are ecosystems characterized by the presence of shallow groundwater (< 1 m depth) and the dominance of herbaceous vegetation found in mountainous terrain (Weixelman et al., 2011). Although generally smaller in land area than other ecosystem types, montane meadows contribute disproportionally to a variety of ecosystem services, including soil carbon (C) sequestration (Norton et al., 2011). High rates of C accumulation in these ecosystems is hypothesized to be driven by both low decomposition rates in their high water content, low oxygen soils (Malmer, 1986; Borken and Matzner, 2009), and high rates of net primary productivity that are comparable to tropical forests (De Deyn, et al., 2009; Scurlock and Olson 2013; Arnold et al., 2014; Chang et al., 2015).

About 40-50% of montane meadows within the Sierra Nevada of California, USA can be classified as at risk or in a degraded condition (Castelli et al., 2000; Krueper and Rich, 2003). Major ecological stressors such as overgrazing, fragmentation, and drought have negatively impacted the structure and function of montane meadow ecosystems (Van de Koppel et al., 1997). These stressors reduce vegetation cover, thus destabilizing stream channel banks and increasing erosion, leading to channel head cutting and increasing channel incision (Miller et al., 2001). Channel incision, in turn, disconnects hydrologically the stream from its floodplain, which causes the stream channel to erode even more rapidly (Merrill, 2012). Channel incision also lowers the groundwater table, decreasing meadow soil water contents and increasing the frequency of more severe drying and wetting (DRW) cycles (Ramstead et al., 2012). Such positive feedbacks in meadow degradation has motivated efforts to restore the structure and function of these ecosystems in the Sierra Nevada and elsewhere in order to reestablish their ecosystem services (Ratliff, 1985; Drew et al., 2016).

Both drying and increased frequency of DRW cycles could increase soil organic matter (SOM) loss, leading to reduced soil total C and nitrogen (N) stores. Soil drying increases oxygen availability to heterotrophic microorganisms, increasing SOM decomposition rates due to the greater metabolic activity of aerobic than anaerobic decomposers (Paul and Clark, 1996). Increased occurrence of DRW cycles can also lead to greater SOM degradation, a phenomenon known as the "Birch effect" (Birch and Friend, 1956; Birch, 1958). The Birch effect describes the often-observed immediate and large increase in organic matter decomposition that occurs within a day of rewetting dry soil (Jarvis et al., 2007). This rapid increase in decomposition leads to increases in carbon dioxide (CO_2) emissions from soil, and frequently increased emissions of nitrous oxide (N_2O; Butterbach-Bahl et al., 2013) and increased rates of net N mineralization (Birch, 1958; Borken et al., 2009).

Both biological and physical mechanisms have been proposed for explaining the Birch effect. Hypothesized biological mechanisms include: cell lysis from the water potential up-shock following a DRW event and the subsequent rapid decomposition of these materials by surviving microorganisms; and the rapid decomposition of osmolytes released by soil microorganisms into the soil solution to reduce cell lysis during the wet-up event (Schimel et al., 2007). Studies demonstrating the elimination of the Birch effect following soil sterilization support these biological hypotheses (e.g., Stevenson, 195

Fraser et al., 2016). Physical mechanisms include aggregate destabilization, dissolution of OM, and forced gas displacement from soil pores following the rewetting of dry soil (Bossuyt et al., 2001; Denef et al., 2001; Saetre et al., 2005; Yepez et al., 2005; Kaiser et al., 2015; Homyak et al., 2018). In most soils, both biological and physical mechanisms are likely involved (Casals et al., 2011; Kim et al., 2012).

The magnitude of the CO_2 emission pulse following rewetting appears to depend on the soil water content prior to the wet-up event. For example, Sun et al. (2018) found that the greater the extent of soil drying prior to the rewetting event, the greater the pulse in microbial respiration for a silt loam grassland soil of northern China incubated under laboratory conditions. Lado-Monserrat et al. (2014) found that the magnitude of the wet-up event following drying was linearly related to the increase in soil microbial respiration for clay loam and sandy loam forest soils from Spain incubated in the laboratory. Under field conditions, Almagro et al. (2009) and Unger et al. (2010) also found that the extent of soil CO_2 pulses following rewetting events were greater under more severe than mild drought conditions for Mediterranean ecosystems in Spain and Portugal, respectively. Clearly, the magnitude of change in soil water content has a strong influence on the magnitude of the CO_2 emission pulse from soil following rewetting. (Lado-Monserrat et al. 2014).

In general, aerobic microbial respiration increases in response to increasing soil water content until the limiting effects of substrate diffusion and O_2 supply are equal (Skopp et al., 1990). Because decomposition of SOM under anaerobic conditions occurs at slower rates, this generally leads to a unimodal "hump-backed" response to increases in soil water content, with maximal microbial respiration rates occurring near or slightly wetter than field capacity (Linn and Doran, 1984). However, recent laboratory studies in some montane meadow soils of the Sierra Nevada of California have shown continued increases in net CO_2 emission at soil water contents higher than water saturation (C. Reed, Univ. of Nevada, *unpublished data*). One possible mechanism for continued increases in CO_2 production at these higher soil water contents is the influence of iron (Fe) or other reduction-oxidation (redox) active metals on organic matter decomposition (e.g., "Fe^{III}–Fe^{II} redox wheel;" Li et al., 2012). For instance, Emsens et al. (2016) found high rates of mobilization of Fe, total inorganic C, and dissolved organic C in re-wetted, Fe-rich but not Fe-poor groundwater-fed peatlands (i.e., fens), which they attributed to increased rates of organic matter oxidation to CO_2 via coupled Fe reduction. However, little is known about the importance of such metal-organic matter redox coupling in contributing to net CO_2 production in montane meadows that are not fens.

Pulses in net N_2O emissions following DRW events have also been documented in soils (Butterbach-Bahl et al., 2013). The increase in N_2O emission can result from increased rates of nitrification, denitrification, or both, with the relative importance of nitrification to denitrification processes following a DRW event depending apparently on the degree of anaerobiosis following rewetting (Davidson et al, 2000). In some cases, abiotic processes such as chemodenitrification may also be involved (Butterbach-Bahl et al., 2013). Nitrification, being an aerobic process, likely contributes the most to the net N_2O emission pulse when rewetting does not induce anaerobic conditions, while denitrification likely contributes to the majority of the N_2O pulse when the rewetting event leads to anaerobic conditions, but not prolonged enough to result in the complete

dissimilatory reduction of N_2O to N_2 (Davidson et al., 2000). However, other factors besides the degree of reducing conditions influence the ratio of N_2O to N_2 production via denitrification; both high C availability and a small nitrate pool size appear to promote reduction of N_2O to N_2 (Weier et al., 1993). Indeed, the relative importance of nitrification compared to denitrification in contributing to net N_2O pulses following a rewetting event appears to depend on the soil type (Priemé and Christensen, 2001).

Responses in net CH_4 emissions following DRW events appear more variable than CO_2 or N_2O (Kim et al., 2012). Similar to net N_2O emissions from soil, the net CH_4 flux is the result of the balance between methanogenesis (microbial production under anaerobic conditions during organic matter degradation by methanogenic archaea) and methanotrophy (microbial consumption by methanotrophs metabolizing CH_4 as their source of C and energy). Hence, the response of net CH_4 emissions from soil to DRW events depends on the response of these competing processes to changes in availability of substrates and availability of electron donors and acceptors resulting from the wet-up event, making both the direction and magnitude of the response hard to predict (Kim et al., 2012). For example, in a mesocosm study in a peatland, Dinsmore et al. (2009) found a large increase in net CH_4 emission within 1–2 days following rewetting. In contrast, several studies have reported enhanced CH_4 oxidation (reduced net CH_4 emissions) following rewetting for days to weeks in other peatland soils (Öquist and Sundh, 1998; Kettunen et al., 1999; Goldhammer and Blodau, 2008). An increase in CH_4 oxidation also occurred nine days after rewetting in an alpine meadow soil under laboratory conditions (West and Schmidt, 1998). As concluded in a recent review by Kim et al. (2010), our understanding of the mechanisms responsible for the response of CH_4 emissions to DRW events have not been well elucidated, making prediction of responses across different ecosystems difficult.

We evaluated the impact of DRW cycles on soil pools and processes in two pairs of montane meadows from the Sierra Nevada, California, USA. Most soils assessed previously for a pulse in soil CO_2 emission following rewetting have been from sites where soils are frequently dry and rarely are saturated with water (i.e., Mediterranean-type climates; Xu and Baldocchi, 2004; Rey et al., 2005; Xiang et al., 2008; Inglima et al., 2009). In these studies, the re-wetted state evaluated is generally around field capacity. However, as noted above, montane meadow soils in an undegraded state are generally found in near or under water-saturated conditions (Loheide and Gorelick, 2007). Hence, we used the water-saturated condition in our study to evaluate DRW cycles in these montane meadow soils. We measured greenhouse gas (CO_2, N_2O, and CH_4) emissions that are largely microbial-mediated, as well as changes in other biological activity measurements and soil chemical pools, during an 84-day laboratory incubation that followed a 7-day preincubation period. Four contrasting montane meadow soils were subjected to five treatments: soils maintained at three constant soil water contents (air-dry, field capacity, and saturated) and two DRW treatments (4 or 12 cycles over the incubation period starting from water-saturated conditions). We hypothesized that the greatest cumulative net CO_2 emissions would occur from the 4-cycle treatment, followed by the 12-cycle, field capacity, saturated, and air-dry treatments. We also hypothesized that the highest cumulative net N_2O emissions would occur from the 12-cycle treatment, followed by the 4-cycle, field capacity, saturated, and air-dry treatments.

Cumulative net CH_4 emissions were hypothesized to be greatest in the saturated treatment, followed by the 12-cycle, 4-cycle, field capacity, and air-dry treatments. Periodic measurements of soil microbial C and N, salt-extractable organic C and N pools, rates of net N transformations, potential exoenzyme activities, organic matter functional composition, and reduction-oxidation (redox) active metals were used to help evaluate the mechanisms potentially responsible for the greenhouse gas emissions gas emission patterns observed among treatments. Our overall goal was to help elucidate the potential impact of ecosystem degradation on greenhouse gas emissions from meadow soils in order to evaluate the long-term potential benefit of meadow restoration on net greenhouse gas emissions from these ecosystems.

2. MATERIALS AND METHODS

2.1. Description of Study Sites

Our study sites consisted of two pairs of montane meadows in the Northern Sierra Nevada, California, USA in the Tahoe and Plumas National Forests (Fig. 1). The former consists of both an undegraded and a degraded meadow, while the latter consists of a restored via the "pond-and-plug" (in 1995, 22 years before sampling; Feather River CRM, 1999) and unrestored (in a degraded state) meadow. Loss of native vegetation, increased surface erosion rates, gully formation, and sporadic water runoff patterns are all signs of meadow degradation (Lindquist and Wilcox, 2000). Upper Loney (undegraded) and Deer Meadow (degraded) are located within an elevational range between 1840 and 1900 m above sea level (asl), with soils classified as Borolls and Aquolls derived from andesitic tuff. Vegetation at both sites is dominated by *Carex* and *Juncus* spp. (Table 1; USDA, 2005). Big Flat (restored) and Coyote Flat (unrestored) meadows are located within an elevational range between 1700 and 1740 m asl. Soils are classified as Aquolls and are derived from basalt and mixed alluvium. The restored meadow is dominated by species typical of healthy wet meadow ecosystems (i.e., *Juncus balticus* and *Carex* spp.; Table 1). The unrestored site was dominated by the shrub *Artemisia tridentata* and the drought resistant native grass species *Poa secunda,* and exhibited characteristics indicative of significant erosion along the unvegetated channel banks (Loheide and Gorelick, 2005). The degraded meadow showed moderate signs of head cutting and, along with the unrestored meadow, the soils were air-dry when sampled. The undegraded and restored meadows showed negligible signs of head cutting (i.e., lush vegetation, shallow creek bed, minimal erosion) and the soils were near-saturated when sampled.

2.2. Soil sampling and preparation

We collected soils in late June/early July 2017 from 12 locations within each meadow along an evenly spaced grid (sample points separated by 15 m in the degraded site or separated by 30 m in the other three sites) established near the center of the meadow (to avoid edge effects). A 5-cm diameter AMS slide hammer (American Falls, Idaho, USA) with an acid-washed polycarbonate liner was used to collect the top 15 cm of mineral soil. In the few instances (mainly in the undegraded meadow) where we were unsuccessful in obtaining an intact soil core due to high soil water content, an AMS volumetric soil recovery auger with similar dimensions was used instead. Samples were immediately placed in a cooler containing Blue Ice (~4 °C) until we returned to the laboratory at University of California, Merced that same day. Intact soil cores were stored in a cold room (4 °C) until soil processing (approximately 3 weeks).

In the laboratory, soils were air-dried, sieved (< 2 mm), and composited and homogenized by meadow. Most of the visible roots remaining in the sieved soil were removed by hand, while indurated peds (primarily for the restored meadow soil) were gently crushed with a rolling pin or a hand sledge. The air-dried soils were stored at laboratory temperature (~20 °C) in covered plastic bins for approximately 75 days prior to initiating the laboratory experiment.

2.3. *Experimental design*

We conducted an 84-d incubation experiment (with a seven-day preincubation) consisting of three static (air-dry, field capacity, and saturated moisture contents) and two DRW treatments (i.e., experimental Birch Effect treatments) that differed in DRW frequencies and intensities. The air-dry (AD) soil moisture treatment served as a negative control where microbial activity should be at a minimum. The field capacity (FC) treatment was used to represent the maximum rate of microbial activity and to evaluate the impact of continuous water saturation on soil microbial pools and processes. The water-saturated (SAT) treatment was used as a control to evaluate the impact of DRW cycles on soil microbial pools and processes. In the 4-cycle DRW treatment, soils were allowed to dry down for three weeks in a forced air-oven set at 20 °C (VWR International, 1380 FM, Radnor, PA, USA) prior to rewetting to saturation, for a total of 4 DRW cycles over the course of the incubation. In the 12-cycle DRW treatment, soils were dried down for one week in the same forced-air oven prior to rewetting to saturation, for a total of 12 DRW cycles over the course of the incubation. We based these drying periods on a preliminary study using a similar montane meadow soil with the objective of reducing the soil gravimetric water content to approximately air-dry soil moisture conditions (~few % of saturation) before rewetting in the 4-cycle treatment, and ~50% of saturation before rewetting in the 12-cycle treatment (Fig. 2).

Field capacity and saturation soil water states for the four meadow soils were determined as follows. Sieved soil duplicates (~100 g oven-dry mass equivalent) were saturated with deionized water and mixed into a paste (Rhoades, 1982). The soil gravimetric water content at saturation was then determined from the mass of water added to reach saturation. Saturated soil samples were then adjusted to field capacity by placing them in Büchner funnels with a pre-wetted, Whatman No. 42 filter paper at the bottom, and then applying a 33 kPa vacuum. Field capacity was assumed to have been reached when the soil no longer eluted water in response to the vacuum (Haubensak et al., 2002). The soil gravimetric water content at field capacity was then determined from the loss of water mass from saturation to reach field capacity.

Experimental units consisted of homogenized, sieved soil placed into 20-ml scintillation vials with soil masses based on adding roughly equivalent soil organic matter to each vial (i.e., 8 g air-dry mass for the undegraded site, 12 g for the degraded site, 10 g for the restored site, and 15 g for the unrestored site; Table 1). Air-dry, field capacity, and saturated treatment vials were placed in ~1 L Mason jars and covered with a 0.03 mm thick polyethylene film to limit moisture loss but allowing for gas exchange (Hart et al., 1994). Soil water contents were maintained in the field capacity and saturated treatments by adding 15 ml of water to the bottom of the Mason jars. Experimental units for the DRW treatments were incubated in open Mason jars placed in a forced-air oven to accelerate soil drying. All Mason jars were periodically repositioned within the forced-air oven and in the laboratory to minimize any environmental differences experienced by the different soils and treatments during the incubation. All experimental units were incubated in the dark either under a laboratory bench (static treatments) or inside a forced air oven (DRW treatments) at temperatures of 20 °C ± 2 °C).

The same experimental units were used for gas sampling throughout the experiment. For periodic destructive sampling of experimental units (to estimate extractable C and N pools, fumigated soils for microbial C and N, and soil enzyme potential activities), experimental units to be used for the same analyses were grouped together in the same jar for all sampling dates (up to five; Fig. 2); on each sampling date, one vial was randomly chosen from each jar (see below). All experimental units were preincubated at their experimental moisture state for seven days (DRW treatments were preincubated at saturated conditions). The purpose of this preincubation was to allow for microbial populations to grow and roughly reach steady state conditions representative of that soil moisture state and soil before initiating the DRW treatments (Horwath and Paul, 1994). All experimental units/analyses were replicated in triplicate.

2.4. Greenhouse gas fluxes

We measured CO_2, N_2O, and CH_4 fluxes throughout the incubation on a weekly basis. For static soil moisture treatments, individual experimental units were kept sealed within Mason jars over the weekly measurement periods. On the seventh day of each week, headspace gas was sampled using a needle and syringe fitted with a gas-tight valve through a butyl rubber septum inserted in the Mason jar lid. After headspace gas sampling, Mason jars were flushed for 30 seconds with ambient air and then resealed. On the sampling dates that the DRW treatments were to be rewetted (i.e., every third week for the 4-cycle treatment and every week for the 12-cycle treatment), the Mason jars containing the experimental units for those treatments were sealed immediately prior to the wet-up event (on the sixth day of the week), and the headspace was sampled after one day. Then, the Mason jars were flushed with ambient air, the soils were rewetted to saturation, and the Mason jars were then resealed for another day. Headspace samples were again collected, and the jars were flushed with ambient air and then returned to the forced-air oven. On sampling dates where the 4-cycle treatment was not to be rewetted, headspace samples were collected on the seventh day only and flushed with ambient air before returning them to the forced-air oven. Headspace samples were then analyzed for CO_2, N_2O, and CH_4 by gas chromatography using a Shimadzu GC-2014 gas chromatograph equipped with a thermal conductivity, electron capture, and flame ionization detectors, respectively (Shimadzu Corporation, Columbia, MD, USA). Daily greenhouse gas fluxes were calculated from changes in headspace gas concentrations over time using the ideal gas law. Cumulative gas fluxes for the static treatments were calculated simply from the integration of these rates over the course of the incubation period. For the DRW treatments, cumulative greenhouse gas fluxes during periods when the jars were drying (i.e., open) were estimated by taking the average daily gas fluxes of the two sequential weekly measurements and multiplying that value by the intervening days.

2.5. *Potential soil exoenzyme activity*

We measured potential soil extracellular enzyme activity of β-glucosidase (BG), N-acetylglucosaminidase (NAG), and alkaline phosphatase (AP) using the "soil slurry" method with 4-methylumbelliferone (MUB)-linked substrates (Bell et al, 2013). These measurements were made at the end of the preincubation period (sampling date 1), after the third week of incubation (sampling date 2, after the first re-wetting of the 4-cycle DRW treatment), and at the end of the 84-d incubation (sampling date 5; Fig. 2). For sampling dates 2 and 5, measurements were taken both before and after wet-up. Briefly, an 800 µl soil slurry consisting of 1 g fresh-weight soil (at the water content of that treatment) in 84 ml of 50 mM sodium acetate buffer (pH = 5.5) was incubated with 200 µl of each of the 100 µM 4-methylumbelliferone (MUB)-linked substrates. After a 3-h incubation at 20 °C, samples were centrifuged at 3000 rpm for 3 minutes and supernatant was transferred to a black, flat-well plates. Fluorescence was measured on a Fluorimeter (Tecan Trading AG, Infinite 200 Pro, Switzerland) using excitation wavelength of 365 nm and emission of 450 nm.

2.6. *Microbial biomass and inorganic N pools*

We measured microbial biomass C and N using a modified chloroform fumigation extraction procedure (Vance et al., 1987; Haubensak et al., 2002) at the end of the preincubation period (sampling date 1), after the first re-wetting of the 4-cycle DRW (sampling date 2,), and at the end of the 84-d incubation (sampling date 5; Fig. 2). Briefly, a pair of vials was removed from each treatment (one from a jar containing the vials that served as the unfumigated controls for that treatment and one from a jar containing the samples to be fumigated) in triplicate. The unfumigated control soils were immediately extracted with 50 mL of 0.5 M K_2SO_4 solution, shaken for 1 h on a reciprocating shaker, and filtered through Whatman #1 filter paper. The other paired vial was brought up to saturation with deionized water (to control for the effect of soil moisture on the efficacy of fumigation; Haubensak et al., 2002) and incubated in a chloroform-filled desiccator for seven days. We used a longer fumigation period to account for the lower diffusion rate of $CHCl_3$ through water-filled than through air-filled pores (Lee et al., 2016). We realize that the efficiency of fumigation in these water-saturated soils may be lower than under unsaturated conditions (Lee et al., 2016; but see Oren et al., 2018), but we fumigated all soils at the same soil water content (saturated) regardless of treatment so that inter-treatment comparisons of microbial C and N within a given soil should be valid. After fumigation, the fumigant was removed using repeated evacuations with ambient air, and samples were then extracted with 50 ml of 0.5 M K_2SO_4, shaken, and filtered as with the unfumigated samples. Filtrates were analyzed for total C and N by catalytic combustion oxidation coupled to non-dispersive infrared (C) and chemiluminescence (N) detectors (Shimadzu TOC-Vcsh with TNM-1 Total Nitrogen Measuring Unit, Kyoto, Japan). No carbonates were present in the soils used in this study (see pH values in Table 1), so total C was assumed to equal organic C. Microbial C was calculated from the total C flush (fumigated C – unfumigated C) divided by the extraction efficiency factor (k_{EC}) of 0.45 (Beck et al., 1997), while microbial was calculated form

the total N flush divided by the extraction efficiency factor (k_{EN}) of 0.69 (Brookes et al., 1985).

We also measured inorganic N pools in the unfumigated extracts to estimate net N mineralization and nitrification across the treatments. These inorganic N analyses were conducted on experimental units destructively sampled on all 5 sampling dates (Fig. 2). Filtrates were analyzed for ammonium (NH_4^+; Lachat Method 12-107-06-1-B) and nitrate (NO_3^-; Lachat Method 10-107-04-1-A) colorimetrically using a Lachat AE Flow-Injection Autoanalyzer (Lachat Instruments, Inc., Milwaukee, WI, USA). The net N mineralization rate was calculated as the net change in the inorganic N pool over the 84-d incubation period; similarly, the net nitrification rate was calculated as the net change in the NO_3^--N pool over this same period (Hart et al., 1994).

2.7. Soil physiochemical measurements

Soil texture was measured using the hydrometer method on duplicates of the initial sieved, air-dry soils, following a three-day 30% hydrogen peroxide wash to remove most of the organic matter (Gee and Or, 2002). Soil pH was measured on initial soil duplicates using an Orion Dual Star benchtop pH meter (Thermo Scientific, Waltham, MA, USA). Measurements were conducted on the supernatant of 10 g air-dry mass to 50 ml of solution using both DI water and 0.01 M $CaCl_2$ after allowing 30 minutes for equilibration following mixing (McLean, 1982). Subsamples from the initial and post-incubation soils (from gas flux measurement vials) were ground to a fine powder with a mortar and pestle and analyzed for total carbon and nitrogen concentrations, and ^{13}C and ^{15}N isotopic ratios (‰) using an elemental analyzer (Costech Analytical, ECS 4010, Italy) coupled to a ThermoFisher Delta V Plus Isotope Ratio Mass Spectrometer (Waltham, MA, USA) at the Stable Isotope Laboratory, University of California, Merced (https://research.ucmerced.edu/core-facilities/stable-isotope-laboratory).

To elucidate possible changes in soil organic matter composition following incubation, initial and treated soils at the end of the incubation period (except the air-dry treatment soils) were analyzed in triplicate using Diffuse Reflectance Infrared Fourier Transform (DRIFT) spectroscopy (Bruker IFS 66vS, Germany). Samples were ground to a fine powder with mortar and pestle, oven dried (105 °C) overnight, and ran at a 6 mm aperture and 100 scans. Potassium bromide (KBr) was used as a background spectrum because it does not exhibit any absorption at the wave number range of 4000 to 400 cm^{-1}. (Parikh et al., 2014). We observed peak heights at Band A and B (2856 ± 20 cm^{-1} to 2928 ± 20 cm^{-1} for A and 1625 ± 20 cm^{-1} for B). In order to relate the C=C stretch (aromatic C group; Band B) with the C-H stretch (aliphatic C group; Band A), we took the B/A ratio normalized to % soil C and compared the resulting values between treated and pre-incubation soils (Kaiser et al., 2014).

2.8 DTPA-extractable metals

Iron (Fe), manganese (Mn), copper (Cu), and Zinc (Zn) were extracted from the constantly saturated and DRW treatment soils following the procedures of Olson and Ellis (1994). These measurements were made after the first three rewetting events of the 4-cycle DRW (sampling dates 2-4) and at the end of the 84-d incubation (sampling date 5; Fig. 2). Twenty mL of Diethylenetriamine Pentaacetic Acid (DTPA) reagent (consisting of 0.005 M DTPA, 0.1 M triethanolamine, and 0.013 M $CaCl_2$) were added to 10 g fresh-weight soil taken from the same experimental units designated for soil enzymes. They were than mixed on a reciprocating shaker for 2 h, centrifuged at 4000 rpm for 3 minutes, and then filtered through Whatman #40 filter paper. The extracts were kept frozen until analysis. Thawed samples were diluted 1:1 with 1% nitric acid and analyzed on an inductively coupled plasma optical emission spectroscopy (ICP-OES; Perkins-Elmer Optima 5300dv, United States).

2.9. Statistical analyses

Prior to running the necessary statistical analyses, all data was converted to an oven-dry soil weight basis. Data were than analyzed for each meadow separately (due to lack of true site replication) using R and the following packages: *dunn.test* (includes the function for the Dunn's Test), and *car* (includes the function for the Levene's Test), and *lsmeans* (includes the function for obtaining least square means and contrasts; Lenth, 2016; Dinno, 2017; Fox and Weisberg, 2019; R Development Core Team 2019). Significance level for all analyses was set priori at $\alpha = 0.05$.

To confirm if a Birch effect occurred (i.e., a statistically significant increase in net gas efflux rate relative to the rate before the wet-up event), a paired t-test was conducted on the pre and post wet-up CO_2, N_2O, and CH_4 fluxes for the DRW soils across all sampling dates. If the t-tests were significant, we followed up for each DRW treatment with a one-way Analysis of Variance (ANOVA) with sampling date as the factor to determine if the magnitude of the efflux pulse changed over time (Montgomery, 2000). Similarly, a paired t-test was used on soil potential exoenzyme activity to determine if there was a significant wet-up effect at both the second and fifth sampling dates (Fig. 2). Again, if the t-tests were significant, we followed up for each DRW treatment with a one-way ANOVA with sampling date as the factor to determine if the magnitude of the wet-up effect on soil exoenzyme activity changed over time.

In order to determine if the response variables were affected by the different SWC conditions, a one-way ANOVA with treatment as the factor was used on net cumulative CO_2, N_2O, and CH_4 emissions, net changes in microbial C and N, and net N transformation rates. If the ANOVA was significant, Sidak adjusted planned contrasts were used to compare mean differences within only the static treatments (AD, FC, and SAT) and within only the DRW (4 and 12 cycle) and SAT treatments.

To establish if there were physiochemical changes between our initial soils and those following the 84-d incubation study, a one-way ANOVA with treatment as the factor was used on total C and N and DRIFT derived B/A ratios. If the ANOVA was

significant, a Sidak adjusted pairwise comparison was run on all treatments using Tukey's Honestly Significant Difference. We used a two-way ANOVA model across the saturated and DRW treatments to evaluate treatment, sampling date, and treatment by sampling date interactions for DTPA-extractable metals.

Normality was checked using both the Shapiro-Wilk test and Q-Q plots. To assess equality in variance, we used the Levene's test. If assumptions were not met, data were transformed using the natural logarithm and reanalyzed. Net Cumulative N_2O across all sites, BG and AP activity within the unrestored site, and NAG activity across all except for the undegraded required transformation using the natural logarithm. Net microbial C within the degraded site, net microbial N within the undegraded site, and net nitrification within the unrestored site required transformation using the natural logarithm after adding 1000 as a constant. If the transformed data still failed to pass the aforementioned tests (Shapiro-Wilk and Levene's) and the residuals continued to show a non-normal distribution on the Q-Q plot, then non-parametric alternatives were used. These included the Krustal-Wallis test by ranks (a non-parametric approach to a one-way ANOVA). If the Krustal-Wallis test was significant, the Dunn's test was used (the post hoc analysis after rank sums for multiple comparisons) on all treatments.

3. RESULTS

3.1 Greenhouse Gas Fluxes

Based on paired t-tests, there were significant differences between the pre and post wet up CO_2 fluxes across all soils ($p < 0.001$) within the 4-cycle DRW treatment. With one exception, substantial increases in net CO_2 emissions occurred during the 1-day period following wet-up relative to the pre-wet-up rates, which were generally close to zero (Fig. 3-6). The exception occurred in the degraded soil during the 4th sampling date (63 days into the incubation) where the DRW pulse in CO_2 appeared to be delayed (i.e., increased net CO_2 emission occurred during gas sampling the following week in the drying phase; Fig. 4). For the undegraded, degraded, and unrestored soils, there was a decrease in the magnitude of the post wet-up CO_2 pulse over time, before increasing at the end of the incubation to rates comparable to those found at the end of the preincubation period (ANOVA: $p = 0.016$, undegraded; $p = 0.024$, degraded; and $p = 0.023$, unrestored). In the restored soil, the magnitude of elevated CO_2 emission post wet-up was similar throughout the incubation; furthermore, elevated CO2 emissions appeared to continue for a week after the second and third DRW cycles (Fig. 5).

For the 12-cycle treatment, there were significant or marginally significant ($p = 0.050$ - 0.100) increases in CO_2 emissions post wet-up across all soils based on paired t-tests ($p = 0.002$, undegraded; $p = 0.014$, degraded; $p = 0.089$, restored; and $p < 0.001$, unrestored). The magnitude of the post wet-up CO_2 pulse changed significantly over time for all soils (ANOVA: $p = 0.001$, undegraded; $p = 0.027$, degraded; $p <0.001$, restored; and $p =0.004$; unrestored). Carbon dioxide pulses were up to ~20,000% higher after wetting in the 4 cycle soils compared to the 12 cycle where CO_2 pulses were up to ~500% higher after wetting.

There were significant differences between pre and post wet up N_2O fluxes across all sites for the 4 cycle treatment ($p <0.001$). Similarly, to CO_2, the occurrence of N_2O pulse spikes coincided consistently with the wet up taking place 24-h prior where pre wet up rates were close to zero (Fig. 3-6). While the size of the post wet up N_2O pulse changed over time ($p = 0.016$ (undegraded), $p = 0.024$ (degraded), $p = 0.038$ (restored), and $p = 0.016$ (unrestored), the pattern was more inconsistent than CO_2. For example, in the undegraded site, the post wet up N_2O pulse peaked at ~2500 $\mu g\ N\ kg^{-1}\ d^{-1}$ at 21-d, ~1800 $\mu g\ N\ kg^{-1}\ d^{-1}$ at 42-d, and ~3000 $\mu g\ N\ kg^{-1}\ d^{-1}$ at 63-d (Fig. 3). Except for the degraded site, there were significant differences between pre and post wet up N_2O fluxes in the 12 cycling treatment ($p < 0.001$). Similar to CO_2, the pulse spikes in N_2O appeared to only coincide with the wet up taking place 24-h prior for the first 30-d. After which, elevated rates following the wet up of dried soils were no longer statistically detectable (Fig. 3-6). Nitrous oxide pulses were up to ~350,000% higher after wetting in the 4 cycle soils compared to the 12 cycle where N_2O pulses were up to ~50,000% higher after wetting. There were no significant post wet-up pulses for CH_4 for both DRW treatments across all our sites.

3.2 Cumulative Greenhouse Gas Production

For net cumulative CO_2, over the 84 day incubation there was a significant difference between the DRW and SAT treatments within the degraded and unrestored sites following the preincubation period ($p < 0.001$ (undegraded, degraded, and restored),

p = 0.031 (unrestored; different only between the 4 cycle and SAT); Table 2). In the degraded site, total CO_2 production was less in the 4 and 12 cycle treatments than the SAT treatment (~45% and ~40% less, respectively). In the unrestored site, total CO_2 production was ~37% less in the 4 cycle than the SAT treatment. In the same site, total CO_2 production was significantly greater in the 12 cycle than the 4 cycle treatment (~180% greater). There was a significant difference in cumulative CO_2 between the static treatments within the undegraded and degraded sites (Table 2). In the case of the restored and unrestored pair, there was no significant difference between the FC and SAT treatments. Within the undegraded and degraded sites, total CO_2 production in the FC treatment was ~19% and 47% less, respectively, than the SAT treatment. Total net CO_2 production within the AD treatments always remained ~30,000% (unrestored) to ~50,000% (restored) lower than the SAT treatment (Table 2).

There was only a significant difference in net cumulative N_2O between the DRW and SAT treatments within the degraded site following the preincubation period (p = 0.005; different only between the 4 cycle and SAT treatments; Table 2). There was a significant difference in cumulative N_2O between the AD and the SAT treatments within all except for the unrestored site (also different between the AD and FC treatments within the restored site; Table 2). In the degraded site total N_2O production was ~92% less in the FC than SAT treatments. Total net CO_2 production within the AD treatments always remained ~140% (unrestored) to 65,000% (undegraded) lower than the SAT treatment (Table 2).

There were no significant differences in net cumulative CH_4 flux among the DRW and SAT or the static treatments across all sites (Table 2). There is also high variability among replicates compared to other greenhouse gases measured. Total CH_4 production was only large in a single replicate (n=3) in the SAT treatment within the restored site (~9832 μg C kg^{-1}; Table 2)

3.3 Exoenzyme Activity

For the 4 cycle treatments, based on the paired t-tests, there were significant differences between pre and post wet up BG activity, within the undegraded and unrestored sites (p = 0.019 and p = 0.037, respectively). With exception of the undegraded site, it appeared that there was an increase in BG activity at 21 and 84-d following wet up 24-h prior across all sites (Fig. 7). In the undegraded site, BG activity there was a decrease in BG activity after rewetting at both sampling dates (Fig. 7). The size of the post wet up change in BG activity was only significantly different over time for the undegraded site (p = 0.039). The post wet up BG activity decreased at a slightly greater degree at 84-d than at 21-d; Fig. 7). For the 12 cycle treatments, there were significant differences between pre and post wet up BG activity for the undegraded and degraded sites (p = 0.048 and p = 0.016, respectively). The magnitude of the post wet up change in BG activity did not change significantly over time in the soils from these two sites. Though, BG activity decreased following wetting in the undegraded site and increased at 21-d only in the degraded site (decreased at 84-d; Fig. 7).

There were no significant differences between pre and post wet up NAG activity across all sites for the 4 cycle treatment. There were significant differences between pre and post wet up

NAG activity within the degraded and restored sites for the 12 cycle treatment ($p = 0.038$ and $p = 0.025$ respectively). The size of the post wet up change in NAG activity did not significantly change over time in these soils. Though, NAG activity appeared to increase at 21-d within the restored site (high variability in replicates; Fig. 7).

For AP activity, there was only a significant difference between pre and post wet up activity within the undegraded site for the 4 cycling treatment ($p = 0.0019$). There was a slightly larger degree of AP activity increase following rewetting at 84-d than there was at 21-d (higher variability in the replicates at the earlier date; Fig. 7). There were no significant differences between pre and post wet up AP activity for the 12 cycle across all sites.

3.4 *Unfumigated EOC and EON*

Net extractable organic carbon (EOC) over the 84-d incubation between the DRW and SAT treatments was only significantly different within the undegraded site following the preincubation period ($p = 0.0027$ (4 vs. SAT), and $p = 0.020$ (12 vs. SAT)). The EOC pool remained relatively unchanged over time in the DRW and SAT treatments (Fig 8). Net extractable organic nitrogen (EON) over the 84-d incubation between the DRW and SAT treatments was only significantly different within the degraded site following the preincubation period ($p < 0.001$). Within the restored site, the EON pool in the 4 cycle treatment was reduced to zero at 21-d before increasing to ~25 mg N kg^{-1} at 84-d. There was an almost complete depletion of the EON pool in all except for the AD treatment at 21-d within the undegraded site and a depletion in EON in the SAT treatment at 84-d within the degraded site (Fig. 8).

There was only a significant difference in net EOC between the AD and the other static treatments within the undegraded and restored site (also different between the FC and SAT treatments within only undegraded site; $p = 0.009$). There was a significant difference in net EON between the AD and SAT treatments in all except for the restored site (also different between FC and SAT within the degraded site).

3.5 Microbial C and N

There were no significant differences in net microbial C over the 84-d incubation between the DRW and SAT treatments across all sites following the preincubation period (Table 3). The net change in microbial C ranged from approximately -340 to -480 mg C kg^{-1} (undegraded), 14 to -208 mg C kg^{-1} (degraded), 71 to -414 mg C kg^{-1} OD (restored), and -55 to -102 mg C kg^{-1} (unrestored; Table 3). There were no significant differences in net microbial N over the 84-d incubation between the DRW and SAT treatments across all sites following the preincubation period (Table 3). Similar to microbial C, microbial N decreased over time in the DRW and SAT treatments especially between 0 and 21-d (Fig. S1). The net change in microbial N ranged from approximately -15 to -112 mg N kg^{-1} (undegraded), -6 to -54 mg N kg^{-1} (degraded), -14 to -181 mg N kg^{-1} (restored), and -4 to -31 mg N kg^{-1} (unrestored; Table 3).

There were only significant differences in the net microbial C between AD and the other static treatments within the degraded and restored site (only significantly different between the AD and SAT treatment within the degraded site; $p = 0.011$; Table

3). In both the degraded and restored sites, there was a net increase in microbial C pools in the AD treatment, while there was a net decrease in microbial C pools in the FC treatment (Fig. S1). The greatest decrease in microbial C within the static treatments occurred in the AD treatment within the undegraded site (Table 3). For the net change in microbial N over the 84-d incubation, there was only a significant difference between the AD and FC treatments within the unrestored site ($p = 0.013$; Table 3). Across all sites, the net decrease in microbial N in the AD treatments was minimal compared to all other treatments (Table 3).

3.6 N Transformations

Net N mineralization over the 84-d incubation was significantly different between the DRW and SAT treatments within the undegraded and restored sites (only marginally different between the 4 cycle and SAT treatments within the restored site; $p = 0.049$; Table 3). In both the undegraded and restored sites, net N mineralization occurred in both DRW treatments, while net N immobilization occurred in the SAT treatment (negative N mineralization; Fig S2). There were significant differences in net nitrification over the 84-d incubation between the DRW and SAT treatments within the undegraded and restored sites (different only between the 4 cycle and SAT treatments within the restored site; $p = 0.028$; Table 3). In both the undegraded and restored sites, net nitrification in the DRW treatments was greater than in the SAT treatment (~900% higher (undegraded) and ~ 470% higher (restored for 4 cycle v. SAT only); Table 3).

There were significant differences in net N mineralization between the AD and other static treatments in all sites except for the restored site (different only between the AD and FC treatments within the undegraded site; $p < 0.001$ Table 3). Across all sites, net N mineralization was highest in the FC than any other static treatment (Table 3) while it remained relatively low in the AD treatment (~7.2 mg N kg^{-1} or below). Similar to the net N mineralization, there were significant differences in net nitrification over the 84-d incubation between the AD and other static treatments in all except for the restored site (different only between the AD and FC treatments within the undegraded site; $p < 0.001$; Table 3). Across all sites, net nitrification was highest in the FC than any other static treatment (Table 3).

3.7 SOM Dynamics

For total soil carbon (TC), the undegraded site had the largest initial pool size (143 g C kg^{-1}), while the unrestored site had the smallest initial pool size and (38.5 g C kg^{-1}; Table 4). There were only significant differences in TC between initial and DRW soils (after 84-d) within the restored site. In the undegraded site, the initial C pool decreased by ~9% within the SAT treatment over the incubation (Table 4). In the restored site, the initial C pool decreased by ~11% within the DRW treatment over the incubation (Table 4). There was only a significant difference in TN between the initial and SAT soils (~6% decrease) within the undegraded soils. Unexpectedly, there was a slight, but statistically significant increase in TN between initial and 12 cycle soils within the unrestored soils (Table 4).

There was only a significant decrease in ^{13}C from initial to the 12 cycle soils within the unrestored site. Within the degraded site, there was a decrease in ^{13}C between initial and SAT treatments. There was an increase in ^{13}C between these same treatments within the restored site. For ^{15}N, there was a significant increase between initial and 12 cycle treatments within the undegraded and the unrestored sites (Table 4). Otherwise, isotopic ratios for ^{13}C and ^{15}N remained unchanged over the course of the 84-d incubation.

For the DRIFT derived ratio in absorbance of aromatic to aliphatic groups (B/A ratio; Fig. S3), we expected it to increase over the course of the incubation for all treatments as labile C substrates gets taken up by surrounding microbial communities. Except for the degraded site, there were significant increases from initial to the 12-cycle treatments across sites (Fig. 9). The largest increase in the B/A ratio occurred between the initial and 4-cycle soils within the unrestored site. The B/A ratio appeared greater across all treatments within the degraded compared to the undegraded sites, and the unrestored compared to the restored sites suggesting greater proportion in aromatics (higher B/A ratios; Fig 9).

3.8 Fe, Mn, Cu, and Zn Pools

Iron (Fe) pool sizes ranged from 89.7 mg kg^{-1} (unrestored) to 584 mg kg^{-1} (undegraded) across the DRW and SAT treatments over time (Table S1). There were higher Fe concentrations in the sites that exhibited the largest CO_2 and N_2O pulses after rewetting (i.e. undegraded). However, there were no significant differences in Fe pools between the DRW and SAT treatments. Unlike iron, the manganese (Mn) pools were largest within the degraded site, (up to 54.6 mg kg^{-1}; Table S1). There were significant treatment effects on Mn pools within the undegraded and restored sites (Table S1). Manganese pools were significantly higher in the 12 cycle than the SAT within these soils (Table S1). There was only a significant decrease in Mn pool size between 21 and 63-d in the SAT treatment within the unrestored site (Table S1).

For the copper (Cu) pools, sizes ranged from 0.83 mg kg^{-1} (degraded) to 4.67 mg kg^{-1} (undegraded) across the DRW and SAT treatments over time (Table S1). There was only a significant interaction effect (sampling date and treatment) on pool size within the undegraded site (Table S1). Copper pool sizes were significantly higher in both DRW than SAT treatments within the restored site. There also appeared to be a net decrease in Cu pool size over time in the 4 cycle treatment within the unrestored site (change not statistically significant; Fig S4). For zinc (Zn) pools, sizes ranged from 0.52 mg kg^{-1} (degraded) to 11.5 mg kg^{-1} (undegraded) across the DRW and SAT treatments over time (Table S1). There were significant treatment effects on Zn pool size within all minus the degraded site. Zinc pool sizes were significantly higher in the both DRW than SAT treatments within the undegraded and restored sites (Table S1). There was a significantly large increase in Zn pools over time in the SAT treatment within the undegraded site (Fig. S4).

4 DISCUSSION

4.1 Evaluating Greenhouse Gas Emissions Following Rewetting of Dried Soils

As has been observed in many other soil types (Kim et al., 2012), we found a significant increase in net CO_2 and N_2O, evolution following DRW across all montane meadow soils evaluated. The elevated CO_2 and N_2O efflux took place within a 24-h period after rewetting. Though the pattern in these pulses was inconsistent for N_2O while CO_2 pulses decreased in size for most of the incubation until they increased at 84-d (Fig. 3-6). For the degraded site, the CO_2 pulse did not occur a day following the third wetting of the dried 4 cycling soils but was found a week later (Fig. 4). Despite the prolonged drier moisture conditions that were present in this treatment, rewetting did not force a larger die off in microbial communities than what we observed within our wetter 12 cycling soils. This suggests that the imbalance in the number of surviving microbes to surrounding substrates was unlikely the reason for this lag especially seeing that respiration increased a day after the fourth wet up period at 84-d even though the microbial biomass continued to decline (Lado-Monserrat et al., 2014; Fig. 4). The frequency of wet up events also affected the magnitude of CO_2 and N_2O pulse following rewetting. More frequent DRW cycles resulted in smaller pulses of CO_2 and N_2O than those observed within soils undergoing more infrequent DRW cycles. These results were consistent with previous studies that observed gas fluxes in real time on soils at different SWC prior to wetting (Unger et al., 2010). The pulses occurring in the more frequent DRW soils also became undetectable after the first 30-40 days, suggesting that microbial tolerance to these cycling conditions increased with time (Evan and Wallenstein, 2012; 2014).

We expected the bulk of the elevated post wet up CO_2 efflux to stabilize to background levels after 1-d (Jarvis et al., 2007), but this was not the case within the restored soils where the elevated flux rates continued for a week after rewetting before stabilizing (Fig. 5). The rates also appeared to peak at about half of those noted at the end of the 1-week preincubation period. This contrasted with the other three sites whose CO_2 pulses matched closely to those initial rates following wet up. The spatial arrangement of substrates, exoenzyme, and microbial pools coupled with an increased drought tolerance in those more active microbial communities may have limited respiration and or allowed it to persist for longer (Berard, et al., 2011; Fierer, et al., 2003; Stoyan et al., 2000; Xiang et al., 2008). Secondly, inundated soil peds that were present in the drying cycling soils could have barred access to available C substrates until disintegration of aggregates by water penetration (Van Veen and Kuikman, 1990).

Despite the elevated CO_2 and N_2O fluxes after wetting, there were no differences in cumulative gas production among the DRW and saturated soils within the majority of our soils. It was only within the degraded soil maintained at saturated resulted in greater cumulative CO_2. While SOM decomposition is indicated by increased CO_2, it can also be indicated by an increase in N mineralization, which was not the case here in comparison to every other treatment (Weintraub and Schimel, 2003). The chemical nature of "younger" SOM would be more abundant in labile N, which enables high rates of N mineralization (Oik et al., 2006). A more degraded system should possess "older" SOM

as the more labile material gets broken down leaving behind more recalcitrant SOM. This idea was reflected in the DRIFT derived B/A ratio data showing greater aromaticity in the degraded site compared to its undegraded counterpart (Fig. 9). However, in our more degraded sites, nitrates were also still present within these saturated soils suggesting that conditions were not completely anaerobic (Table 3). If these saturated conditions were not reduced enough to affect the redox state of the metals, they may still impact CO_2 production within the degraded site. Though these metals still require DRW conditions to become alternating electron acceptors in the absence of oxygen (Stumm and Sulzberger, 1992; Weber et al., 2006). Considering there was no significant change in extractable total metals over time to support our original hypothesis regarding them aiding in the oxidation of SOM under more anaerobic conditions, it is unlikely that they had an effect on cumulative CO_2. in our soils. It is also in only the degraded site where there was greater N_2O production within the DRW soils than those maintained at saturation. Nitrifying and denitrifying bacteria seem to be well adapted to surviving extreme drought conditions and become active within minutes of a wetting event (Davidson, 1992).

Methane production was unaffected by soil rewetting and remained low during the 84-d incubation. We expected the generation of methane to occur under anaerobic soils as long as CO_2, was the dominant electron acceptor resulting in the reduction of CO_2 to CH_4 (Villano et al., 2010). However, this was not the case as the saturated soils among our sites did not produce significantly more CH_4 than any other treatment. This and the presence of NO_3^- for the duration of the incubation further indicated aerobic conditions persisted in the saturated soils. In order to minimize disturbances to the soil structure following mixing, samples were rarely stirred upon addition of water. Similar to what we would expect to find with a rain event, water percolating down from the soil surface should still leave air filled microsites for a while. There is also a possibility that later in the study, the top of the water table existed slightly below the soil's surface. Both of these instances will result in the presence of aerobic zones in the soil and if pertinent methanotrophic species are inhabiting these areas, they may oxidize the CH_4 being generated from the water-filled and more anaerobic areas into CO_2 (Ball et al., 1997, Knorr et al., 2008). This may further explain the CO_2 production observed across the saturated treatments for our sites.

4.2 Assessing Possible Mechanisms for the "Birch Effect"

Because the Birch effect is driven at least partially by biological processes, an increase in exoenzyme activity after wetting of the both DRW treatments was predicted to occur as both exoenzymes and cellular metabolism play a role in the decomposition of SOM (Blankinship et al., 2014). However, it was only within the unrestored site for the 4-cycle treatment where there was an increase in the C degrading enzyme (BG; Fig. 7). In the same treatment within the undegraded site, BG activity decreased at 21 and 84-d after rewetting. While water-logging can affect enzyme activity, its effects are only really apparent on soils that are allowed to remain at waterlogged conditions where aerobic treatments can decrease activity especially in soils that are typically saturated to begin with (Xiao-Chang and Qin, 2006). Lower to nil detected activity within the other

sites for the 4-cycle treatment could have resulted from a decrease enzyme production from the longer drying periods than those occurring in soils subjected to the 12-cycle treatment. The osmotic stresses introduced in the 4 cycle treatment can force microbial communities to focus on intercellular maintenance and production of osmolytes in order to prevent plasmolysis in more air-dried soils (Schimel et al., 2007). The lack of microbial investment to replenish these pools could also be representative of a lower C demand in the soils undergoing more frequent wet-up events especially as there is a high microbial C to N mass ratio present within the undegraded site (Allison and Vitousek, 2005). However, even with slower production and the possibility that not all enzymes in the pool activate during a wet-up event, the pool size can continue to increase during the drier period and activity can become detectable at a later wetting period (Steinweg et al., 2013). This would possibly explain why there was a detectable increase in the N-acquiring (NAG) enzyme activity at 84-d following a decrease or no change in activity at 21-d (specifically within the degraded and unrestored sites; Fig. 7).

While the net change in C and N over the incubation remained unaffected by soil water content treatments, the net change in microbial C and N was more limited (30-40% decline) in the degraded and unrestored sites compared to the 60-70% decline in the undegraded and restored site. Microbial communities in the former pair could be responding to the water deficits that matched their historical regime either through the accumulation of osmolytes or the re-allocation of C to the cell membrane (Kakumanu et al., 2013; Schimel et al., 2007). Extractable organic carbon (EOC) and nitrogen (EON) have been analyzed in the past (i.e., Xiang et al., 2008) as a potential substrate for the Birch effect. However, in our study, EOC remained relatively the same over the 84-d study. There was a depletion in EON in the DRW soils within the undegraded site (Fig. 8). This depletion in EON at 21-d might explain the N_2O pulses following rewetting within the 12 cycling soils as pulses stopped occurring shortly after this time point in the incubation. Though pulses in N_2O continued to occur within the 4-cycle treatment soils suggesting that EON may be a more prominent source for the Birch effect under wetter cycling conditions.

Inorganic N pools in our soils were mainly dominated by NO_3^- throughout the 84-day incubation, apparently because NH_4^+ was being nitrified to NO_3^-. Nitrification appeared to occur at faster rates than denitrification as the NO_3^- pools steadily grew throughout the laboratory study especially under DRW and our more aerobic controls as per our prediction (Fig 8). Net nitrification only decreased over time within the undegraded site where N immobilization also occurred in the saturated soils specifically within the undegraded site (indicative by the negative mineralization rate; Table 3). This could be due to the high C:N ratio present in the microbial biomass leading to a N deficiency in the surrounding soil (Biagodatsky and Richter, 1998). Though exact quantification of N_2O produced by denitrification was impossible due to lack of gaseous nitrogen (N_2) collection especially under the most reduced soil conditions (Galloway et al., 2004).

Even within soils with low SOM (i.e., degraded and unrestored sites), the 84-d incubation had only minor effects on the soil total C and N. This suggests that the biological process we observed were not limited by the SOM pool size. The incubation did however increase the aromaticity of SOM (increase in B/A) except for soils within

the degraded site. This is indicative of the utilization of high C quality substrates in the form of aliphatic C. Though the DRW treatments did not significantly alter this pattern over the study period. Soils in a more degraded state tended to have higher aromaticity relative to aliphatic C, supporting the identification of these soils as degraded. In general, like previous studies, it seems apparent that DRW cycles does not have a large effect on the decomposition of native SOM (i.e., Magrid, et al., 1999).

4.3 Implications for Montane Meadow Restoration and GHG Mitigation

There is currently great interest in wet meadow restoration. Because meadows perform a wide array of ecosystem and hydrological benefits, manipulations of stream channels have been considered in order to resurrect floodplain function (Ramstead et al., 2012). For example, the “pond-and-plug” method was implemented in our restored study site of Big Flat over 20 years ago. This large-scale approach is meant to remove any pre-existing incised or “gullied” streams by redirecting water flow up towards the ground’s surface spreading over a broad area. The effectiveness in this technique is dependent on the length and detail of monitoring following application since during peak flow events, flooding may affect the integrity of these created “plugs.” (Rodriguez and McMahon. 2017). While successful restoration can help reverse the pattern of C loss especially by converting oxidizing meadow soils into sinks, the reintroduction of water into the dry environment can potentially cause a short-term increase in CO_2 and N_2O emissions (as per the Birch effect) and in the long term, greater CH_4 if the area that remains flooded. The seasonal water content fluctuations will still occur as flood waters run back down into the ponds and streams (likely to occur more rapidly on eroded and sloping sections). Though as long as the water table does not lower enough to cause a full dry-down of the soils, microbial communities should still be able to adapt to the water content fluctuations and not become too active upon wet up therefore minimizing loss in soil C and N (Schimel et al., 2007; Evan and Wallenstein, 2012; 2014).

Soils with greater SOM content also appear more vulnerable to cycling moisture conditions revolved around air dried soils. The undegraded and restored soils resulted in larger CO_2 and N_2O pulses than their more degraded counterparts. Healthy wet meadow systems have a potential to release significant amounts of CO_2 and N_2O if their typically saturated soils are forced undergo severe DRW events (Gronlund et al., 2006; Wang et al., 2010). Meadows with lower SOM content may produce less GHG upon wetting due to less readily available substrates, but the positive effects of restoration should outweigh the consequences to surrounding ecosystem health and function from continued mismanagement. Overall, based on our study, in order to minimize pulses in CO_2 and N_2O, sites should be allowed to cycle around saturation while simultaneously preventing the soils from drying down to air dry between wet ups. This will also prevent anaerobically driven CH_4 emissions, while continuing to support high aboveground productivity that will result in more SOM accumulation.

5 CONCLUSIONS

We hypothesized that drying and rewetting of montane meadow soils would affect GHG emissions, producing more CO_2 and N_2O resulting from the Birch effect compared to soils kept at a constant moisture content. While pulses of CO_2 and N_2O did occur following wet up of dried soils, they were smaller in soils that underwent more frequent drying and rewetting cycles. Despite the increased post wet-up CO_2 and N_2O fluxes, cumulative gas production remained greater or similar to DRW soils in those maintained at saturation. The only exception existing within the degraded site where N_2O production was higher in the DRW treatment soils than those that remained at saturation. Methane was unaffected by soil rewetting with total CH_4 emissions remaining low across treatments. Various information on biological and physical aspects were collected from our soils over the course of the 84-d incubation with the goal of pinpointing possible mechanisms behind the Birch effect. There were only minor differences between our static and DRW treatments over time. Any significance that was present was distinct to each soil. Therefore, we are unable to form strong conclusions about the prominent sources for the CO_2 and N_2O pulses. Laboratory studies also cannot accurately simulate field conditions well enough to generalize our results in the context of Sierra Nevada meadow soils as a whole. Various caveats such as unnatural disturbances to soil structure from field coring and soil preparation and other ecological factors that were controlled for (i.e., ambient temperature fluctuations and foreign OM inputs). Hence, there is justification for further experimentation to be conducted in situ on a greater number of sites coupled with longer time scales to better understand the effect that drying and rewetting frequencies have on greenhouse gas emissions. Lastly, it should also be important to account for the Birch effect when monitoring meadows for restoration as a potential catalyst for further SOM loss from at risk and degraded meadow ecosystems.

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TABLES

Table 1: Selected study site characteristics. Elevation data is a.s.l. (above sea level) © Google Earth (Accessed April 27, 2017). Soil suborders, common parent material, and dominant vegetation were taken from the USGS Soil Web Survey and soil surveys for Tahoe and Plumus National Forest regions. (USDA 2002; USDA and NRCS, 2005; USDA and NRCS, 2019). Means (and standard errors, n=3) are shown for soil texture, pH, and total carbon (C) and nitrogen (N). Soil pH was measured using a 1:5 air dry mass to DI water (w) or 0.01 M $CaCl_2$ (s).

Site Name*	**Elevation (m)**	**Soil Suborder**	**Common Parent Material**	**Dominant Vegetation**	**% Sand**	**% Clay**	**pHw**	**pHs**	**Total C (g kg^{-1})**	**Total N (g kg^{-1})**
Undegraded (Upper Loney)	~1844	Aquolls and Borolls	Andesite Tuff	*Carex* spp., *Juncus* spp.	49.9 (0.5)	11.5 (0.2)	5.21 (0.00)	4.65 (0.06)	143 (1)	9.6 (0.2)
Degraded (Deer Meadow)	~1889	Aquolls and Borolls	Andesite Tuff	*Carex* spp., *Juncus* spp.	70.6 (1.3)	9.8 (0.2)	5.19 (0.06)	4.70 (0.07)	56.1 (1.6)	4.4 (0.2)
Restored (Big Flat)	~1738	Aquolls	Basalt and Mixed Alluvium	*Carex* spp. *Juncus balticus*	29.6 (0.1)	10.6 (0.6)	5.73 (0.05)	4.95 (0.05)	93.4 (1.1)	7.3 (0.1)
Unrestored (Coyote Flat)	~1700	Aquolls	Basalt and Mixed Alluvium	*Artemisia tridentate*, *Poa secunda*	17.8 (1.3)	45 (1.1)	5.61 (0.04)	4.36. (0.01)	38.5 (0.4)	3.0 (<0.1)

Table 2: Mean (and standard error; n=3) net cumulative carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4) efflux from soil over an 84-d laboratory incubation. Specified contrasts were used to determine whether a significant difference existed between static treatment means (indicated by different lower case letters) or between DRW vs. SAT treatment means (indicated by different upper case letters; α = 0.05). Treatment key: AD = air dry, FC = field capacity, SAT = saturation, 4 Cycle = 4 DRW cycles, 12 Cycle = 12 DRW cycles.

Soil	Treatment	Net cumulative CO_2 (mg C kg^{-1} soil)		**Net cumulative N_2O (µg N kg^{-1} soil)		Net cumulative CH_4 (µg C kg^{-1} soil)	
Undegraded	**AD**	23.0 a	(5.5)	62.5 a	(9.3)	64.5 a	(69)
	FC	2488 b	(93)	9961 ab	(9552)	-126 a	(15)
	SAT	3020 Ac	(141)	40892 Ab	(15156)	228 Aa	(406)
	4 Cycle	3310 A	(72)	30880 A	(9192)	-539 A	(193)
	12 Cycle	3283 A	(143)	9420 A	(4457)	-151 A	(210)
Degraded	**AD**	-4.8 a	(5.7)	17.9 a	(3.4)	72.4 a	(32.0)
	FC	720 b	(11)	88.6 a	(3.3)	-79.6 a	(4.3)
	SAT	1345 Bc	(30)	1141 Ab	(389)	89.1 Aa	(149)
	4 Cycle	746 A	(55)	16484 B	(3920)	-230 A	(155)
	12 Cycle	814 A	(41)	9277 AB	(6650)	5.3 A	(132)
Restored	**AD**	7.2 a	(1.4)	115 a	(35)	255 a	(165)
	FC	2904 b	(202)	17354 b	(11722)	-250 a	(12)
	SAT	3567 Ab	(326)	14992 Ab	(5961)	9832 Aa	(9628)
	4 Cycle	2341 A	(113)	60663 A	(12303)	-391 A	(174)
	12 Cycle	2780 A	(88)	55259 A	(13680)	-203 A	(188)
Unrestored	**AD**	3.1 a	(6.2)	31.6 a	(25.4)	17.0 a	(13.8)
	FC	898 b	(15)	51.3 a	(11.7)	-171 a	(7)
	SAT	941 Bb	(86)	43.5 Aa	(6.0)	-187 Aa	(13)
	4 Cycle	597 A	(11)	227 A	(30)	-252 A	(17)
	12 Cycle	1061 B	(125)	267 A	(125)	-223 A	(24)

*** All data for this gas flux were transformed using the natural logarithm prior to running statistical analyses*

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Table 3: Mean (and standard error; n=3) net change in microbial carbon (C) and nitrogen (N), net N mineralization, and net nitrification over an 84-d laboratory incubation. Shows mean with the standard error in parentheses (n=3). Specified contrasts were used to determine whether a significant difference existed between static treatment means (indicated by different lower case letters) or between DRW vs. SAT treatment means (indicated by different upper case letters; $\alpha = 0.05$). Treatment key: AD = air dry, FC = field capacity, SAT = saturation, 4 Cycle = 4 DRW cycles, 12 Cycle = 12 DRW cycles.

Soil	Treatment	Net Microbial C (mg C kg^{-1})		Net Microbial N (mg N kg^{-1})		Net N Mineralization (mg N kg^{-1})		Net Nitrification (mg N kg^{-1})	
Undegraded	**AD**	-339 a	(43)	-14.8 a	(3.7)**	-7.1 a	(0.5)**	0.19 a	(0.0)
	FC	-411 a	(31)	-112 a	(9)	167 b	(7)	261 b	(7.3)
	SAT	-456 Aa	(34)	-25.2 Aa	(39.7)	-86.7 Aa	(7.2)	22.5 Ba	(14.3)
	4	-482 A	(40)	-90.9 A	(18.3)	163 B	(33)	192 A	(26)
	12	-453 A	(30)	-79.4 A	(41.9)	112 B	(31)	190 A	(28)
Degraded	**AD**	14.1 b	(40.3)**	-5.9 a	(6.0)	2.0 a	(0.8)	1.1 a	(0.1)
	FC	-118 ab	(7)	-29.1 a	(6.4)	90.9 b	(4.1)	106 b	(3)
	SAT	-159 Aa	(13)	-51.5 Aa	(18.8)	50.4 Aab	(25.0)	68.3 Ab	(27.2)
	4	-118 A	(33)	-37.4 A	(8.7)	79.3 A	(3.2)	90.2 A	(3.1)
	12	-208 A	(32)	-54.4 A	(11.0)	63.5 A	(4.7)	77.3 A	(4.6)
Restored	**AD**	71.5 b	(15.5)	-14.5 a	(2.3)	7.2 a	(0.2)	0.4 a	(0.0)
	FC	-203 a	(53)	-92.9 a	(17.9)	102 a	(70)	131 a	(72)
	SAT	-351 Aa	(20)	-68.6 Aa	(52.1)	-6.1 Aa	(23.0)	41.2 Aa	(21.3)
	4	-363 A	(89)	-181 A	(29)	153 B	(14)	195 B	(17)
	12	-414 A	(54)	-161 A	(28)	60.3 A	(14.6)	103 A	(15)
Unrestored	**AD**	-102 a	(45)	-3.9 b	(1.0)	3.1 a	(0.4)	0.1 a	(0.0)**
	FC	-72.6 a	(11.3)	-27.0 a	(1.0)	105 b	(7.6)	111 b	(22)
	SAT	-55.4 Aa	(12.1)	-19.6 Aab	(3.2)	78.8 Ab	(1.3)	79.6 Ab	(4.2)
	4	-88.1 A	(12.6)	-31.4 A	(5.6)	82.2 A	(1.1)	77.7 A	(0.4)
	12	-82.5 A	(17.9)	-29.8 A	(5.8)	96.2 A	(12.2)	92.2 A	(9.8)

*** All response variables from this soil were transformed using the natural logirithm after adding a constant (i.e. log(x+1000)) prior to running statistical analyses*

Table 4: Mean (and standard error; n=3) soil total carbon (C), total nitrogen (N), ^{13}C content, and ^{15}N content of initial and treated soils after a 7-d preincubation and an 84-d laboratory incubation. All pairwise comparisons were used to determine whether a significant difference existed between treatment means (indicated by different lower case letters; α = 0.05). Treatment key: AD = air dry, FC = field capacity, SAT = saturation, 4 Cycle = 4 DRW, 12 Cycle = 12 DRW cycles.

Soil	Treatment	Total C (g kg^{-1})		Total N (g kg^{-1})		$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
Undegraded	**Initial**	143 c	(0.7)	9.6 ab	(0.2)	-25.5 b	(0.8)	2.7 a	(0.1)
	AD	139 b	(1.8)	9.3 ab	(0.1)	-27.1 ab	(0.0)	2.5 a	(0.1)
	FC	130 a	(2.5)	9.0 a	(0.1)	-27.1 ab	(0.0)	2.9 ab	(0.1)
	SAT	130 a	(1.3)	9.0 a	(0.2)	-27.1 ab	(0.0)	3.0 ab	(0.04)
	4	144 c	(2.4)	9.6 b	(0.2)	-27.1 a	(0.1)	3.1 bc	(0.1)
	12	143 c	(0.6)	9.8 b	(0.0)	-27.1 a	(0.1)	3.4 c	(0.0)
Degraded	**Initial**	56.1 b	(1.6)	4.4 a	(0.2)	-26.2 b	(0.1)	5.0 a	(0.00)
	AD	57.6 b	(1.4)	4.2 a	(0.1)	-26.0 b	(0.1)	4.8 a	(0.2)
	FC	53.6 a	(4.4)	4.0 a	(0.3)	-26.0 b	(0.1)	5.1 a	(0.3)
	SAT	51.1 a	(2.4)	4.1 a	(0.1)	-27.0 a	(0.1)	4.9 a	(0.1)
	4	56.7 b	(4.1)	4.2 a	(0.3)	-26.6 a	(0.2)	4.9 a	(0.0)
	12	56.6 b	(3.9)	4.3 a	(0.3)	-25.8 b	(0.0)	4.8 a	(0.1)
Restored	**Initial**	93.4 b	(1.1)	7.3 a	(0.1)	-27.0 b	(0.02)	4.5 b	(0.1)
	AD	95.7 b	(1.8)	7.5 a	(0.2)	-27.0 b	(0.04)	4.1 ab	(0.1)
	FC	87.5 ab	(2.7)	7.3 a	(0.1)	-26.7 a	(0.08)	4.3 ab	(0.0)
	SAT	83.7 a	(1.6)	7.1 a	(0.1)	-27.0 b	(0.05)	4.0 a	(0.1)
	4	84.5 a	(1.7)	7.2 a	(0.1)	-27.0 b	(0.03)	4.2 ab	(0.1)
	12	82.9 a	(2.9)	7.0 a	(0.1)	-27.0 b	(0.04)	4.3 ab	(0.1)
Unrestored	**Initial**	38.5 ab	(0.4)	3.0 a	(0.0)	-26.3 a	(0.03)	4.1 a	(0.2)
	AD	37.6 ab	(0.2)	3.0 a	(0.0)	-26.3 a	(0.03)	4.2 ab	(0.1)
	FC	37.1 a	(0.1)	3.0 a	(0.0)	-26.3 a	(0.02)	4.6 bc	(0.1)
	SAT	39.5 b	(1.0)	3.1 a	(0.1)	-26.4 a	(0.05)	5.5 c	(0.6)
	4	40.4 b	(0.5)	3.1 a	(0.0)	-26.4 a	(0.26)	5.5 c	(0.1)
	12	40.0 b	(0.6)	3.4 b	(0.1)	-27.0 b	(0.08)	5.7 c	(0.1)

FIGURES

Fig. 1. Locations of the montane meadow study sites in the Sierra Nevada of California, USA. The undegraded and degraded pair (Upper Loney (UL) and Deer Meadow (DM)) and the restored and unrestored pair (Big Flat (BF) and Coyote Flat (CF)).

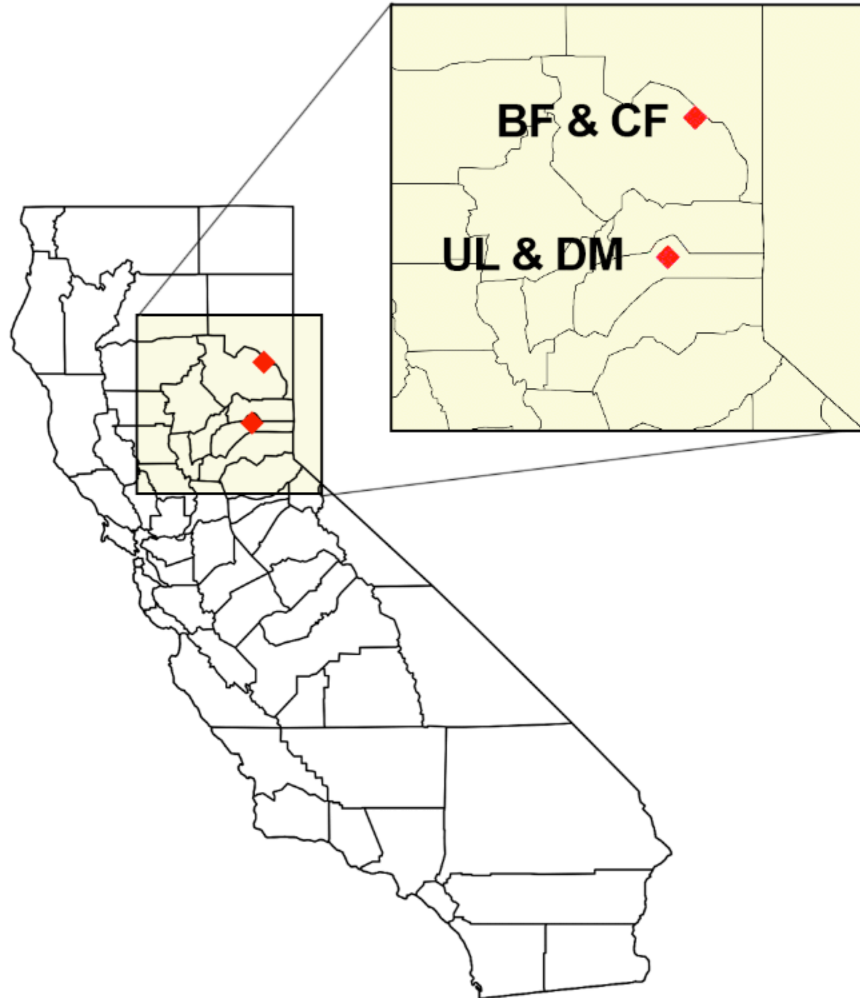


Fig. 2. Schematic of the experimental design showing the treatments and sampling timelines over the 84-d laboratory incubation, following a 7-d preincubation period (indicated by the -7 to 0-d period). Treatments were designed around varying soil water content (SWC) and included two drying rewetting (DRW) treatments: 4-cycle (A), 12-cycle (B), and three static controls (C) maintained at a contant soil water content (air-dry, field capacity, and saturated). Greenhouse gas sampling was based around the 12-cycle treatment (open circles represent times of sampling). Potential soil exoenzyme activity, microbial biomass carbon (C) and nitrogen (N), extractable organic C and N and inorganic N pool sizes, and extractable metals sampling are based around the 4-cycle treatment (numbers 1-5 represent a sampling date). Soil exoenzyme activities on sampling dates 2 and 5 were evaluated both pre- and post-wetting for the DRW soils (represented by the arrows).

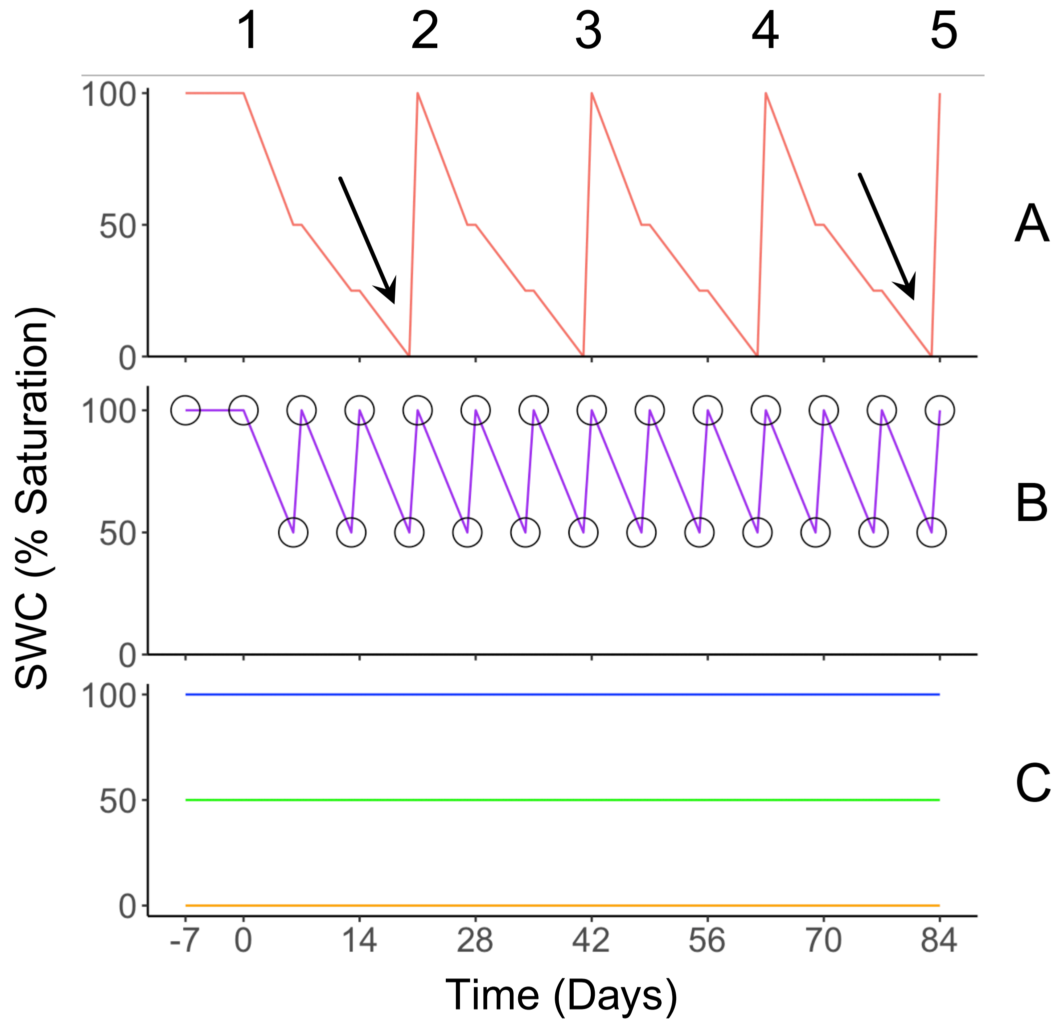


Fig. 3. Changes in mean carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4) efflux within the undegraded site during the 84-d laboratory incubation. Figure panels showing gas efflux rates are stacked vertically for each DRW treatment (4-cycle (red), 12-cycle (purple)) or static treatment group ((saturated (blue), field capacity (green), air-dried (orange)) above their corresponding changes in SWC (expressed relative to saturation) shown in the bottom row. Vertical bars denote ± one standard errors (n = 3).

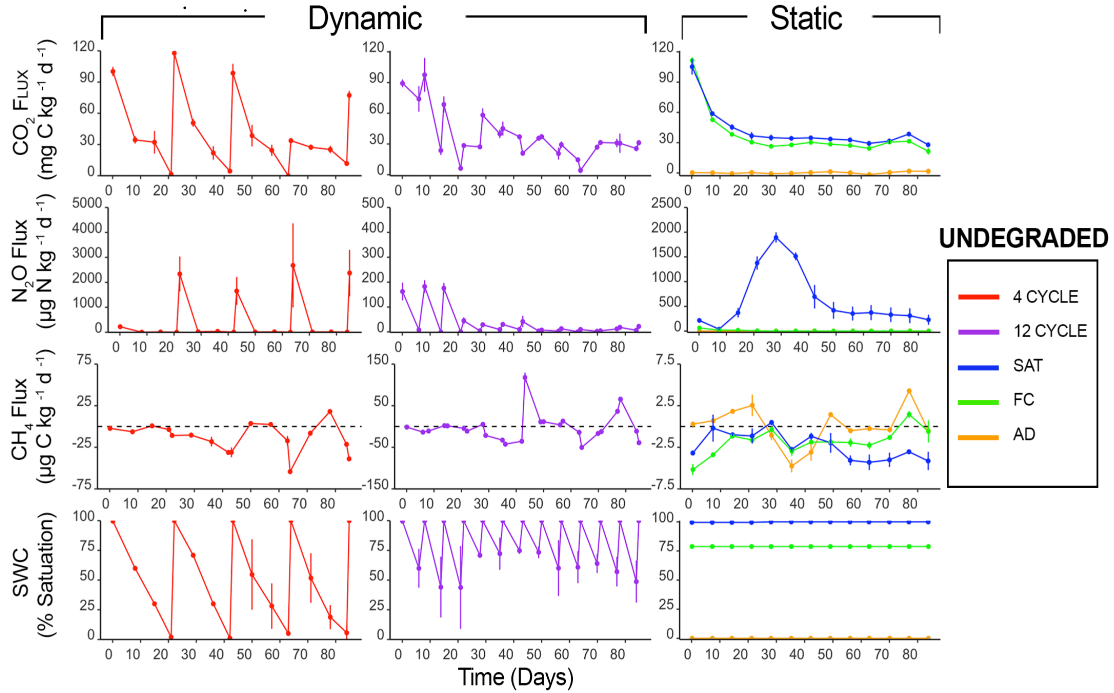


Fig. 4. Changes in mean carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4) efflux within the undegraded site during the 84-d laboratory incubation. Figure panels showing gas efflux rates are stacked vertically for each DRW treatment (4-cycle (red), 12-cycle (purple)) or static treatment group ((saturated (blue), field capacity (green), air-dried (orange)) above their corresponding changes in SWC (expressed relative to saturation) shown in the bottom row. Vertical bars denote ± one standard errors (n = 3).

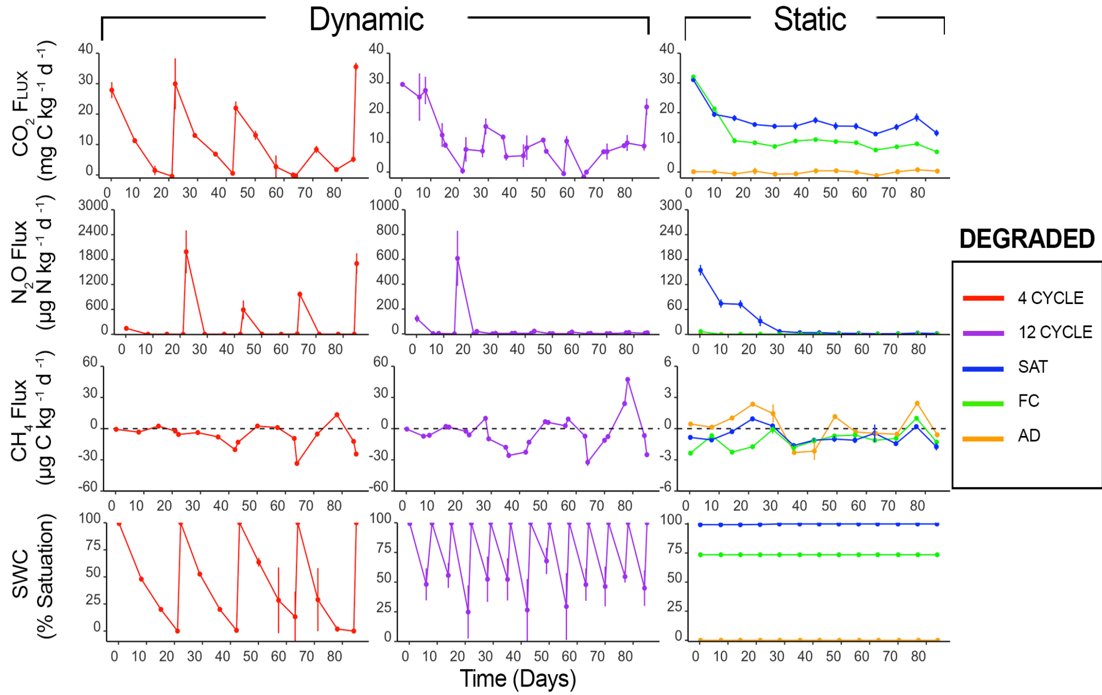


Fig. 5. Changes in mean carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4) efflux within the restored site during the 84-d laboratory incubation. Figure panels showing gas efflux rates are stacked vertically for each DRW treatment (4-cycle (red), 12-cycle (purple)) or static treatment group ((saturated (blue), field capacity (green), air-dried (orange)) above their corresponding changes in SWC (expressed relative to saturation) shown in the bottom row. Vertical bars denote ± one standard errors (n = 3).

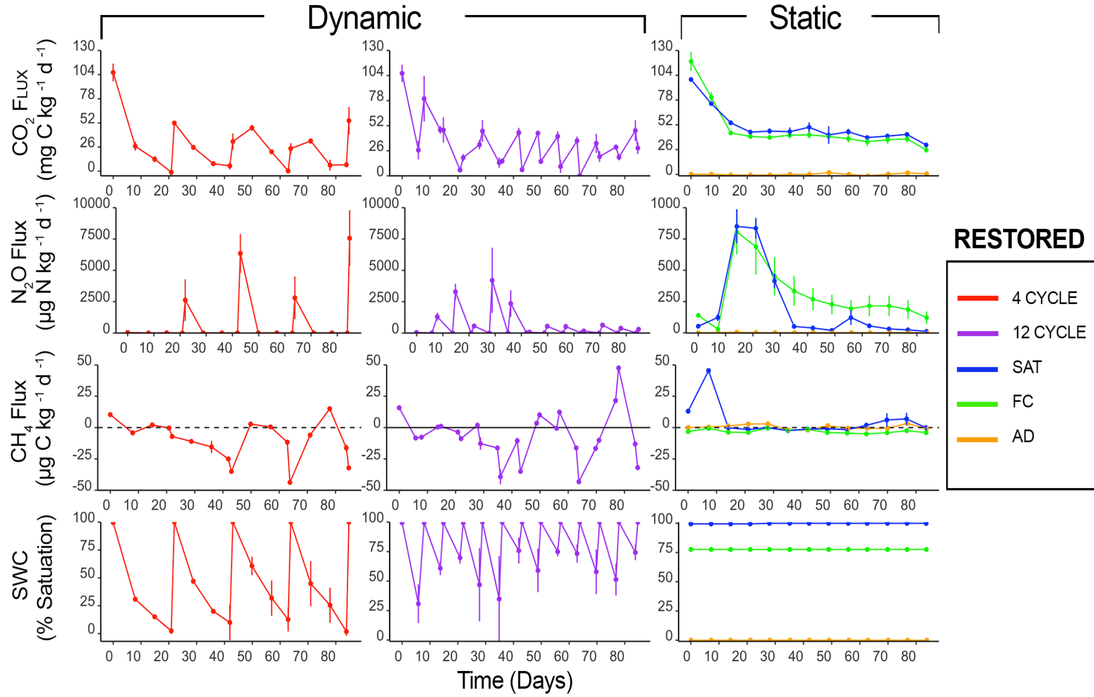


Fig. 6. Changes in mean carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4) efflux within the unrestored site during the 84-d laboratory incubation. Figure panels showing gas efflux rates are stacked vertically for each drying rewetting treatment (4-cycle (red), 12-cycle (purple)) or static treatment group ((saturated (blue), field capacity (green), air-dried (orange)) above their corresponding changes in SWC (expressed relative to saturation) shown in the bottom row. Vertical bars denote ± one standard errors (n = 3).

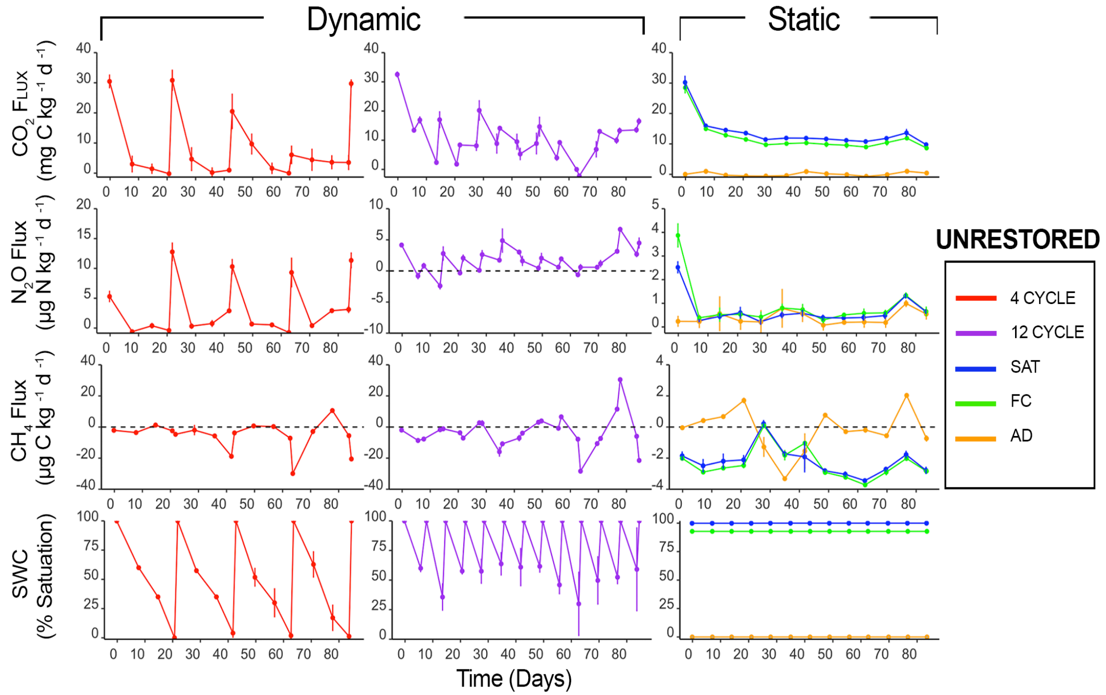


Fig. 7. Changes in mean potential β-glucosidase (BG), N-acetylglucosaminidase (NAG), and alkaline phosphatase (AP) activities in montane meadow soils over the 84-d laboratory incubation. For both drying rewetting treatments, activity was assayed twice (before and after wet up) at 21 and 84-d. Vertical bars denote ± one standard errors (n = 3). Treatment key: air dry = orange, field capacity = green, saturated = blue, 4 cycle = red, and 12 cycle = purple.

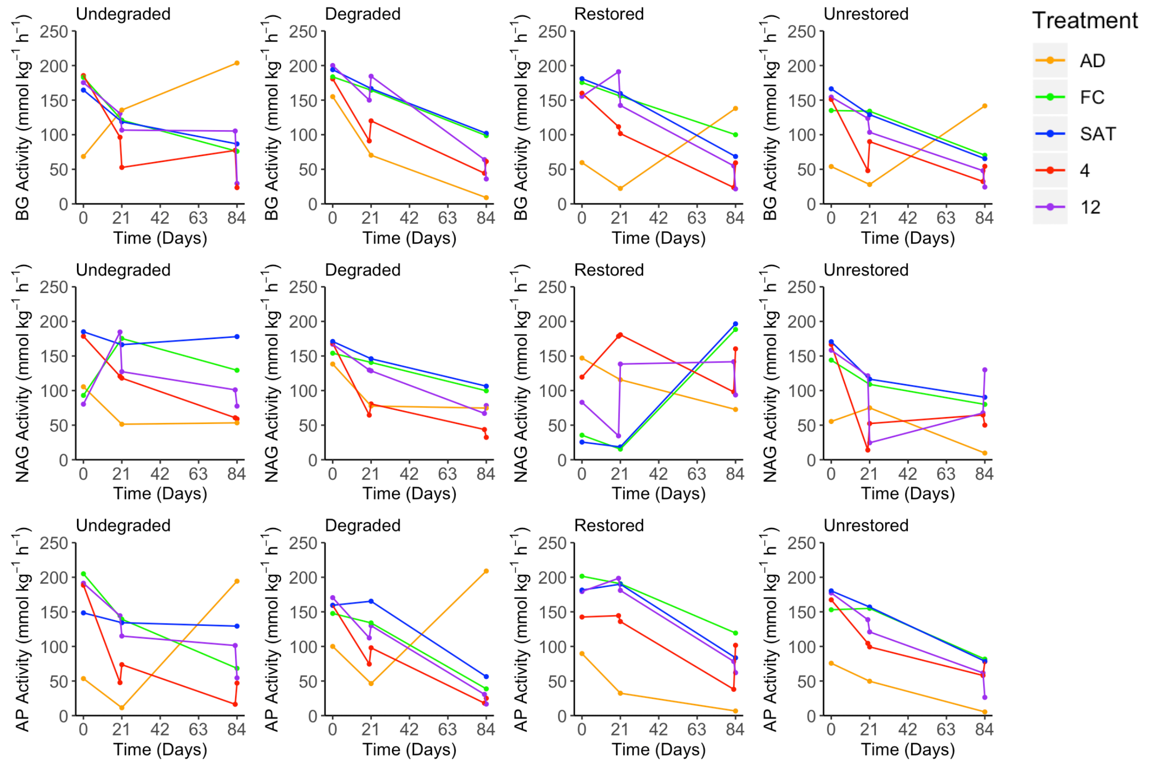


Fig. 8. Changes in mean extractable organic carbon (EOC) and extractable organic nitrogen (EON) in montane meadow soils over the 84-d incubation. Vertical bars denote ± one standard errors (n = 3). Treatment key: air dry = orange, field capacity = green, saturated = blue, 4 cycle = red, and 12 cycle = purple.

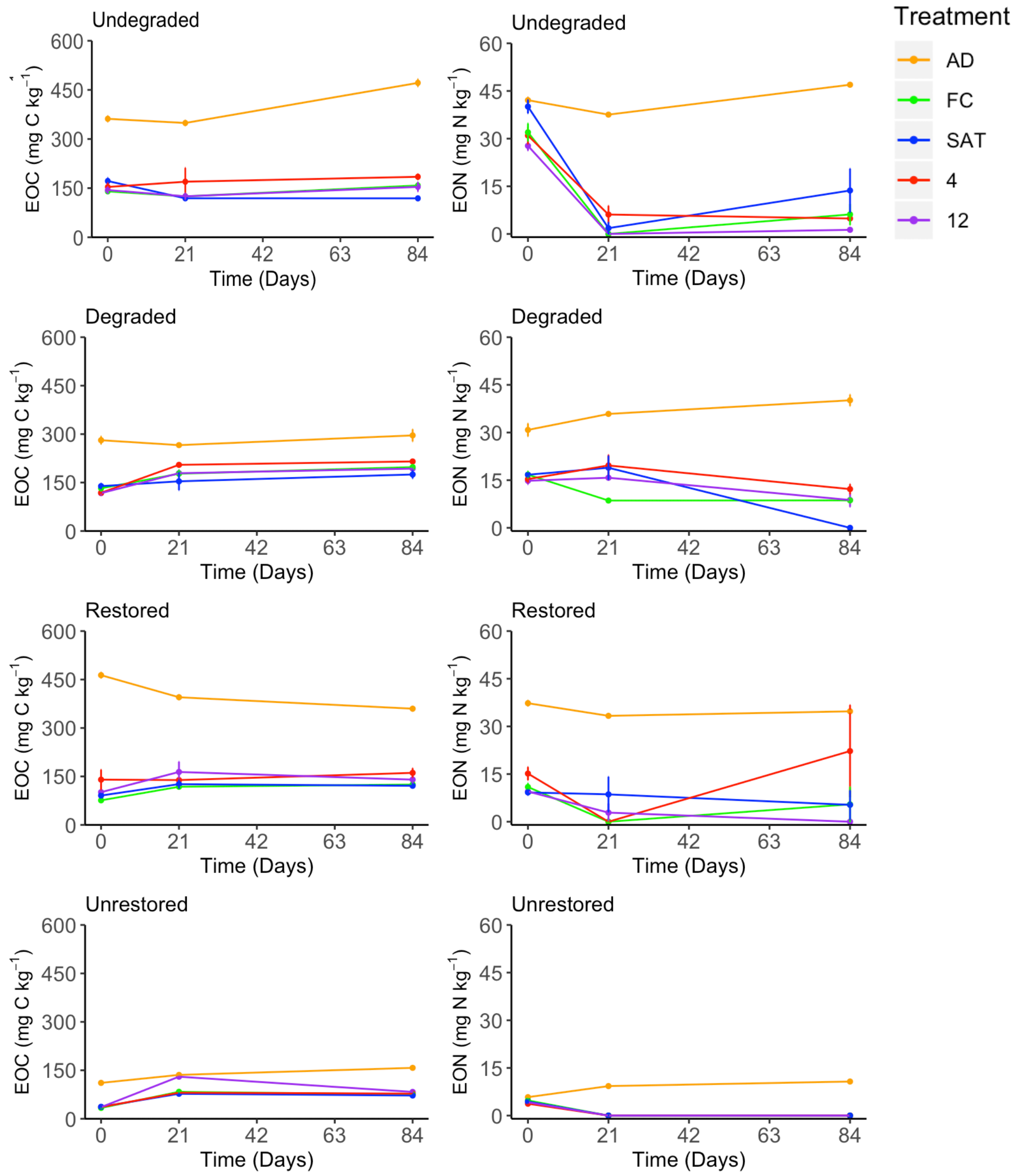
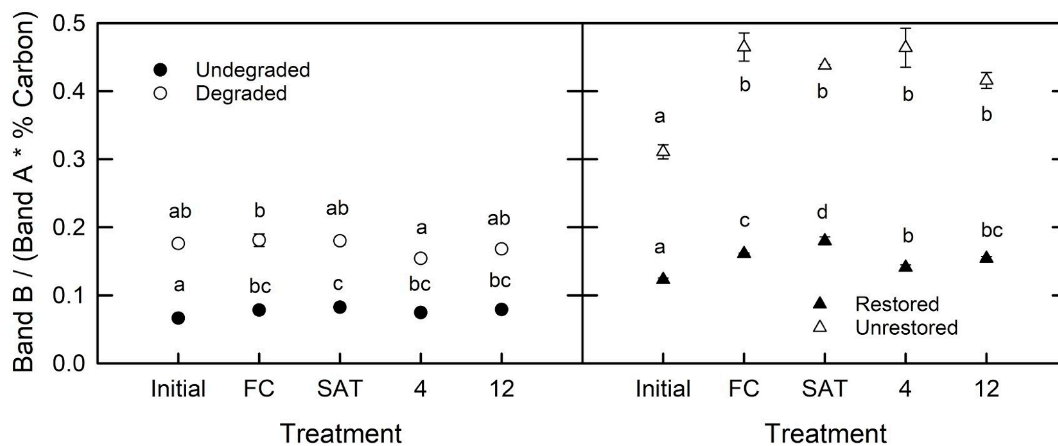


Fig. 9. Change in aromatic to aliphatic groups (Band B/Band A; see Materials and Methods) from initital to treated soils at the end of the 84-d laboratory incubation (n = 3). Ratios of spectral bands were derived from Fourier-transform infrared spectroscopy. Multiple pairwise comparisons were used to determine whether a significant difference existed between treatment means (indicated by different lower case letters; $\alpha = 0.05$). Treatment key: Initial = soil before preincubation, FC = field capacity, SAT = saturation, 4 Cycle = 4 drying-rewetting cycles, 12 Cycle = 12 drying rewetting cycles.



SUPPLEMENTAL TABLES

Table S1. Mean Diethylene Triamine Pentaacetic Acid (DTPA)-extractable iron (Fe), manganese (Mn), copper (Cu), and Zinc (Zn) pools in montane meadow soils from the continuously saturated and drying-rewetting treatments during laboratory incubation. Results from two-factor Analyses of Variance are also shown. T = treatment, D = Days Incubated, TxD = interaction. **Bolded values** denote significant factors (α = 0.05). Where Treatment was a significant factor, Treatment means with different lower-case letters are significant different (shown in first row only). Where Days Incubated was a significant factor, Days Incubated that have different upper-case letters are significantly different (shown in first column only). Where a significant TxD interaction occurred, treatment effects are shown separately for each number of days incubated.

Soil	Days Incubated	Fe			Mn			Cu			Zn		
		---mg kg^{-1} soil---											
		Sat	4 Cycles	12 Cycles	Sat	4 Cycles	12 Cycles	Sat	4 Cycles	12 Cycles	Sat	4 Cycles	12 Cycles
Undegraded	**21**	514^{a}	615^{a}	552^{a}	7.10^{a}	12.4^{ab}	14.2^{b}	1.69^{a}	3.18^{a}	4.87^{b}	1.92^{aA}	5.90^{b}	9.16^{b}
	42	584^{a}	488^{a}	484^{a}	8.10	12.3	11.4	1.18^{a}	4.23^{b}	4.04^{b}	1.87^{B}	9.42	8.52
	63	529^{b}	369^{a}	469^{ab}	11.5	24.1	27.4	2.06^{a}	3.21^{a}	3.54^{a}	5.49^{B}	6.76	7.82
	84	584^{a}	514^{a}	464^{a}	3.87	15.0	20.9	3.96^{a}	5.06^{a}	4.67^{a}	8.25^{C}	11.5	10.8
	T		**0.046**			**0.020**			**<0.001**			**<0.001**	
	D		**0.018**			0.087			**0.001**			**<0.001**	
	TxD		**0.033**			0.859			**0.009**			0.061	
Degraded	**21**	216^{b}	149^{a}	105^{a}	23.8	35.0	24.0	0.88	0.99	0.93	0.52^{A}	0.81	0.72
	42	214	113	79.7	54.6	29.6	30.6	0.98	0.74	0.65	0.87^{AB}	1.03	0.90
	63	289	102	113	36.9	33.3	28.4	0.83	0.72	1.31	0.74^{B}	1.02	1.56
	84	184	128	141	22.9	44.3	42.3	1.13	0.82	0.86	1.16^{B}	1.19	1.23
	T		**<0.001**			0.799			0.519			0.065	
	D		0.801			0.504			0.633			**0.005**	
	TxD		0.604			0.210			0.232			0.282	
Restored	**21**	284^{a}	419^{b}	444^{b}	14.4^{a}	10.2^{a}	18.7^{b}	1.06^{a}	1.50^{b}	2.49^{b}	1.03^{a}	2.19^{b}	3.61^{b}
	42	405^{a}	376^{a}	366^{a}	16.2	12.6	26.5	1.71	1.63	2.05	2.83	2.94	3.89
	63	429^{a}	375^{a}	413^{a}	14.8	12.2	18.1	0.89	2.52	2.43	0.99	4.94	4.39
	84	401^{a}	464^{a}	467^{a}	14.2	19.7	23.1	1.69	2.41	2.79	2.11	4.35	5.12
	T		0.175			**0.007**			**0.001**			**<0.001**	
	D		0.082			0.285			0.244			0.088	
	TxD		**0.040**			0.637			0.354			0.274	
Unrestored	**21**	89.7	120	117	28.9^{AB}	26.4	35.1	1.62^{A}	1.96	1.96	1.50^{aA}	1.73^{ab}	1.94^{b}
	42	129	108	89.3	24.5^{AB}	30.7	30.9	1.10^{A}	1.87	1.45	1.36^{A}	2.07	1.84
	63	88.3	144	82.7	22.9^{A}	21.6	25.9	1.51^{A}	1.60	1.37	1.87^{AB}	1.98	1.88
	84	117	106	129	30.2^{B}	31.8	35.8	1.85^{A}	1.69	1.97	2.08^{B}	2.11	2.27
	T		0.315			0.076			0.124			**0.029**	
	D		0.794			**0.018**			**0.016**			**0.011**	
	TxD		0.064			0.838			0.176			0.328	

SUPPLEMENTAL FIGURES

Figure S1: Changes in mean microbial carbon (C) and nitrogen (N) in montane meadow soils over the 84-d laboratory incubation Vertical bars denote ± one standard errors (n = 3). Treatment key: air dry = orange, field capacity = green, saturated = blue, 4 cycle = red, and 12 cycle = purple.

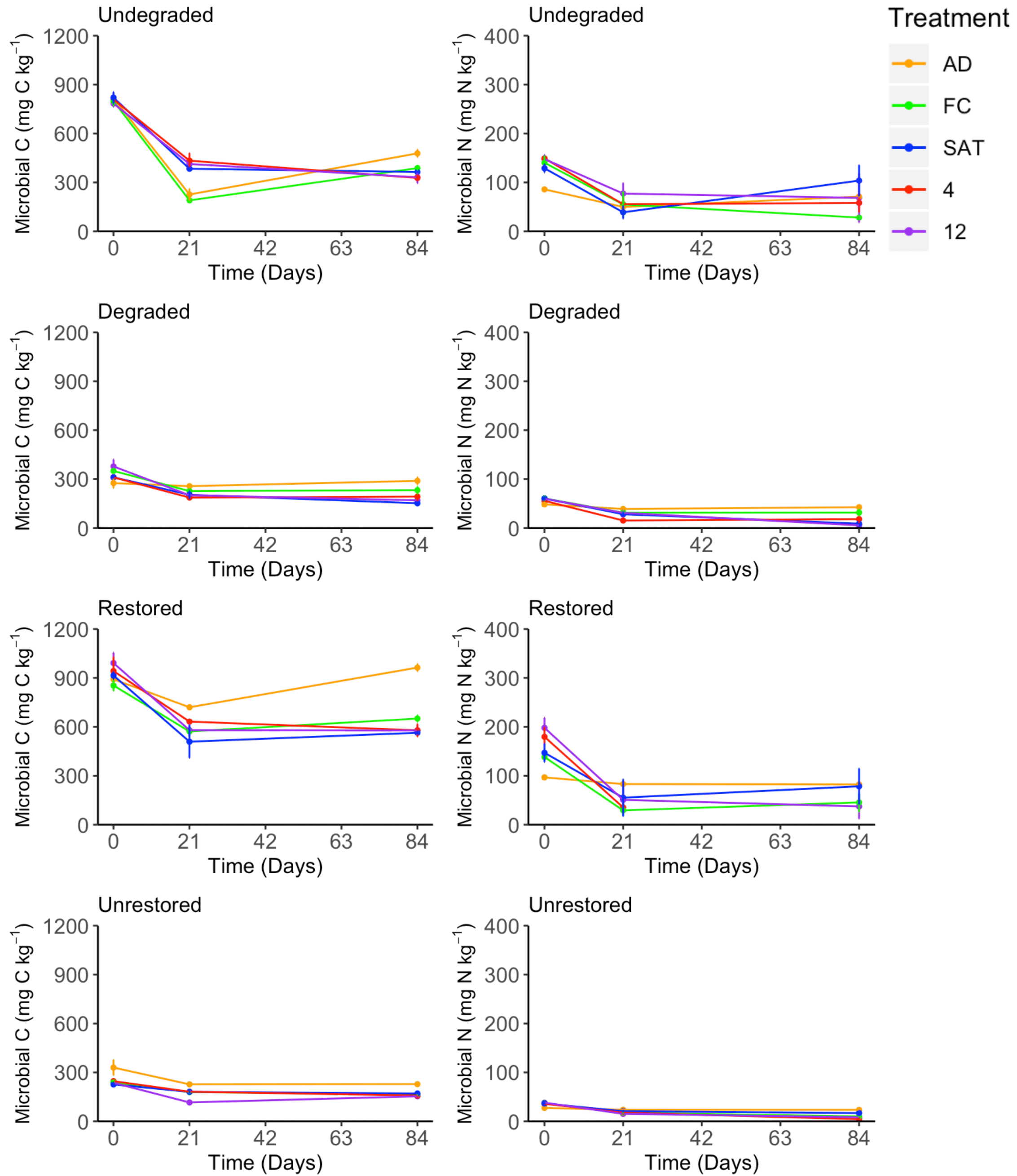


Figure S2: Changes in mean total inorganic nitrogen (N; $NH_4^+ + NO_3^-$) and NO_3^- pool sizes in montane meadow soils over the 84-d laboratory incubation. Vertical bars denote ± one standard errors (n = 3). Treatment key: air dry = orange, field capacity = green, saturated = blue, 4 cycle = red, and 12 cycle = purple.

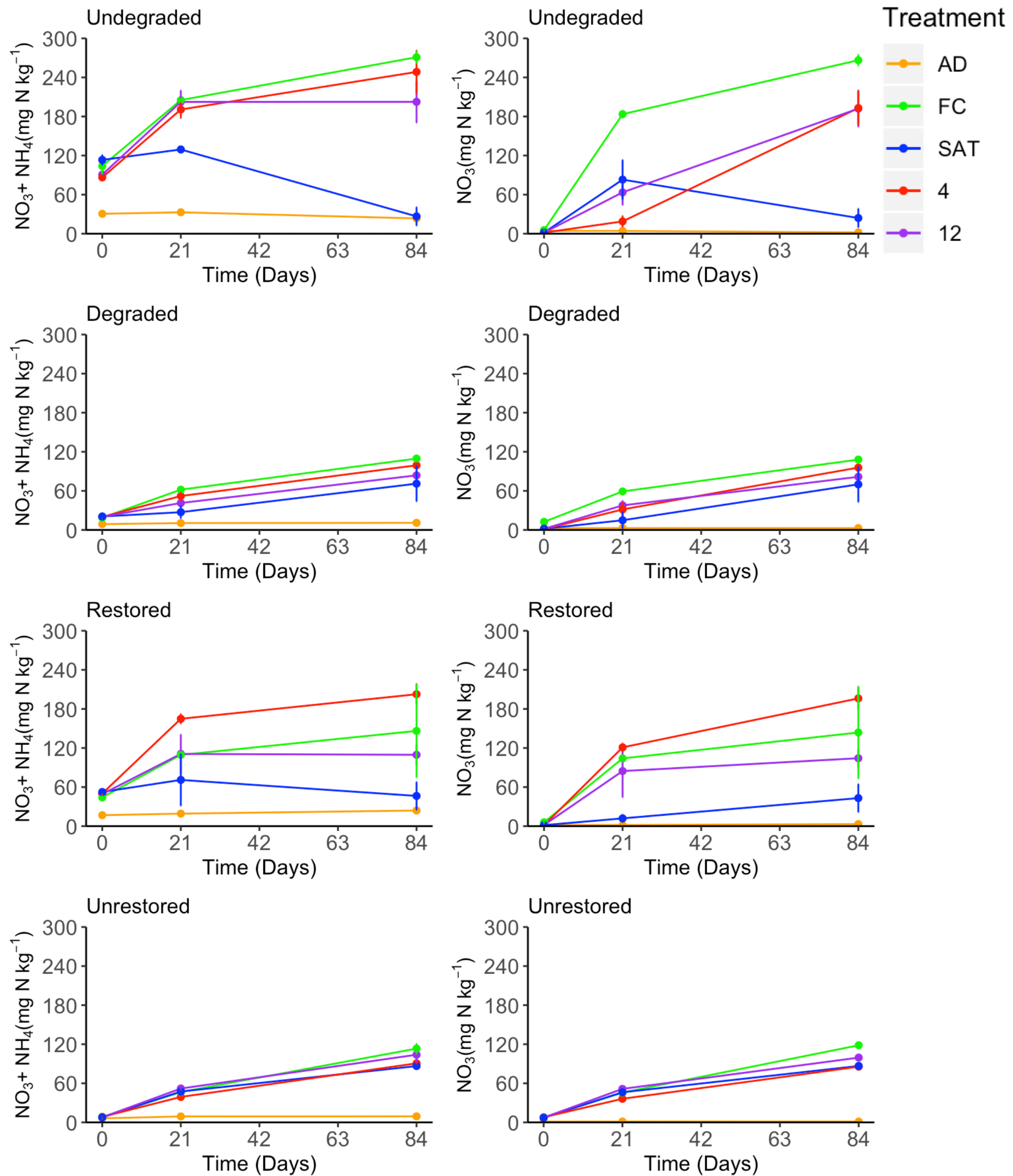


Fig. S3. Mean (n = 3) Diffuse Reflectance Infrared Fourier Transform spectroscopy (DRIFT) spectra for montane meadow soils before (initial) and after an 84-d laboratory incubation under various soil water content treatments. The pairs of dotted vertical lines show the range of wavelengths of interest for calculating the Band B/Band A ratios shown in Fig. 11 (see Materials and Methods). Treatment key: initial, incubated soil = orange, field capacity = green, saturated = blue, 4 cycle = red, and 12 cycle = purple.

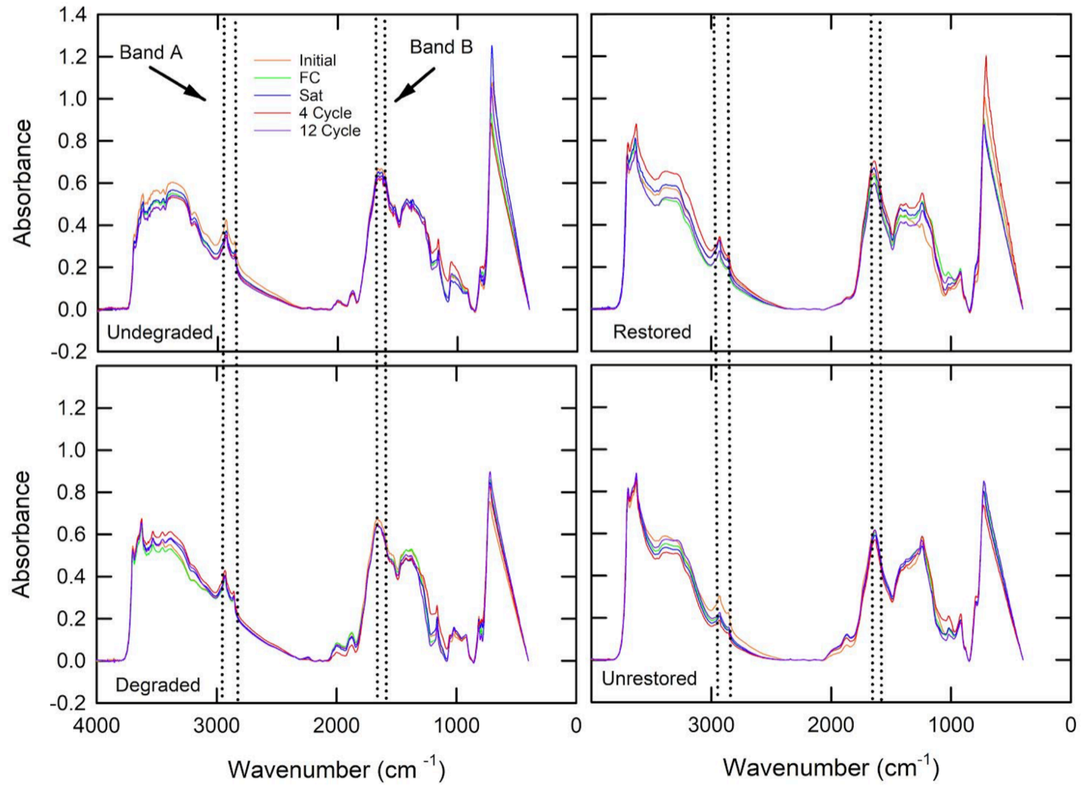


Fig. S4. Changes in Diethylene Triamine Pentaacetic Acid (DTPA)-extractable iron (Fe), manganese (Mn), copper (Cu), and Zinc (Zn) pools in montane meadow soils from the continuously saturated and drying-rewetting treatments during laboratory incubation. soils over the 84-d incubation. Vertical bars denote ± one standard errors (n = 3). Treatment key: saturated = blue, 4 cycle = red, and 12 cycle = purple.