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Quantifying the legacy of snowmelt timing on soil greenhouse gas emissions in a seasonally dry montane forest

Joseph C. Blankinship[1] | Emma P. McCorkle[1] | Matthew W. Meadows[2] | Stephen C. Hart[1]

[1]Life & Environmental Sciences and Sierra Nevada Research Institute, University of California at Merced, Merced, California

[2]Sierra Nevada Research Institute, University of California at Merced, Merced, California

Correspondence
Joseph C. Blankinship, Life & Environmental Sciences and Sierra Nevada Research Institute, University of California at Merced, Merced, CA.
Email: jblankinship@email.arizona.edu

Present address
Joseph C. Blankinship, Department of Soil, Water, and Environmental Science, University of Arizona, Tucson, Arizona.
Emma P. McCorkle, California Regional Water Quality Control Board- Colorado River Basin Region, Palm Desert, California and
Matthew W. Meadows, Kings River Water Association, Fresno, California.

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Abstract

The release of water during snowmelt orchestrates a variety of important belowground biogeochemical processes in seasonally snow-covered ecosystems, including the production and consumption of greenhouse gases (GHGs) by soil microorganisms. Snowmelt timing is advancing rapidly in these ecosystems, but there is still a need to isolate the effects of earlier snowmelt on soil GHG fluxes. For an improved mechanistic understanding of the biogeochemical effects of snowmelt timing during the snow-free period, we manipulated a high-elevation forest that typically receives over two meters of snowfall but little summer precipitation to influence legacy effects of snowmelt timing. We altered snowmelt rates for two years using black sand to accelerate snowmelt and white fabric to postpone snowmelt, thus creating a two- to three-week disparity in snowmelt timing. Soil microclimate and fluxes of carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) were monitored weekly to monthly during the snow-free period. Microbial abundances were estimated by potential assays near the end of each snow-free period. Although earlier snowmelt caused soil drying, we found no statistically significant effects ($p < 0.05$) of altered snowmelt timing on fluxes of CO_2 or N_2O, or soil microbial abundances. Soil CH_4 fluxes, however, did respond to snowmelt timing, with 18% lower rates of CH_4 uptake in the earlier snowmelt treatment, but only after a dry winter. Cumulative CO_2 emission and CH_4 uptake were 43% and 88% greater, respectively, after the dry winter. We conclude that soil GHG fluxes can be surprisingly resistant to hydrological changes associated with earlier snowmelt, likely because of persistent moisture and microbial activities in deeper mineral soils. As a result, a drier California in the future may cause seasonally snow-covered soils in the Sierra Nevada to emit more GHGs, not less.

KEYWORDS
methane oxidation, nitrous oxide, snow manipulation, soil respiration, Southern Sierra Critical Zone Observatory

1 | INTRODUCTION

Climatic warming and eolian dust deposition are causing the snowpack to melt prematurely in seasonally snow-covered ecosystems. Earlier snowmelt timing is already advancing snowmelt runoff by weeks, and potentially months later this century (Barnett, Adam, & Lettenmaier, 2005; Painter et al., 2007; Rauscher, Pal, Diffenbaugh, & Benedetti, 2008; Stewart, 2009; Xu, Liu, Williams, Yin, & Wu, 2016). These

changes in the timing of hydrological processes in seasonally snow-covered ecosystems will likely influence important belowground biogeochemical processes that control ecosystem carbon storage, nutrient retention, and feedbacks to global climate (Brooks et al., 2011; Hinckley, Barnes, Anderson, Williams, & Bernasconi, 2014; Monson et al., 2005). However, there remains a need for quantitative, empirical information about the effects of earlier snowmelt on soil processes in order to better identify and predict effects of winter climate change on summer biogeochemistry. This requires a more integrated understanding of cold- and warm-season processes.

The occurrence of seasonal snowmelt determines the timing of resource availability for soil microorganisms that control ecosystem-scale greenhouse gas (GHG) fluxes of carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O; Aurela, Laurila, & Tuovinen, 2004; Brooks, Williams, & Schmidt, 1998; Liptzin et al., 2009; Sullivan, Dore, Montes-Helu, Kolb, & Hart, 2012). Therefore, earlier snowmelt might modify net GHG emissions from soils in the future if microbial and plant communities are unprepared for the earlier pulse of resources in the spring, or if conditions later in the summer become drier and more limiting to biological activity. Alternatively, effects of snowmelt timing on biogeochemical fluxes might be undetectable because of spatial variation in vegetation structure and soil properties such as profile depth, texture, and organic matter content (Conner, Gill, & Belnap, 2016; Maurer & Bowling, 2015).

Persistent effects of earlier snowmelt and increased temperature on soil moisture during the snow-free period (Blankinship, Meadows, Lucas, & Hart, 2014; Maurer & Bowling, 2014) suggest that there may be changes in soil GHG fluxes lasting months after snow disappears (Figure 1). Earlier snowmelt might increase summer GHG emissions if it causes belowground resources to accumulate because plant roots and soil microorganisms are unprepared for nutrient uptake during the "hot moment" of snowmelt water release (Aanderud, Jones, Schoolmaster, Fierer, & Lennon, 2013; Monson et al., 2005, 2006), possibly leaving behind "hot spots" of microbial resources during summer. Alternatively, earlier snowmelt might lead to decreased soil GHG emissions during summer if associated soil drying exacerbates microbial metabolic stress and limits plant root respiration. Therefore, empirical data are needed to quantify the influence of snowmelt timing on multiple GHGs (i.e., CO_2, CH_4, and N_2O) in conjunction with measurements of soil microclimate at multiple depths. The *amount* of snowfall during winter is known to influence summer soil respiration (Blankinship & Hart, 2012; Concilio, Chen, Ma, & North, 2009), but does the *timing* of seasonal snowmelt have a similar legacy?

The most commonly used approach for simulating winter climate change in seasonally snow-covered ecosystems is by altering snow depth (Blankinship & Hart, 2012; Wipf & Rixen, 2010) using fences (Chimner & Welker, 2005; Williams, Brooks, & Seastedt, 1998) or manual shoveling (Groffman et al., 2001; Knight, Weaver, Starr, & Romme, 1979). However, manipulative experiments that remove snow to simulate earlier snowmelt do not necessarily isolate "the snowmelt effect" because they simultaneously alter water input to soil, which could by itself alter soil GHG fluxes. Natural snowmelt gradients that occur across landscapes may not suffice either because of soil heterogeneity associated with vegetation, topography, and other edaphic properties (Baptist, Yoccoz, & Choler, 2010; Stanton, Rejmánek, & Galen, 1994). Warming lamps can successfully accelerate snowmelt without altering water input (Dunne, Harte, & Taylor, 2003; Meromy, Molotch, Williams, Musselman, & Kueppers, 2015); however, effects of warming after soils are snow-free may misconstrue effects of snowmelt timing.

Therefore, to isolate effects of earlier snowmelt on soil GHG fluxes during the snow-free period, we used field manipulations that did not alter water input and located the experiment in a Mediterranean-type climate to eliminate effects of summer precipitation (Blankinship et al., 2014; Hinckley, Ebel, Barnes, Murphy, & Anderson, 2017). Many seasonally snow-covered ecosystems (e.g., Rocky Mountains and arctic tundra) experience rain during the snow-free period (Conner et al., 2016), which makes it difficult or impossible to distinguish the hydrological effects of spring snowmelt versus summer rain. Therefore, our first objective was to develop a more mechanistic understanding of the effects of snowmelt timing on soil GHG fluxes during the snow-free period. Our previous comparison of earlier and later snowmelt at the same site showed a strong signal of snowmelt timing on soil moisture in the top 30 cm, but deeper soils (30–60 cm) showed no correlation (Blankinship et al., 2014). Particularly during the drier year, near-surface soil drying due to a two- to three-week advancement of snowmelt timing persisted for months after snow disappeared. Do these snowmelt timing-induced changes in near-surface moisture influence soil GHG fluxes? If so, then microbes in near-surface soils are likely more responsible for determining responses of GHG emissions to earlier snowmelt. If not, then microbes (and roots) in deeper soils are probably the dominant control, maintaining their activities despite intra- and interannual variation in snowmelt timing. Our second objective was more broadly related to GHG accounting with earlier snowmelt: are CH_4 and N_2O quantitatively important? Or can the effects of earlier snowmelt on net soil GHG emissions (i.e., total CO_2-equivalents) be adequately estimated by measuring CO_2 alone?

2 | MATERIALS AND METHODS

2.1 | Site description

Field manipulations of snowmelt timing were located in an upper montane mixed-conifer forest in the southern Sierra Nevada (2,365 m ASL; 37.068°N; 119.191°W), approximately 30 km east-southeast of Shaver Lake, California. The site is colocated in the Kings River Experimental Watersheds, a project operated by the US Forest Service Pacific Southwest Research Station, and the Southern Sierra Critical Zone Observatory. The mature forest vegetation is composed of red fir (*Abies magnifica*), sugar pine (*Pinus lambertiana*), and Jeffrey pine (*Pinus jeffreyi*; Johnson, Hunsaker, Glass, Rau, & Roath, 2011). The Sierra Nevada experiences a Mediterranean-type climate with cold wet winters and warm dry summers. Mean annual temperature and precipitation at the elevation of our site are 8°C and 100 cm, respectively. Most precipitation (75%–90%) falls as

snow at this elevation, and 95% of annual precipitation falls between October and May (Hunsaker, Whitaker, & Bales, 2012).

The soil is a member of the Cagwin soil series within the mixed, frigid Dystic Xeropsamments Soil Taxonomic family. The soil is coarse-textured, well-drained, and derived from granitic parent material. The soil profile is 50–150 cm thick with a field capacity of ~20% volumetric water content (VWC; $m^3\ m^{-3} * 100\%$) in the upper 30 cm (Bales et al., 2011). The mean organic (O) horizon thickness is 2.1 with a standard error of 0.5 cm. The top 15 cm of mineral soil is in the A horizon and has a bulk density of 0.75 ± 0.04 Mg/m (mean ± *SE*), water-holding capacity of 45% ± 8% VWC, 81 ± 11 g of total carbon (C) per kg dry soil, and 3.0 ± 0.4 g of total nitrogen (N) per kg dry soil.

2.2 | Snowmelt timing manipulations

Experimental plots with earlier and later snowmelt were established during the summer of 2010 on a relatively flat (<5% slope), southwest-facing slope in forest canopy gaps to minimize tree shading, thereby increasing the efficacy of the snowmelt manipulations. See Blankinship et al. (2014) for further details on the site and treatments. The site layout consisted of 12 blocks in canopy gaps (each approx. 10 × 20 m), each containing two 16 m^2 plots (4 × 4 m) of both accelerated and delayed snowmelt spaced 1.0–1.5 m apart and marked at the corners with steel T-posts attached to PVC pipes for a total height of 2.5 m. Plant communities were undisturbed except inside the collars used for gas flux sampling where seedlings were removed whenever they emerged so that plant presence/absence would not be introduced as a variable. However, seed germination was rare.

The melting of seasonal snowpack was advanced in one randomly selected plot in each block (i.e., "earlier snowmelt" treatment) using black vitreous smelter slag, henceforth referred to by the trade name "black sand" (Waxie Sanitary Supply, San Diego, CA; manufactured by Mission Laboratories, Los Angeles, CA). The black sand was 38.1% silicon dioxide, 27.4% iron oxide, 23.8% calcium oxide, 5.7% aluminum oxide, 3.9% magnesium oxide, and <1% other fused oxides. To create a layer of sand roughly 0.5 mm thick, we used a handheld fertilizer spreader to add 800 g/m for a total of 12.8 kg of sand per plot. A thin layer (<5 mm) of dark-colored particles can accelerate snowmelt by reducing the snow surface albedo (from roughly 0.8–0.2) and thus increasing absorption of shortwave and longwave radiation (Drake, 1981; Warren, 1984). In wetter 2011, we added sand on 25 April and 10 May, as soon as possible after plot markers (i.e., tops of PVC pipes) were visible. In drier 2012, we added sand on 16 April after peak snow depth. The sand application resulted in a bowl-shaped melting pattern, with the highest rates of melting near the center of each plot.

To maximize variation in when soils became snow-free, the melting of seasonal snowpack was delayed in one randomly selected plot in each block—henceforth referred to as the "later snowmelt" treatment. We used two crossed layers (3.1 × 2.8 m) of 0.15 mm thick white Tyvek® HomeWrap fabric (DuPont Corporation, Wilmington, DE) that were secured to a 3.1 × 3.1 m frame. Reflective tarps have been shown to be effective in slowing snowmelt rate (Stinson, 2005). Tyvek® fabric was chosen because it is durable and shades most sunlight, thus primarily reducing the solar radiation component of the snowpack's energy balance, but also by reducing ablation. The snowmelt-delaying frames were constructed from 2.5 cm diameter white PVC pipe, corner connectors (90° angle), and T-connectors to attach 3.1 m long cross pipes on top of the fabric. In 2011, we installed the frames on 25 April or 10 May, as soon as possible after the plot markers were visible above snow. In 2012, we installed the frames at the same time as black sand addition (16 and 17 April). We began with 12 replicates but four of the replicates became unusable because the snowmelt-delaying frames were moved by wind in 2011 (the windblown frames did not disturb the adjacent treatments). Therefore, for both the 2011 and 2012 snow-free periods, we only measured soil gas fluxes from the eight blocks where the delayed snowmelt treatment functioned properly. The frames were removed from the delayed snowmelt plots as soon as possible (one day to one week) after the center of each plot was snow-free.

2.3 | Soil microclimate

Soil volumetric water content (VWC) was measured at a depth of 0–12 cm inside each soil gas flux chamber in the center of each plot

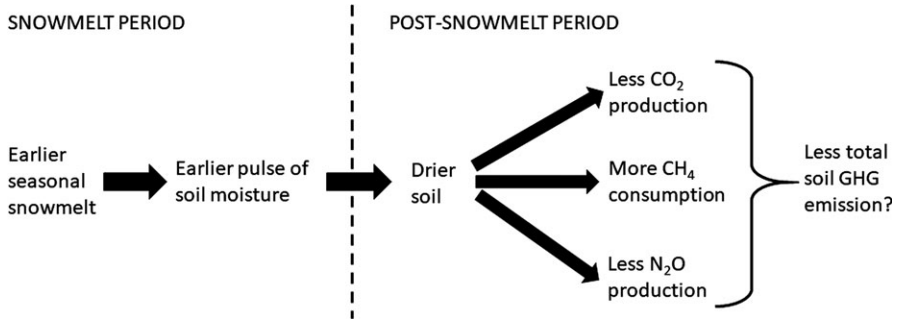

FIGURE 1 Hypothesized control of seasonal snowmelt timing on net greenhouse gas (GHG) emission from soil during the snow-free period. Drier soil is expected to decrease carbon dioxide (CO_2) production because of reduced microbial access to organic matter, increase methane (CH_4) consumption because of greater diffusion of oxygen and atmospheric CH_4 into soil, and decrease nitrous oxide (N_2O) production because of fewer wet aerobic and anaerobic microsites for nitrification and denitrification, respectively

using a portable time domain reflectometer (CD620 Hydrosense System; Campbell Scientific, Inc., Logan, UT). The two 12 cm probes were inserted into the same vertical holes on every sampling date to minimize soil disturbance. To prevent artifacts of soil disturbance, VWC was measured on each date after gas flux sampling. In our previous work (Blankinship et al., 2014), we used time domain reflectometry to monitor permanently installed probes adjacent to the gas flux chambers at depths of 0–15, 15–30, and 30–60 cm. These data are presented again here to better understand how moisture in different soil depths controls net CO_2, CH_4, and N_2O fluxes.

Soil temperature (7.5 cm deep) was measured adjacent to gas flux chambers in the center of each plot at the start and end of gas flux sampling using a handheld digital thermometer (VWR International, Radnor, PA). The mean of the initial and final temperature is henceforth referred to as "soil temperature during gas flux sampling." In addition, soil temperature was logged hourly to determine the exact day when the center of each plot became snow-free (see Blankinship et al., 2014). Soil thermometers with dataloggers were installed 7.5 cm below the ground surface in the center of each plot (HOBO Pendant temperature and light data logger 64K; Onset Computer Corporation, Bourne, MA).

2.4 | Gas flux sampling

Field CO_2, CH_4, and N_2O fluxes were measured in "ambient collars" in the center of each plot. The collars were open at the bottom to include roots. Each ambient collar consisted of a 20 cm long PVC pipe that was sunk 10 cm into the soil. Fine roots are in relatively low abundance in this depth because of seasonal drying in this ecosystem (Johnson et al., 2009). Gas fluxes were sampled monthly before the snowmelt treatments began (i.e., fall 2010) to insure similar initial fluxes in the paired-block design. After the two subsequent winters, gas fluxes were sampled approximately weekly during the first month following the disappearance of snow, then every two weeks during the second month, and then monthly, for a total of three pretreatment sampling dates in 2010 (August 18, September 19, October 16), seven sampling dates in 2011 (June 24, July 8, July 20, July 28, August 17, September 17, October 15), and nine sampling dates in 2012 (January 19, May 9, May 16, May 24, June 1, June 14, June 25, July 17, August 15). Fluxes were always measured between 11:00 and 14:00 using the static chamber technique (Hart, 2006; Hutchinson & Mosier, 1981).

Chamber tops were constructed from a 10.2 cm diameter white PVC pipe closed at one end with a 4 cm tall PVC cap equipped with a rubber septum and vent tube. The length (10 cm) and diameter (0.5 cm) of the vent tube were calculated to minimize chamber air mixing with outside air due to sample collection and perturbations from wind (i.e., the Venturi effect). Headspace gas samples (18 ml) were collected from each chamber using a 20 ml polyethylene syringe with stopcock and 20 gauge needle. Gas samples were collected 0, 30, and 60 min after sealing the chamber top and applying a latex band as a secondary airtight seal between the chamber top and soil mesocosm. Gas samples were injected into 12 ml evacuated glass vials with rubber septa (Exetainer, Labco, LLC, Lampeter, Ceredigion, UK) until laboratory analysis (2 ml injection volume) within two weeks on a gas chromatograph system (GC 2014 Greenhouse Gas Analyzer; Shimadzu Scientific Instruments, Inc., Columbia, MD) with Combi Pal AOC 5000 auto injector (CTC Analytics AG, Zwingen, Switzerland). The gas chromatograph used packed stainless-steel columns (oven temperature = 80°C) and was equipped with a thermal conductivity detector (TCD) to measure CO_2 concentration, a flame ionization detector (FID) to measure CH_4 concentration, and an electron capture detector (ECD) to measure N_2O concentration.

Carbon dioxide and CH_4 fluxes were linear during the 60 min sampling period ($r^2 > 0.90$), and N_2O fluxes were approximately linear (r^2 between 0.70 and 0.85). Rates of soil CO_2 production, CH_4 consumption, and N_2O production/consumption were expressed as mg C m^{-2} hr^{-1}, μg C m^{-2} hr^{-1}, and μg N m^{-2} hr^{-1}, respectively. Positive rates indicate net gas emission from soil to the atmosphere, and negative rates indicate net gas uptake from the atmosphere into soil.

2.5 | Soil sampling and microbial assays

We estimated abundances of microbes (in both O horizon and mineral soil) associated with each GHG near the end of each dry season in mid-August (17 August 2011 and 15 August 2012) to see whether there were any lasting effects of altered snowmelt timing on belowground microbial communities. Heterotrophic microbial biomass was measured by substrate-induced respiration to possibly explain field CO_2 fluxes. Methane oxidation potential was measured to possibly explain field CH_4 fluxes. Denitrification potential was measured to possibly explain field N_2O fluxes.

After field collection, intact soil cores (10 cm diameter, 0–15 cm deep) from adjacent to the gas sampling collars were transported cold (4°C) to the laboratory at the University of California, Merced and stored cold until processing (within 1 week). For the O horizon, any material >1 cm in diameter was discarded and any material <1 cm in diameter (e.g., 8 cm long pine needles and twigs) was cut into smaller pieces <2 cm in length using scissors. The mineral soil was sieved field-moist through a 4 mm mesh and any material >4 mm in diameter was discarded. We chose a 4 mm mesh for the mineral soil rather than 2 mm mesh to include mineral soil that was clearly attached to particulate organic matter in the 2–4 mm size fraction.

Substrate-induced respiration (SIR) was used to assess the relative abundance of microorganisms that were active near the end of the dry season (West & Sparling, 1986). Field-moist mineral soil (15 g) or O horizon material (3 g) was combined with 30 ml of glucose solution (30 mg glucose per ml H_2O) in a 250 ml flask. The flasks were sealed with a rubber stopper with septum and placed on an orbital shaker (180 rpm) for 2.5 hr at room temperature (23°C). At 0.5, 1.5, and 2.5 hr after adding glucose, 15 ml of headspace gas inside each flask was sampled for CO_2 and stored in an evacuated 12 ml glass vial until analysis. Respiration rates were calculated by dividing net CO_2 production by the mass of soil or O horizon

material and exact elapsed time; rates were expressed as mg CO_2-C per kg soil or O horizon material per hour.

Potential rates of CH_4 oxidation were used to estimate the abundance of CH_4-oxidizing microbes in soil. Field-moist soil (10 g) and O horizon material (3 g) were weighed into 250 ml flasks and adjusted to 35% of water-holding capacity (WHC; 22% gravimetric water content for the mineral soil and 74% gravimetric water content for the O horizon material), an assumed optimum for high-affinity CH_4-oxidizing bacteria (Gulledge & Schimel, 1998). The flasks were sealed with a rubber stopper and septum, and then 2 ml of 1% CH_4 (Air Liquide America Specialty Gases, Plumsteadville, PA) was injected into each flask to elevate the initial CH_4 concentration to approximately 125 ppmv. This concentration is high enough to relieve limitation on high-affinity CH_4-oxidizing bacteria without also promoting the activity of low-affinity CH_4-oxidizing bacteria (Bender & Conrad, 1992). The mineral soil and O horizon materials were incubated in the dark at room temperature (23°C) for 48 hr. The first headspace sample (15 ml) was collected 1 hr after injecting CH_4, and then again 24 and 48 hr later. Each gas sample was stored in an evacuated 12 ml glass vial until analysis. Potential rates of CH_4 oxidation were calculated by dividing net CH_4 consumption over 48 hr by the mass of dry soil and exact elapsed time; rates were approximately linear ($r^2 > 0.90$) and expressed as μg CH_4-C per kg soil or O horizon material per hour.

Potential rates of denitrification were measured using a shaken-slurry method (Smith & Tiedje, 1979). To insure unlimited resources for denitrifying microorganisms, field-moist soil (50 g) or O horizon material (5 g) was combined with nitrate (NO_3^-) and labile C substrates (0.1 g NO_3^--N, 1 g glucose-C, and 1 g glutamic acid-C per kg material) in a 250 ml flask. After sealing each flask with a rubber stopper and septum, the headspace was made anaerobic by triplicate cycles of vacuum and flushing with dinitrogen (N_2) gas. After equilibrating the headspace pressure with a bubble trap, 20 ml of acetylene (generated using calcium carbide) was injected to produce a ~ 10% v/v acetylene atmosphere in order to inhibit the reduction of N_2O to N_2. The soil and O horizon materials were incubated at room temperature (23°C) on an orbital shaker (180 rpm) for 90 min. The headspace in each flask (15 ml) was sampled 30 and 90 min after adding the NO_3^- and C solution. Gas samples were stored in evacuated 12 ml glass vials until N_2O analysis. Potential rates of denitrification were calculated by dividing net N_2O production by the mass of soil or O horizon material and exact elapsed time; rates were expressed as μg N_2O-N/kg soil or O horizon material per hour.

2.6 | Data analysis

Means and standard errors of soil microclimate (moisture and temperature), gas fluxes (CO_2, CH_4, and N_2O), and microbial assays (substrate-induced respiration, methane oxidation potential, and denitrification potential) were calculated for each sampling date and snowmelt treatment. Cumulative, time-integrated, full-season gas fluxes were calculated for the precipitation-free period between the completion of snowmelt (i.e., snow-free date) until September 1. The flux during the first snow-free sampling date for each snowmelt treatment was averaged across the period until the second sampling date, and so forth until September. For the purposes of these full-season calculations, gas emissions above snowpack were assumed to be zero due to diffusion limitation.

Radiative forcing calculations were based on CH_4 and N_2O being 25 and 298 times stronger per mole, respectively, than CO_2 as a GHG during the next 100 years (Forster et al., 2007). Hourly fluxes of CO_2, CH_4, and N_2O in each chamber were converted to g CO_2-equivalents (CO_2e) m^{-2} day^{-1}. In the case of CH_4 consumption, values of CO_2e were negative. We totaled CO_2e for each chamber on each date (i.e., net GHG emission). We also calculated the contribution of CH_4 and N_2O to net GHG emission by dividing CH_4- and N_2O-associated CO_2e by the total CO_2e and multiplying by 100%.

For soil microclimate and gas fluxes, we ran a two-way analysis of variance (ANOVA) test with snowmelt treatment, year, and block as single factors, and snowmelt treatment by year as the interactive effect, using an alpha level of 0.05 (JMP Pro 13 software; SAS Institute, Cary, NC). For this statistical analysis, we focused on the dry season between the snow-free date and September 1. No data transformation was required for near-normal distribution or heteroscedasticity. Linear regressions of GHG fluxes (*y*-axis) versus soil microclimate (*x*-axis) were performed for each combination of snowmelt treatment, GHG flux, and depth of soil VWC measurement (i.e., 0–12 cm inside gas sampling collar and 0–15 cm, 15–30 cm, and 30–60 cm adjacent to collar). Linear regressions were performed individually for each date as well as across all sampling dates. Effects of snowmelt timing on soil microbial assays at the end of each dry season were analyzed similarly, except with only one date per year. The mineral soil and O horizon were analyzed separately.

3 | RESULTS

3.1 | Soil microclimate

The mean difference in snow-free date between the earlier and later snowmelt treatments was 14 days in 2011 and 20 days in 2012. Water year 2011 was extremely wet with 196% of MAP and a mean snow-free date of June 11 (±1.0 day, standard error) in the earlier snowmelt plots and June 25 (±1.7 days) in the later snowmelt plots. Water year 2012 was drier with 69% of MAP and a mean snow-free date of April 22 (±0.5 day) in the earlier snowmelt plots and May 12 (±2.4 days) in the later snowmelt plots. In both years of the study, no precipitation fell between the snow-free date and September 1.

During the precipitation-free period between snowmelt and September 1, soil moisture inside the gas sampling collars was significantly drier with earlier snowmelt (Table 1), averaging 5.1% VWC in the later snowmelt treatment and 4.3% VWC in the earlier snowmelt treatment. This effect did not depend on block (i.e., spatial variation) or year (i.e., interannual variation in precipitation amount). In 2010 before the snowmelt treatments began, soil moisture was not statistically different across plots (Figure 2a). Despite the large interannual difference in precipitation amount, surface soils (i.e., top 12 cm) started the snow-free period in both years around 12% VWC and

TABLE 1 Two-way ANOVA results for effects of altered snowmelt timing and interannual variation on soil microclimate and fluxes of carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O), and their combined contribution to net radiative forcing

	Block		Snowmelt Timing		Year		Snowmelt Timing x Year	
Response Variable	*F* stat	*p* value	*F* stat	*p* value	*F* stat	*p* value	*F* stat	*p* value
Soil moisture	0.81	0.58	3.75	0.05*	1.30	0.26	0.03	0.85
Soil temperature	9.76	<0.0001*	3.29	0.07	41.98	<0.0001*	4.55	0.03*
Mean CO_2 flux	13.18	<0.0001*	0.02	0.88	22.65	<0.0001*	0.80	0.37
Mean CH_4 flux	13.86	<0.0001*	29.85	<0.0001*	3.76	0.05*	6.52	0.01*
Mean N_2O flux	0.72	0.66	1.89	0.17	1.39	0.24	0.01	0.91
Seasonal CO_2 flux	8.07	<0.0001*	1.54	0.23	40.16	<0.0001*	2.25	0.15
Seasonal CH_4 flux	7.07	0.0002*	6.72	0.02*	125.01	<0.0001*	8.65	0.008*
Seasonal N_2O flux	1.00	0.46	1.32	0.26	0.04	0.84	0.27	0.61
CO_2-equivalents	8.10	<0.0001*	1.60	0.22	39.52	<0.0001*	2.19	0.15
CH_4 contribution	11.26	<0.0001*	6.78	0.02*	20.63	0.0002*	0.89	0.36
N_2O contribution	1.13	1.13	0.78	0.39	0.75	0.40	0.34	0.57

Note. "Seasonal" fluxes are cumulative across the period from the completion of snowmelt (i.e., snow-free date) until September 1.
*$p \leq 0.05$.

finished around 2% VWC. In 2011, mean soil VWC was lower in the earlier snowmelt treatment until precipitation fell in September and October. In 2012, mean soil VWC was consistently lower in the earlier snowmelt treatment throughout the dry season.

During the precipitation-free period between snowmelt and September 1, soil temperature during gas sampling ranged from 6.4°C in the later snowmelt treatment to 23.3°C in the earlier snowmelt treatment (Figure 2b). Unlike soil moisture, soil temperature showed significant spatial variation and was influenced by an interactive effect of year and altered snowmelt timing (Figure 3). After the wet winter (2011), earlier snowmelt was associated with soil warming of 2.1°C. However, after the dry winter (2012), soil temperature was 2–5°C cooler on average with no effect of altered snowmelt timing.

3.2 | Soil greenhouse gas fluxes

3.2.1 | Carbon dioxide

Fluxes of CO_2 were not statistically different across plots in fall 2010 before the snowmelt treatments began (Figure 4a). During the precipitation-free periods in 2011 and 2012 between snowmelt and September 1, soil CO_2 fluxes showed significant spatial variation (i.e., block effect) and interannual variation (i.e., year effect), but there was no effect of altered snowmelt timing (Table 1). Mean rates of soil CO_2 emission were 19% lower after the dry winter (50.6 mg C m^{-2} hr^{-1}) as compared to after the wet winter (62.3 mg C m^{-2} hr^{-1}).

In terms of microclimatic predictors of soil CO_2 flux, VWC at a depth of 15–30 cm was the most consistent statistically significant predictor, but only in the later snowmelt treatment (Table 2). Also in the later snowmelt treatment, significant positive correlations occurred at a depth of 0–15 cm in the wet year and at a depth of 30–60 cm in the dry year. Across all dates, soil VWCs at all depths were positively correlated with soil CO_2 fluxes. In the earlier snowmelt treatment, soil VWC at a depth of 15–30 cm was never a significant predictor of soil CO_2 fluxes. The only significant positive correlation between soil VWC and CO_2 flux in the earlier snowmelt treatment occurred at a depth of 0–12 cm, and only after the wet winter. Across all dates, soil VWC was positively correlated with soil CO_2 fluxes in the 0–12 cm and 15–30 cm depths. Soil temperature was never a significant predictor of CO_2 fluxes in the later snowmelt treatment, but temperature was sometimes negatively correlated in the earlier snowmelt treatment (i.e., lower CO_2 fluxes in warmer soils).

3.2.2 | Methane

Soil CH_4 fluxes always showed net consumption of atmospheric CH_4, ranging from −13 μg C m^{-2} hr^{-1} in the earlier snowmelt treatment in June 2012 to −26 μg C m^{-2} hr^{-1} in the later snowmelt treatment in September 2011 and July 2012. Fluxes of CH_4 were not statistically different across plots in fall 2010 before the snowmelt treatments began (Figure 4b). During the precipitation-free periods in 2011 and 2012 between snowmelt and September 1, soil CH_4 fluxes showed significant spatial variation and an interactive effect between year and altered snowmelt timing (Table 1). Earlier snowmelt significantly decreased soil CH_4 uptake rates by 24% (i.e., less negative fluxes) after the dry winter but not after the wet winter (Figure 5).

Overall, soil moisture was a weak predictor of soil CH_4 fluxes (Table 2). The only significant positive correlation between soil VWC and CH_4 flux (i.e., higher rates of CH_4 uptake in drier soils) occurred at a depth of 15–30 cm in the later snowmelt treatment, and at a depth of 0–12 cm in the earlier snowmelt treatment after the wet winter. Negative correlations (i.e., higher rates of CH_4 uptake in wetter soils) were also observed for depths of 0–15 cm and 30–60 cm.

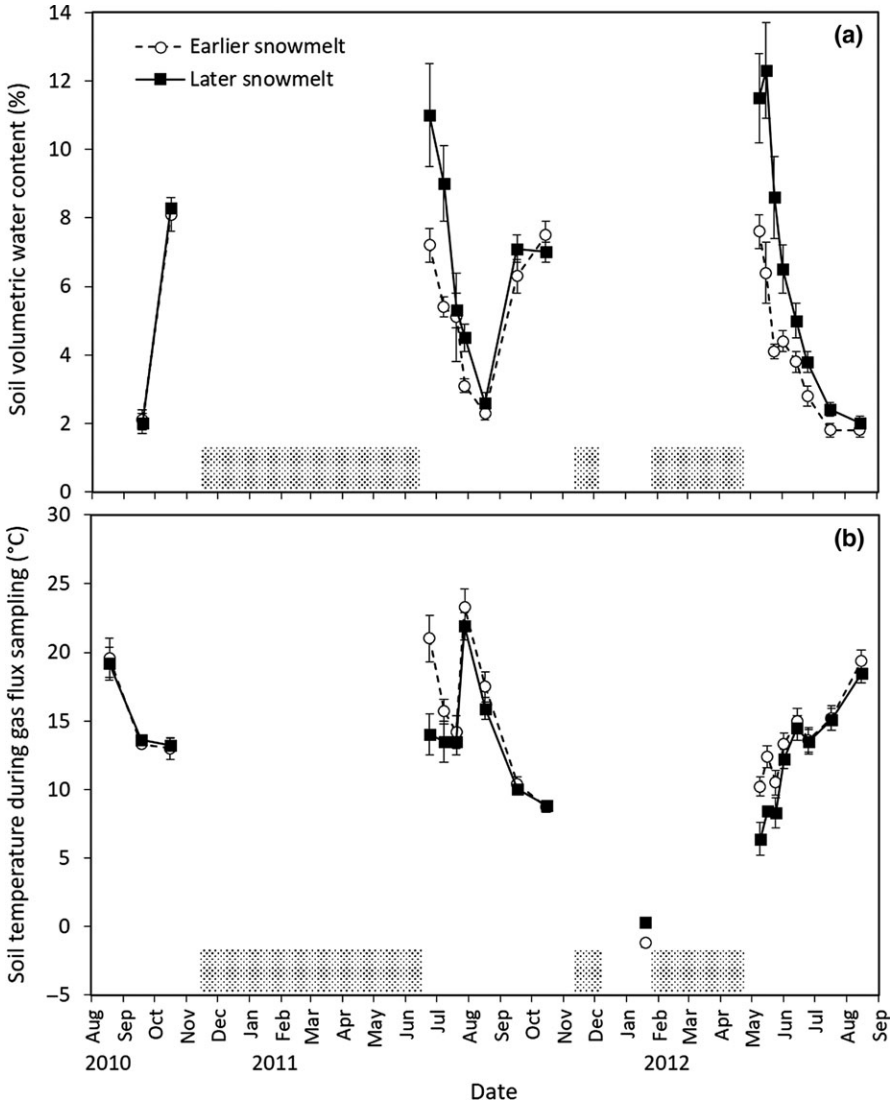

FIGURE 2 Effect of altered snowmelt timing on (a) soil volumetric water content (depth of 0–12 cm; mean ± *SE*; *n* = 8) and (b) soil temperature (depth of 7.5 cm) across all sample dates. Shaded areas indicate when soils were snow-covered and inaccessible

Soil temperature was never a significant predictor of CH_4 fluxes in the later snowmelt treatment, but it was negatively correlated (i.e., higher rates of CH_4 uptake in warmer soils) in the earlier snowmelt treatment after the wet winter.

3.2.3 | Nitrous oxide

During the precipitation-free periods in 2011 and 2012 between snowmelt and September 1, soil N_2O fluxes varied from net uptake to net emission, ranging from −0.7 μg N m^{-2} hr^{-1} in the later snowmelt treatment in July 2011 to 3.8 μg N m^{-2} hr^{-1} in the earlier snowmelt treatment in June 2011 (Figure 4c). Net N_2O consumption was observed both near the beginning (2011) and end (2010 and 2012) of the snow-free period. Fluxes of N_2O were not significantly different across plots in fall 2010 before the snowmelt treatments began. Soil N_2O fluxes were not significantly affected by altered snowmelt timing, spatial variation, or year (Table 1).

Overall, soil moisture was a weak predictor of soil N_2O fluxes (Table 2). The exceptions were (a) in the earlier snowmelt treatment at a depth of 0–12 cm (i.e., inside gas sampling collars) where N_2O emission was positively correlated with soil VWC across all dates; (b) in the later snowmelt treatment where soil VWC at a depth of 30–60 cm was positively correlated with N_2O emission in both years roughly one month after snowmelt; (c) in the later snowmelt treatment where soil VWC at a depth of 0–15 cm was positively correlated with N_2O emission after the dry winter; and (iv) in the earlier snowmelt treatment where soil VWC at a depth of 30–60 cm was positively correlated with N_2O emission after the dry winter. Soil temperature was only a significant predictor for the later snowmelt treatment, where it was negatively correlated with N_2O emission after the dry winter.

3.3 | Cumulative seasonal gas emission/uptake

When integrated across the precipitation-free periods in 2011 and 2012 between snowmelt and September 1, statistically significant effects of altered snowmelt timing were found for CH_4, but not for CO_2 or N_2O (Table 1). The earlier snowmelt treatment had no

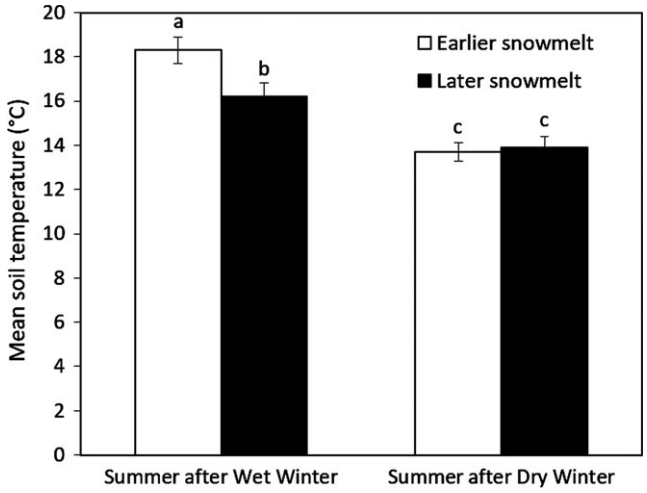

FIGURE 3 Significant interactive effect of interannual variation and snowmelt manipulation on the mean soil temperature (depth of 7.5 cm) during the summer dry season after wet (2011) and dry (2012) winters (see Table 1). Different letters indicate significant differences in Tukey HSD post hoc tests at an alpha level of 0.05

effect on cumulative soil CH_4 uptake after the wet winter, but it did have an effect after the dry winter when it caused a 21% decrease (Figure 6). Cumulative soil CH_4 uptake roughly doubled in the dry winter compared to the wet winter, particularly in the later snowmelt treatment. Cumulative CO_2 emission was roughly 40% greater after the dry winter as compared to after the wet winter. Cumulative N_2O emission was not significantly affected by interannual variation.

3.4 | Microbial assays

Altered snowmelt timing did not affect assays of soil microbial abundances associated with CO_2 production, CH_4 consumption, or N_2O production in either the O horizon or mineral soil (Table 3). For all microbial assays, the O horizon had rates (per unit mass) roughly an order of magnitude greater than the mineral soil. Substrate-induced respiration and CH_4 oxidation potential did not vary significantly between years, but denitrification potential did vary, with two- to threefold higher rates after the dry winter.

3.5 | Net radiative forcing

When fluxes of GHGs were combined in terms of CO_2 equivalents (CO_2e), net GHG emission tracked soil CO_2 fluxes because CH_4 and N_2O typically contributed less than 1% to net radiative forcing (Figure 7). During the precipitation-free periods in 2011 and 2012 between snowmelt and September 1, net GHG emission was significantly affected by spatial variation and year, but not by snowmelt treatments (Table 1). Although net GHG fluxes were 23% greater after the wet winter (5.58 ± 0.26 g CO_2e m^{-2} day^{-1}) than after the dry winter (4.52 ± 0.26 g CO_2e m^{-2} day^{-1}), when integrated across the snow-free period, this pattern reversed, with 335 ± 20 g CO_2e/m^2 emitted after the wet winter and 478 ± 32 g CO_2e/m^2 emitted after the dry winter because of a longer snow-free period.

The contribution of N_2O to net GHG emission was not affected by snowmelt timing, spatial variation, or year (Table 1), with an average net radiative forcing contribution of 0.13%. The contribution of CH_4 to net GHG emission, however, was significantly affected by all three factors. The average "atmospheric cooling effect" of soil CH_4 uptake was −0.33% after the wet winter, −0.41% after the dry winter, −0.33% in the earlier snowmelt treatment, and −0.39% in the later snowmelt treatment.

4 | DISCUSSION

Our overarching goal was to improve mechanistic understanding of how snowmelt timing influences soil GHG dynamics by manipulating snowpack duration in a forest ecosystem without summer precipitation or altering water input. We asked: do altered snowmelt timing and associated soil drying modify GHG fluxes? If not, then spatial and interannual heterogeneity of soil moisture were likely more important than snowmelt timing in controlling soil GHG fluxes. The multiweek disparity in snowmelt timing that we created also occurred naturally during highly contrasting wet and dry years when there was a multimonth disparity in snowmelt timing and a threefold difference in snowfall amount. These results inform baseline soil GHG dynamics during the main drying period following snowmelt. These results also inform what may occur if a typically wet ecosystem experiences summer drought or a more permanent future shift to a drier climate. When summer drought occurs, it is critical to know the biogeochemical legacy of snowmelt timing because it becomes one of the main hydrological events of the year.

For soil CO_2 fluxes, the primary restraint was less about snowmelt timing and more about interannual variation of soil moisture. We hypothesized that earlier snowmelt would reduce rates of CO_2 emission during the snow-free period because of less soil moisture in the 0–15 cm and 15–30 cm layers (Blankinship et al., 2014). The response of soil CO_2 emission to earlier snowmelt was in the expected direction, but not nearly as strong as the 35% decrease predicted by reduced snow depth (Blankinship & Hart, 2012). Therefore, previously observed effects of altered snowmelt timing created by snow removal and addition (e.g., Maljanen, Kohonen, Virkajärvi, & Martikainen, 2007; Nobrega & Grogan, 2007) are more likely explained by the amount of water input rather than the timing of water input.

Although the snowmelt treatments did not significantly affect the magnitude of soil CO_2 fluxes, they did influence the strength of the relationship between CO_2 fluxes and soil moisture. The mechanism by which soil moisture affected CO_2 fluxes appeared different for the earlier and later snowmelt treatments; soil moisture was a consistent and strong positive predictor of CO_2 fluxes in the later snowmelt treatment but not in the earlier snowmelt treatment. If earlier snowmelt induced microbial carbon limitation (Brooks, McKnight, & Elder, 2005; Edwards, Scalenghe, & Freppaz, 2007), partly due to reduced plant root inputs (Scott-Denton, Rosenstiel, &

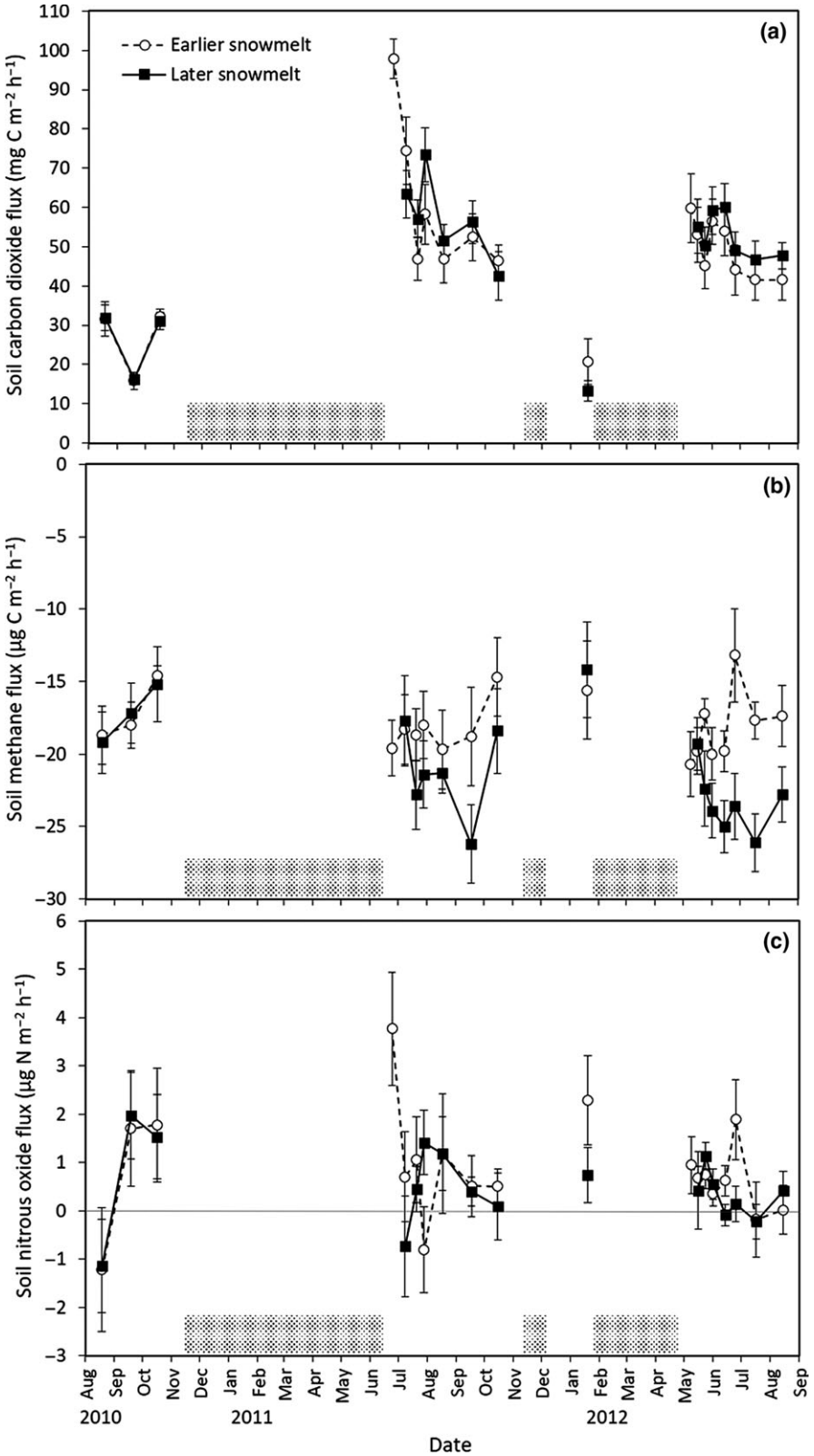

FIGURE 4 Effect of altered snowmelt timing on soil fluxes of (a) carbon dioxide (CO_2), (b) methane (CH_4), and (c) nitrous oxide (N_2O) across all sample dates (mean ± *SE*; *n* = 8). Shaded areas indicate when soils were snow-covered and inaccessible. Negative fluxes indicate net consumption of atmospheric CH_4 and N_2O, presumably by soil microorganisms

Monson, 2006), then this could explain the lack of moisture response in the earlier snowmelt treatment (i.e., substrate rather than water limitation). In the later snowmelt treatment, the soil depth that was the best predictor of surface CO_2 fluxes was not at the surface but instead in the 15–30 cm layer. This was also the layer where soil moisture responded most persistently to altered snowmelt timing (Blankinship et al., 2014), which suggests that microbes at intermediate soil depths play a major role in controlling soil CO_2 emission in this ecosystem, at least when snowmelt occurs later in the spring.

TABLE 2 Linear regression results for effects of soil microclimate predictors (*x*-axis) on greenhouse gas fluxes (*y*-axis) in later and earlier snowmelt treatments

Gas	Snowmelt Treatment	Predictor	6/24/11	7/8/11	7/20/11	7/28/11	8/17/11	5/9/12	5/16/12	5/24/12	6/1/12	6/14/12	6/25/12	7/17/12	8/15/12	All Dates
CO_2	Later	Soil Temp	N/A	+	–	–	–	N/A	–	+	–	–	–	–	–	+
		VWC 12 cm	N/A	–	+	+	+	N/A	+	+	+	+	+	+	–	+
		VWC 15 cm	N/A	N/A	+	+	+	N/A	+	+	+	+	+	–	+	+
		VWC 30 cm	N/A	N/A	+	+	+	N/A	+	+	+	+	+	+	+	+
		VWC 60 cm	N/A	N/A	+	+	+	N/A	+	+	+	+	+	+	+	+
	Earlier	Soil Temp	+	–	–	–	–	+	+	–	–	–	–	–	–	+
		VWC 12 cm	+	+	–	+	+	+	+	–	+	–	+	–	–	+
		VWC 15 cm	N/A	N/A	–	–	–	–	–	–	–	–	–	–	–	+
		VWC 30 cm	N/A	N/A	–	–	–	+	–	+	+	–	–	–	–	+
		VWC 60 cm	N/A	N/A	–	–	+	+	+	–	–	–	–	–	–	+
CH_4	Later	Soil Temp	N/A	–	+	–	+	N/A	+	+	+	+	+	–	–	–
		VWC 12 cm	N/A	+	–	+	+	N/A	+	–	–	–	–	–	–	+
		VWC 15 cm	N/A	N/A	–	–	+	N/A	+	–	–	–	–	–	–	+
		VWC 30 cm	N/A	N/A	+	+	+	N/A	+	+	+	+	+	+	+	+
		VWC 60 cm	N/A	N/A	–	+	+	N/A	+	–	–	–	–	–	+	+
	Earlier	Soil Temp	–	+	+	–	+	–	–	–	+	+	+	–	+	+
		VWC 12 cm	+	+	–	+	+	–	–	–	+	–	–	–	+	–
		VWC 15 cm	N/A	N/A	–	+	+	–	–	–	–	–	–	–	+	–
		VWC 30 cm	N/A	N/A	+	–	–	–	–	+	+	–	+	–	+	–
		VWC 60 cm	N/A	N/A	–	–	–	–	–	–	–	–	+	+	+	–
N_2O	Later	Soil Temp	N/A	–	+	–	+	N/A	+	+	+	–	–	–	–	+
		VWC 12 cm	N/A	+	–	+	–	N/A	+	+	+	+	+	–	–	+
		VWC 15 cm	N/A	N/A	–	+	–	N/A	+	+	+	+	+	–	+	+
		VWC 30 cm	N/A	N/A	+	+	–	N/A	–	+	–	+	–	+	–	+
		VWC 60 cm	N/A	N/A	+	+	–	N/A	+	–	+	+	+	+	–	+
	Earlier	Soil Temp	–	+	–	+	–	–	+	+	+	+	–	–	+	–
		VWC 12 cm	+	–	+	–	+	–	+	+	–	–	–	–	–	+
		VWC 15 cm	N/A	N/A	+	–	–	–	+	+	–	+	–	–	+	+
		VWC 30 cm	N/A	N/A	+	+	–	+	–	+	–	+	+	–	+	+
		VWC 60 cm	N/A	N/A	+	–	–	+	–	+	+	+	–	–	+	+

Note. Only precipitation-free periods were included in this analysis, spanning from the completion of snowmelt (i.e., snow-free date) until the end of August; "All Dates" indicates overall test combining all sampling dates; "+" or "–" indicates direction of linear regression slope; bold with gray shading indicates $p \leq 0.05$ ($n = 8$); soil temperature measured at depth of 7.5 cm; soil volumetric water content (VWC) measured using time domain reflectometry (TDR) at depths of 0–12 cm inside gas sampling collars and adjacent to the collars (Blankinship et al., 2014) at depths of 0–15 cm, 15–30 cm, and 30–60 cm; "N/A" indicates data not available because TDR probes were not installed yet (2011) and/or plots were snow covered (2012).

Our results highlight the biogeochemical importance of moisture in mineral soils that are buffered from summer drought. Microbes living in water films in deeper mineral soils may have been buffered from low atmospheric humidity to sustain their metabolism under otherwise dry conditions. Unfortunately, we only measured microbial abundances in near-surface soils. Remnant water in mineral soils, combined with the well-drained nature of this ecosystem, might explain why there was little variation in soil CO_2 flux despite extreme intra- and interannual variation in soil moisture. This pattern agrees with constant CO_2 fluxes along a soil moisture gradient in a Sierra Nevada subalpine meadow (Blankinship & Hart, 2014). Another possible explanation for relatively constant CO_2 production is the contribution of plant root respiration. Although roots are rare in the top 15 cm of Sierra Nevada soils (Hart & Firestone, 1991; Johnson et al., 2009), perhaps root respiration in the 15–30 cm layer maintained CO_2 production through dry periods. In terms of rates of soil CO_2 emission, the Sierra Nevada seems surprisingly resistant to hydrological change.

However, because soil CO_2 fluxes in this montane forest were so resistant to snowmelt timing and precipitation amount, less

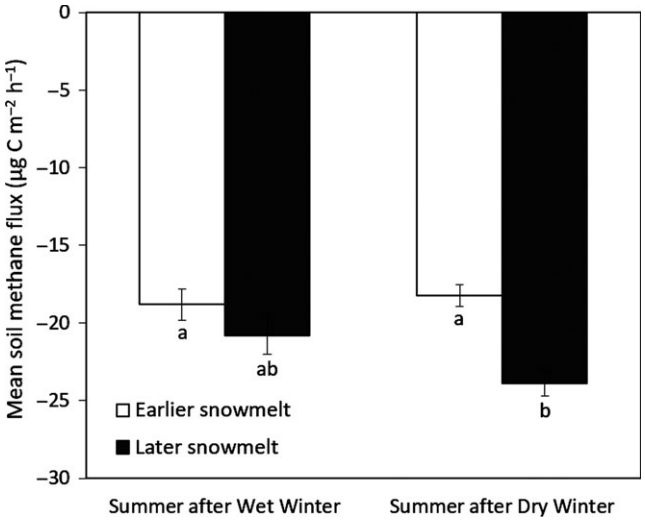

FIGURE 5 Significant interactive effect of interannual variation and snowmelt manipulation on the mean soil methane flux during precipitation-free summers after wet (2011) and dry (2012) winters. Different letters indicate significant differences in Tukey HSD post hoc tests at an alpha level of 0.05

snowfall translated into a longer snow-free period and an *increase* in cumulative soil CO_2 emission in the drier year. The slightly higher mean rates of soil CO_2 emission in the wet year were compensated by the longer snow-free period in the dry year, resulting in greater cumulative CO_2 emission during the dry year. We did not measure diurnal variation or snow-covered CO_2 fluxes, which would confirm the accuracy of these calculations, but we did find low rates when soils were near-frozen in January. Cumulative soil CO_2 emission during the snow-free period appears to be more reflective of precipitation amount than snowmelt timing. Studies demonstrating long-lasting (i.e., months rather than weeks) negative effects of reduced winter snow depth on summer soil CO_2 emission are common (Chimner & Welker, 2005; Maljanen et al., 2007; Moyes & Bowling, 2013; Rogers, Sullivan, & Welker, 2011) and show decreases in cumulative soil CO_2 emission in drier years. However, quantifying effects of snow depth and snowmelt timing on the annual ecosystem carbon balance requires also assessing the subsequent summer-to-winter transition, which is another time of year when soil GHG fluxes are dynamic in seasonally dry California ecosystems (Miller, Schimel, Meixner, Sickman, & Melack, 2005).

Of the three GHGs studied, soil CH_4 fluxes responded most strongly to altered snowmelt timing. However, effects of snowmelt timing on CH_4 fluxes only occurred after the dry winter, and the effect went in a surprising direction. Typically, drier soils show more CH_4 uptake (Blankinship, Brown, Dijkstra, Allwright, & Hungate, 2010; Conrad, 1996; Hanson & Hanson, 1996), but we found *less* CH_4 uptake in the drier soils under earlier snowmelt. This result supports that methanotrophic bacteria can experience metabolic stress due to desiccation (Hanson & Hanson, 1996; Schnell & King, 1996). For example, in soils at a depth of 30–60 cm in the earlier snowmelt treatment, drier soils correlated best with less CH_4 uptake, but only after the dry winter. Whereas in the later snowmelt treatment, a

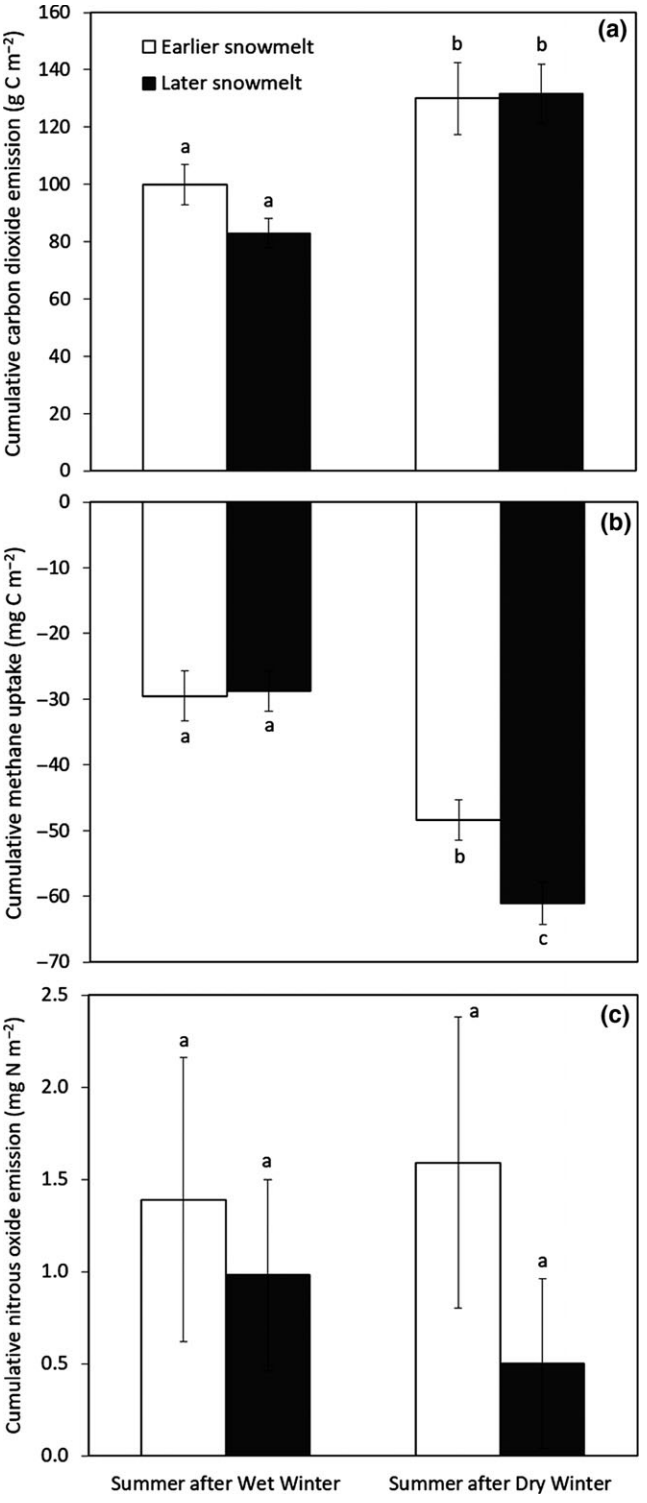

FIGURE 6 Cumulative, time-integrated, full-season fluxes of (a) CO_2, (b) CH_4, and (c) N_2O spanning the precipitation-free period between the completion of snowmelt (i.e., snow-free date) until September 1 following wet (2011) and dry (2012) winters. Different letters indicate significant differences in Tukey HSD post hoc tests at an alpha level of 0.05

stronger relationship between moisture and CH_4 flux was observed at a depth of 15–30 cm. In an excessively well-drained soil with high potential rates for diffusion—such as the one we studied—it is

TABLE 3 Laboratory assays of soil microbial abundances at the end of the snow-free period in the organic horizon (O) and mineral soil (MS) after exposure to altered snowmelt timing

			Aug 2011		Aug 2012	
Variable	Units	Layer	Later Snowmelt	Earlier Snowmelt	Later Snowmelt	Earlier Snowmelt
SIR assay	mg CO_2-C kg^{-1} hr^{-1}	O	N/A	N/A	60.5 (9.9)	49.7 (10.2)
		MS	5.16 (0.66)	5.51 (0.46)	5.24 (0.50)	5.38 (0.42)
MOP assay	μg CH_4-C kg^{-1} hr^{-1}	O	N/A	N/A	15.9 (5.5)	18.2 (4.4)
		MS	4.18 (1.69)	5.16 (1.31)	2.48 (0.95)	3.14 (1.10)
DP assay	μg N_2O-N kg^{-1} hr^{-1}	O	N/A	N/A	52.2 (23.5)	59.8 (15.4)
		MS	2.98[a] (0.94)	2.50[a] (0.86)	7.63[b] (2.46)	8.43[b] (3.17)

Note. Values show mean with standard error in parentheses; "SIR" refers to substrate-induced respiration; "MOP" refers to methane oxidation potential; "DP" refers to denitrification potential; n = 8; "N/A" indicates data not available because of lack of organic material; effects of snowmelt timing and year were not statistically significant ($p > 0.05$), except for DP assay in mineral soil which was higher in 2012 than in 2011 ($p = 0.018$) as indicated by different superscript letters. There were no statistically significant two-way interactions between snowmelt timing and year.

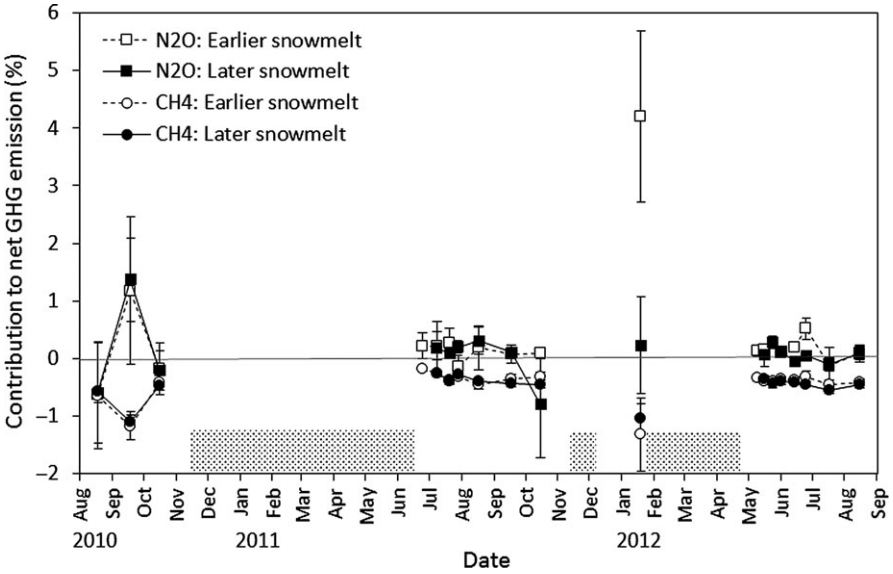

FIGURE 7 Effect of altered snowmelt timing on the contribution of soil methane (CH_4) and nitrous oxide (N_2O) fluxes to net radiative forcing in terms of CO_2-equivalents (mean ± *SE*; n = 8). Positive contributions indicate net warming effect and negative contributions indicate net cooling effect. Shaded areas indicate when soils were snow-covered and inaccessible. Snowmelt treatments began in April 2011

entirely possible that methanotrophic microbial activities in deeper soils affect surface CH_4 fluxes (Adamsen & King, 1993; Bender & Conrad, 1994). We hypothesized that earlier snowmelt would increase soil CH_4 uptake during the snow-free period because of drier soils with less diffusional limitation (Smith et al., 2003; Striegl, 1993), but our data did not support this hypothesis.

After the wet winter, our estimate of cumulative soil CH_4 uptake was relatively low, regardless of snowmelt timing. After the dry winter, on the other hand, cumulative CH_4 uptake was roughly two times greater. Therefore, our results partly agree with the prediction that a longer snow-free period will cause more soil CH_4 uptake in the future (Borken, Davidson, Savage, Sundquist, & Steudler, 2006). The caveat we found is that for the greatest soil CH_4 uptake, the ideal combination is a slow-melting snowpack in a drier-than-average year. The combination of a fast-melting snowpack in a dry year appeared to be detrimental to net CH_4 uptake at a seasonal temporal scale. Reduced soil CH_4 uptake following earlier snowmelt seems most likely in drier climates, during drought (e.g., the second year of our study), and in coarse-textured soils, all due to a greater susceptibility of microbes to desiccation.

For soil N_2O fluxes, our prediction was that earlier snowmelt would reduce soil N_2O emission during the snow-free period due to microbial water limitation (Blankinship & Hart, 2012; Filippa et al., 2009). This prediction was not supported in the ecosystem we studied, likely because these well-drained soils were relatively dry during the entire snow-free period—regardless of snowmelt timing—thus providing few wet microsites for nitrification and few anaerobic microsites for denitrification (Bateman & Baggs, 2005; Bollmann & Conrad, 1998). Sierra Nevada soils show low rates of N_2O emission (Blankinship & Hart, 2014) compared to other snow-covered ecosystems (e.g., Groffman, Hardy, Driscoll, & Fahey, 2006; Filippa et al., 2009). Rather, nitric oxide (NO) emission from soils appears more important in the Sierra Nevada, especially during the summer dry season (Homyak & Sickman, 2014). The absence of a response of N_2O fluxes to snowmelt timing may also reflect the high spatial heterogeneity of soil microbial processes and associated lack of statistical power (Hixson, Walker, & Skau, 1990; McClain et al., 2003).

The only potentially consistent predictor for N_2O fluxes occurred with soil moisture roughly one month after snow disappeared. At this time, regardless of year or snowmelt treatment, there was a

positive correlation across soil depths (sometimes statistically significant and sometimes not) with greater soil N_2O emission in wetter soils. Peak soil N_2O emission commonly occurs during seasonal snowmelt or within weeks of the completion of snowmelt (Brooks, Williams, & Schmidt, 1996; Christensen & Tiedje, 1990), and then emission generally decreases as soils become drier and both nitrification and denitrification become water limited (Bollmann & Conrad, 1998; Filippa et al., 2009; Smith et al., 2003). Our results mostly agree with this expected pattern, except that denitrifying microorganisms were more abundant after the drier year. Soil microbial abundances overall were resistant to snowfall amount and snowmelt timing, but denitrifying microorganisms showed more plasticity.

The potential for increased soil N_2O emission following earlier snowmelt agrees with the increased soil N_2O emission commonly observed after reducing winter snow depth (Groffman et al., 2006; Maljanen et al., 2007, 2009 ; Williams et al., 1998). However, we found that neither snowfall amount nor snowmelt timing exerted a strong control on soil N_2O fluxes. This serves as an example of when winter climate change may only have a weak link to summer soil biogeochemistry. Soil N_2O fluxes at this site are perhaps more strongly controlled by longer-term changes in vegetation and soil organic matter accumulation.

Our second objective was to combine results from all three GHGs to determine whether altered snowmelt timing affects net GHG emission (in terms of CO_2-equivalents) or the contribution of CH_4 and N_2O. Most notably, our results predict a 43% increase in soil GHG emission in dry years as compared to wet years. This effect may be a surprise to GHG accountants in California who assume less soil GHG emission in the Sierra Nevada during drought conditions with shallower and earlier-melting snowpack. Although the "cooling effect" of soil CH_4 uptake on net GHG emission changed from −0.39% with later snowmelt to −0.33% with earlier snowmelt, this change was insignificant in terms of net GHG emission. In this ecosystem, net soil GHG emission can be adequately quantified without considering CH_4 and N_2O fluxes, but this would not be the case in the future if soil CO_2 fluxes decrease due to less plant root respiration or soil organic matter (e.g., after wildfire).

In conclusion, our original conceptual model (Figure 1) overestimated the ability of near-surface soil moisture to explain responses of GHG fluxes to altered snowmelt timing. The strongest legacy of earlier snowmelt was found for soil CH_4 fluxes, but the direction of the effect (i.e., less CH_4 uptake with earlier snowmelt) would not have been predicted without doing the field experiment. Soil CO_2 fluxes in the Sierra Nevada appear surprisingly insensitive to snowmelt timing and interannual variation in precipitation amount. Based on our results, the revised conceptual model should include mechanisms related to microbial resistance to desiccation, persistent activities of microbes and plant roots in deeper mineral soils (at least in forests), and differential control of soil moisture depending on snowmelt timing. Because rates of soil CO_2 emission were similar in extremely wet and dry years, and assuming low rates of CO_2 emission from snowpack, then snowmelt timing becomes the primary determinant of seasonal CO_2 emission. Instead of a longer snow-free period emitting less CO_2, it emitted more. Therefore, with the likely possibility of a shallower and earlier-melting snowpack in the future, these results suggest that the Sierra Nevada may become a larger contributor of GHGs in Calfornia.

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ORCID

Joseph C. Blankinship http://orcid.org/0000-0001-5154-7354

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