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Key Points:
- Rock glacier meltwaters have higher metal concentrations than glacier meltwaters
- Organic matter composition differs between glacier types
- Microbial diversity is higher in rock glaciers than glaciers

Supporting Information:
- Supporting Information S1
- Table S1

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The differing biogeochemical and microbial signatures of glaciers and rock glaciers

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Abstract Glaciers and rock glaciers supply water and bioavailable nutrients to headwater mountain lakes and streams across all regions of the American West. Here we present a comparative study of the metal, nutrient, and microbial characteristics of glacial and rock glacial influence on headwater ecosystems in three mountain ranges of the contiguous U.S.: the Cascade Mountains, Rocky Mountains, and Sierra Nevada. Several meltwater characteristics (water temperature, conductivity, pH, metals, nutrients, complexity of dissolved organic matter (DOM), and bacterial richness and diversity) differed significantly between glacier and rock glacier meltwaters, while other characteristics (Ca^{2+}, Fe^{3+}, SiO_2 concentrations, reactive nitrogen, and microbial processing of DOM) showed distinct trends between mountain ranges regardless of meltwater source. Some characteristics were affected both by glacier type and mountain range (e.g., temperature, ammonium (NH_4^+) and nitrate (NO_3^-) concentrations, and bacterial diversity). Due to the ubiquity of rock glaciers and the accelerating loss of the low-latitude glaciers, our results point to the important and changing influence that these frozen features place on headwater ecosystems.

1. Introduction

Across the American West alpine glaciers and rock glaciers are contracting due to rising air temperatures [*Diaz and Eischeid*, 2007; *McCabe and Fountain*, 2013]. The resulting changes in volume, timing, and chemistry of meltwater discharged by these features appear to be having significant effects on the adjacent alpine headwater ecosystems they feed [*Battarbee et al.*, 2009; *Bogdal et al.*, 2009]. For example, glacial-derived dissolved organic matter (DOM) from ice can be an important source of chemical energy to headwater ecosystems that in some cases fuels heterotrophic respiration much farther downstream [*Hood et al.*, 2009, 2015; *Singer et al.*, 2012]. In addition, it is clear that both glaciers and rock glaciers influence hydrographs and water temperatures of alpine streams [*Fountain and Tangborn*, 1985; *Cable et al.*, 2011; *Dunnette et al.*, 2014; *Millar et al.*, 2013]. The loss of these important ice features is reducing the magnitude of downstream temperature gradients, altering stream microbial community structure [*Wilhelm et al.*, 2013]. Whereas both glaciers and rock glaciers are sources of seasonal meltwater, sediment, and solutes to headwater ecosystems [*Baron et al.*, 2009; *Saros et al.*, 2010; *Singer et al.*, 2012; *Thies et al.*, 2007], the differences between meltwater characteristics of each glacier type are poorly documented.

Glaciers are massive ice bodies that form and persist in areas where annual snow accumulation is greater than annual snow ablation at decadal or longer time spans. Rock glaciers are flowing bodies of permafrost, composed of coarse talus and granular regolith both bound and lubricated by interstitial ice [*Clark et al.*, 1996; *Berthling*, 2011]. Alpine ice glaciers (hereafter simply identified as "glaciers") are discriminated from rock glaciers primarily on the basis of surface appearance and estimated rock content contained within the feature. Glaciers have surfaces of snow and ice and contain relatively low concentrations of rock debris. Rock glaciers have surfaces composed of rock debris whose internal structure may be composed of either rock debris with void spaces between the rocks filled with ice [*Haeberli*, 1985] or bulk ice, like a glacier, mantled with a veneer (approximately less than 1 m thick) rock debris [*Potter*, 1972]. This latter form is known as a debris-covered glacier. It is not possible to easily distinguish between a debris-covered glacier and a rock glacier [*Clark et al.*, 1994]; therefore, here we refer to both as "rock glaciers." Across the contiguous United States rock glaciers are far more common both in number and occupy a much wider geographic range than glaciers (Figure 1). There are approximately 8300 glaciers and perennial snowfields in the contiguous United States, of which about 2000 are considered to be glaciers [*Fountain et al.*, 2007]. In comparison the contiguous United States contains more than 10,000 identified rock glaciers [*Johnson and Fountain*, 2016]. Glaciers, however, have received far more attention than rock glaciers, largely due to their ease of visual identification both in the field and remotely.

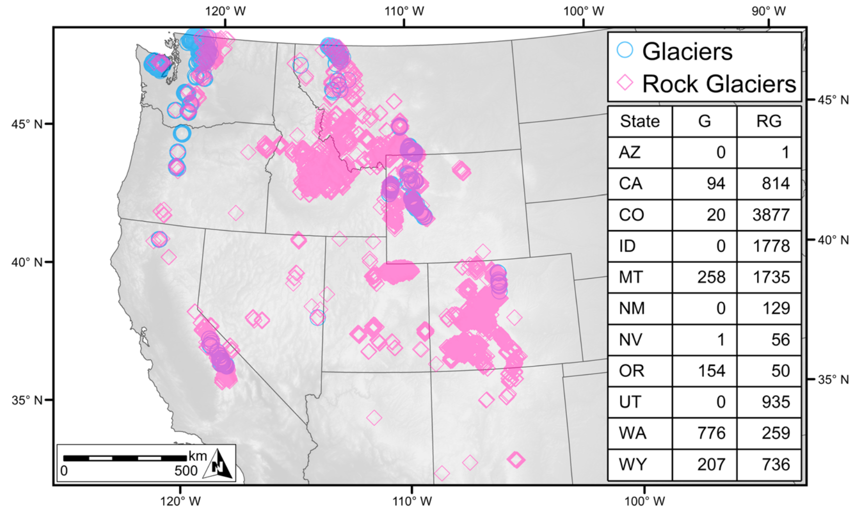

Figure 1. Glacier and rock glacier distribution map. Locations of contiguous U.S. glaciers and perennial ice features drawn from the Randolph Glacier Inventory and rock glaciers drawn from the Fountain Rock Glacier Inventory. Approximately 1500 glacial and perennial ice features are identified, yet >90% of them are clustered in just four states. Conversely, over 10,000 rock glaciers are identified and distributed across a broader geographic range.

The geomorphological characteristics between glaciers and rock glaciers are likely to strongly influence their meltwater characteristics [*Mattson*, 2000; *Williams et al*., 2006]. For example, the continuous talus surface of rock glaciers thermally insulates internal ice (reducing melt) and lowers direct connectivity between the internal ice fraction and the free atmosphere, inhibiting sublimation [*Janke*, 2007]. Consequently, daily runoff volume from rock glaciers is not as variable compared to that of glaciers. Rock glaciers have slower recession rates than glaciers, with the potential to affect headwater biogeochemistry further into the future than glaciers [*Millar and Westfall*, 2008; *Woo*, 2012]. Given the much greater fraction of rock within rock glaciers compared to glaciers, far more mineral surface area is in contact with ice and undergoing active chemical weathering [*Ilyashuk et al*., 2014]. Relative to glaciers, these greater rock glacier meltwater solute concentrations can more readily alter community assemblages of primary producers [*Ilyashuk et al*., 2014; *Thies et al*., 2013]. Nutrient release can also be higher from rock glaciers than glaciers [*Williams et al*., 2007]. Additionally, rock glaciers can change the characteristics and biological processing of carbon compounds entering alpine watersheds [*Williams et al*., 2006].

Here we compare physical, chemical, and microbiological characteristics between glacier and rock glacier meltwaters collected from three mountain ranges of the American West. We asked whether meltwater chemistry and microbiology differed between glaciers and rock glaciers. We also asked if there were characteristic differences in glacier and rock glacier meltwater among mountain ranges.

2. Methods

We conducted a survey of glacier and rock glacier meltwater streams drawn from three geographically distinct alpine regions of the American West (the volcanoes of the Cascade Range of Washington, Oregon, and northern California; the Rocky Mountains of Colorado and Wyoming; and the Sierra Nevada of southern California) (Figure 1). We selected our sample sites to be representative of mountain ranges with different geologies and climates and of both types of glaciers. In total, 25 glaciers and 24 rock glaciers were sampled, during the summers of 2012–2014 (Figure 2).

2.1. Regional Feature Descriptions

Cascade Mountain features were characterized by relatively low mean elevations (2563 ± 503 m) and low mean slopes (23.8° ± 5.4°) and were predominantly underlain by volcanic bedrock. Rocky Mountain features sampled were characterized by relatively high mean elevations (3678 ± 223 m) on steep mean slopes (34.4° ± 7.5°) and underlain by both plutonic and metamorphic bedrock. Sierra Nevada features sampled were characterized by relatively high mean elevations (3679 ± 193 m) on steep mean slopes (30.9° ± 3.8°)

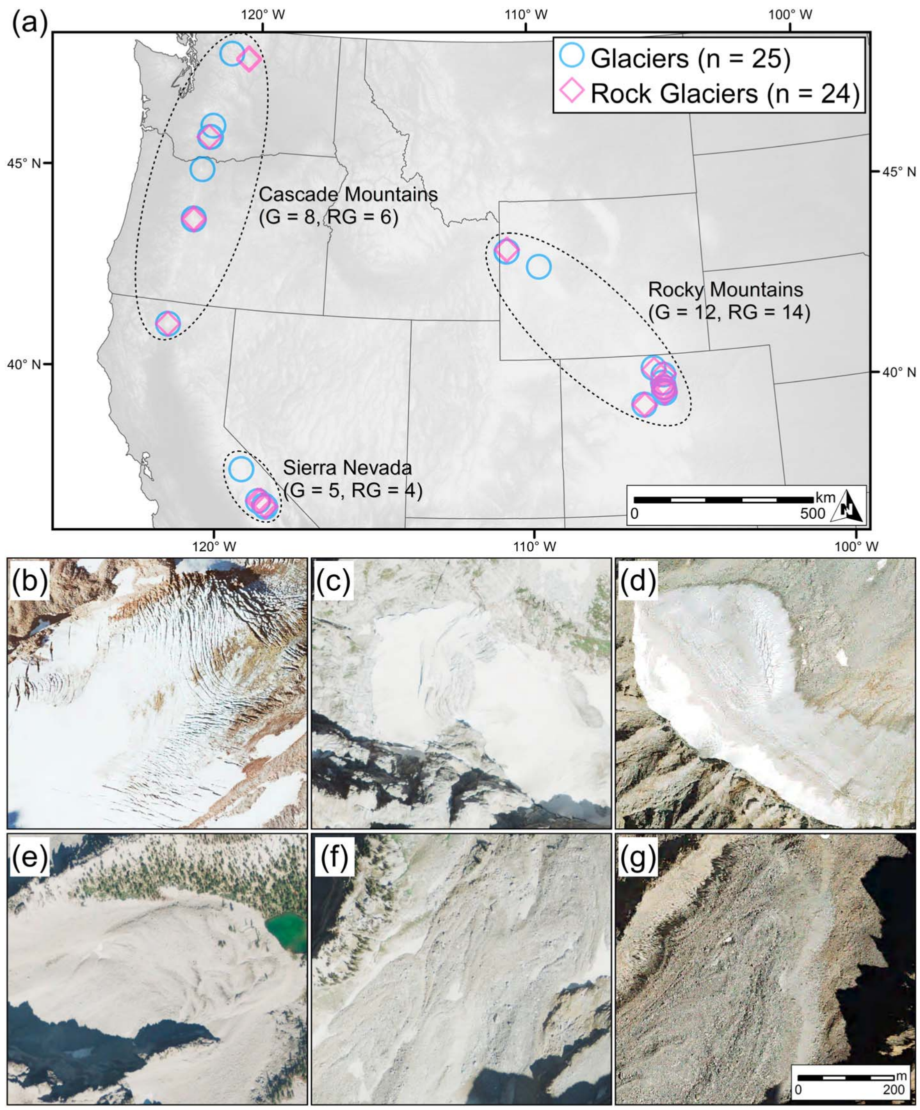

Figure 2. Sample site location map with examples. (a) Sample site locations and (b–g) examples of representative features from each of the three mountain ranges. Eliot Glacier (Figure 2b) and North Cascade Rock Glacier (Figure 2e) are Cascade Mountain sites, Teton Glacier (Figure 2c) and Paintbrush Rock Glacier 3 (Figure 2f) are Rocky Mountain sites, and Middle Palisade Glacier (Figure 2d) and Agassiz Rock Glacier (Figure 2g) are Sierra Nevada sites.

and were predominantly underlain by plutonic and metamorphic bedrock. Detailed topographic characteristics, including contributing drainage area, aspect, and relief, for each alpine region sampled are provided as Supporting Information S1.

The three mountain ranges have different climates. Climatic data were drawn from PRISM modeled 1981–2010 normal atmospheric conditions [*PRISM Climate Group*, 2015]. Cascade Mountain sites have relatively high mean annual precipitation (2675 ± 588 mm, ≈58% ± 18% as snow) and mean annual air temperatures of −0.2 ± 2.1°C. Rocky Mountain sites are relatively drier, with mean annual precipitation of 1237 ± 331 mm (≈49% ± 7% as snow) but with similar mean annual air temperatures of −2.2 ± 1.1°C. Sierra Nevada sites are also dry and cold, with mean annual precipitation of 1092 ± 229 mm (≈57% ± 22% as snow) and mean annual air temperatures of −0.5 ± 1.2°C. Wet atmospheric deposition data, taken from the National Atmospheric Deposition Program, show that Rocky Mountain sites receive greater inorganic reactive nitrogen (N) deposition than the other two regions, with the Colorado Front Range reporting the greatest N deposition of approximately 3.0 kg N ha^{-1} yr^{-1} (Table 1) [*National Atmospheric Deposition Program*, 2015] (http://nadp.isws.illinois.edu/data/). The Colorado Front Range, in particular, is a hot spot of N deposition due to the

Table 1. Site Parameters

Site	Mountain Range	Sample Coordinates	Sample Elevation (m)	Contributing Drainage Area (km^2)	Air Temperature (°C)	Precipitation (mm)	Precipitation as Snow (%)	Wet NO_3^- Deposition ($kg\ ha^{-1}$)	Wet NH_4^+ Deposition ($kg\ ha^{-1}$)
Individual Glaciers									
Adams Glacier	Cascade	46.225340°, -121.524370°	2257	2.29	-3.5	2547	77	5.64	5.22
Bolam Glacier	Cascade	41.428681°, -122.204342°	3100	1.03	-3.8	2208	83	4.29	2.57
Diller Glacier	Cascade	44.140898°, -121.763392°	2274	0.40	1.2	3098	43	3.30	4.06
Eliot Glacier	Cascade	45.394917°, -121.660903°	1890	2.70	-0.2	3652	67	8.70	8.33
Lava Glacier	Cascade	46.232268°, -121.491400°	2399	0.41	-1.2	2613	69	5.30	4.90
McCall Glacier	Cascade	46.519019°, -121.450510°	2053	0.25	0.9	2090	59	4.49	4.17
Prouty Glacier	Cascade	44.112986°, -121.758203°	2436	0.42	0.9	3432	31	3.29	4.03
South Cascade Glacier	Cascade	48.362333°, -121.054929°	1826	2.12	1.3	2791	57	6.23	4.73
Andrews Glacier	Rocky	40.288579°, -105.680264°	3462	0.32	-2.2	1183	48	10.30	5.71
Arapaho Glacier	Rocky	40.023378°, -105.646351°	3737	0.24	-3.5	1134	48	9.32	4.69
Continental Glacier	Rocky	43.341513°, -109.689746°	3682	1.96	-4.9	1045	54	5.46	3.50
Gore Glacier	Rocky	39.752469°, -106.332046°	3496	0.22	-1.7	883	45	6.88	3.83
Isabelle Glacier	Rocky	40.063373°, -105.640994°	3634	0.36	-2.7	1185	48	9.13	4.62
Middle Teton Glacier	Rocky	43.732330°, -110.802640°	3271	0.63	-3.1	2430	61	10.07	6.44
Peck Glacier	Rocky	40.068332°, -105.663810°	3461	0.19	-1.2	1129	45	8.99	4.57
Powell Glacier	Rocky	39.762535°, -106.338675°	3817	0.03	-2.9	911	44	6.86	3.82
Rawah Glacier	Rocky	40.670189°, -105.957956°	3499	0.19	-2.1	1144	47	8.32	4.71
Rowe Glacier	Rocky	40.487127°, -105.645890°	3999	0.02	-4.0	1282	62	7.49	3.94
Saint Vrain Glacier	Rocky	40.162104°, -105.659327°	3551	0.05	-2.4	1196	45	9.15	4.81
Teton Glacier	Rocky	43.740928°, -110.790954°	3206	0.48	-3.2	2473	61	10.28	6.59
East Conness Glacier	Sierra	37.968609°, -119.313354°	3527	0.06	0.1	1266	55	3.42	2.02
Goethe Glacier	Sierra	37.210199°, -118.707668°	3667	0.14	-1.2	1099	67	3.26	2.03
Middle Palisade Glacier	Sierra	37.076582°, -118.458395°	3518	0.58	-1.4	1212	67	3.25	1.98
North Palisade Glacier	Sierra	37.111465°, -118.506498°	3603	1.49	-1.9	1217	67	3.32	2.04
West Conness Glacier	Sierra	37.971285°, -119.318549°	3492	0.31	0.2	1266	55	3.44	2.04
Individual Rock Glaciers									
Adams Rock Glacier	Cascade	46.227090°, -121.552670°	1910	0.11	2.2	2915	43	5.95	5.52
Bolam Rock Glacier	Cascade	41.429724°, -122.209437°	3011	0.46	-1.5	2118	73	4.33	2.59
Diller Rock Glacier	Cascade	44.145730°, -121.765737°	2320	0.53	0.7	3157	42	3.38	4.18
North Cascades Rock Glacier 1	Cascade	48.250517°, -120.406968°	2164	0.08	0.8	1439	62	3.32	2.57
North Cascades Rock Glacier 3	Cascade	48.290884°, -120.413696°	2182	0.30	0.2	1427	62	3.29	2.54
Prouty Rock Glacier	Cascade	44.106983°, -121.750503°	2443	0.60	0.8	3513	42	3.36	4.11
Arapaho Rock Glacier	Rocky	40.022482°, -105.637699°	3583	0.47	-3.0	1151	49	9.26	4.65
Confusion Rock Glacier	Rocky	39.749054°, -106.307559°	3558	0.04	-0.6	831	33	6.84	3.80
Duck Lake Rock Glacier	Rocky	39.759668°, -106.331853°	3702	0.11	-2.6	904	44	6.88	3.83
Gibraltar Rock Glacier	Rocky	40.155336°, -105.654799°	3463	0.03	-2.0	1170	45	8.54	4.46
Ilans Rock Glacier	Rocky	40.627544°,-105.943468°	3396	0.18	-1.1	1188	48	8.48	4.76
Louise Rock Glacier	Rocky	40.508941°, -105.625321°	3419	0.37	-1.4	1125	48	7.06	3.73
Navajo Rock Glacier	Rocky	40.061200°,-105.636092°	3496	0.15	-2.0	1200	49	9.46	4.77
Paintbrush Rock Glacier 1	Rocky	43.783379°, -110.803140°	2974	0.09	-0.6	1630	57	9.43	6.03
Paintbrush Rock Glacier 3	Rocky	43.790463°, -110.778199°	2720	1.29	0.0	1668	57	7.79	4.97
Paintbrush Rock Glacier 2	Rocky	43.783451°, -110.797469°	2866	0.13	-0.3	1635	47	9.53	6.10
Peck Rock Glacier	Rocky	40.071642°, -105.664310°	3272	0.11	-0.6	1126	35	8.93	4.54
Powell Rock Glacier	Rocky	39.764031°, -106.339080°	3769	0.09	-2.8	915	44	6.85	3.81
Saint Vrain Rock Glacier	Rocky	40.163962°, -105.667730°	3704	0.30	-2.7	1196	45	8.91	4.66
Taylor Rock Glacier	Rocky	40.276985°, -105.669918°	3318	0.66	-2.0	1213	48	10.69	5.91
Agassiz Rock Glacier	Sierra	37.123760°, -118.519432°	3578	1.02	-1.4	1053	66	2.94	1.80

Table 1. (continued)

Site	Mountain Range	Sample Coordinates	Sample Elevation (m)	Contributing Drainage Area (km^2)	Air Temperature (°C)	Precipitation (mm)	Precipitation as Snow (%)	Wet NO_3^- Deposition ($kg\ ha^{-1}$)	Wet NH_4^+ Deposition ($kg\ ha^{-1}$)
Goethe Rock Glacier	Sierra	37.220051°, -118.714092°	3596	0.28	-0.4	1104	67	3.26	2.03
Middle Palisade Rock Glacier	Sierra	37.084854°, -118.449419°	3342	1.63	-0.6	1090	67	2.99	1.81
North Lake Rock Glacier	Sierra	37.230261°, -118.620354°	2830	0.41	2.1	519	0	1.80	1.11
				Mountain Range Summaries					
Cascade Mountain glaciers	Cascade	45.302055°, -121.613506°	2279(374)	1.203(0.94)	-0.54(1.94)	2804(520)	61(16)	7.79(4.97)	1.5(0.7)
Cascade Mountain rock glaciers	Cascade	45.408488°, -121.349835°	2338(342)	0.347(0.202)	0.52(1.06)	2428(819)	54(12)	9.53(6.1)	1.14(0.45)
Rocky Mountain glaciers	Rocky	41.007738°, -106.987388°	3568(213)	0.391(0.505)	-2.84(0.96)	1333(512)	51(7)	8.93(4.54)	2.62(0.62)
Rocky Mountain rock glaciers	Rocky	40.894153°, -106.918331°	3374(309)	0.287(0.33)	-1.54(0.99)	1211(255)	46(6)	6.85(3.81)	2.6(0.5)
Sierra Nevada Glaciers	Sierra	37.467628°, -118.860893°	3561(65)	0.514(0.517)	-0.85(0.86)	1212(61)	62(6)	8.91(4.66)	1.83(0.1)
Sierra Nevada Rock Glaciers	Sierra	37.164731°, -118.575824°	3336(309)	0.836(0.535)	-0.06(1.3)	941(245)	50(29)	10.69(5.91)	1.47(0.3)
All glaciers	All	41.259140°, -115.820595°	3154(254)	0.68(0.77)	-1.7(1.7)	1779(842)	56(12)	6.41(2.54)	2.11(0.77)
All rock glaciers	All	41.155790°, -115.614663°	3109(546)	0.39(0.40)	-0.8(1.4)	1470(729)	49(15)	6.39(2.71)	2.05(0.81)

combination of wind patterns and concentrated human settlement and agricultural activity directly to the east [*Baron et al.*, 2000].

2.2. Glacier and Rock Glacier Descriptions

We visited the 25 glacier and 25 rock glaciers, some more than once, collecting 37 glacier meltwater samples (Cascade Mountains $n = 12$, Rocky Mountains $n = 20$, and Sierra Nevada $n = 5$) and 33 rock glacier meltwater samples (Cascade Mountains $n = 9$, Rocky Mountains $n = 20$, and Sierra Nevada $n = 4$). Glaciers and rock glaciers sampled within our survey were chosen to be representative active features from each range based on their size (greater than 0.5 km^2) and apparent activity level (movement of the feature). Glaciers sampled in the survey were determined to be active based on the presence of crevasses. Rock glaciers sampled in the survey were determined to be active based on the presence of surficial ridges and swale flow banding. Glaciers and rock glaciers were also chosen by proximity to trailhead to allow for proper preservation and short field handling times of samples. Some conveniently accessible sites were sampled more than once to estimate how representative single samples were and did they account for interannual variability. For all analysis where features were sampled more than once, average values for each site were used for statistical analyses and figures. While in absolute terms fewer samples were collected within the Sierra Nevada compared to the other mountain ranges, in relative terms this simply reflects the much smaller total number of extant large glaciers (fewer than 10 large ice glaciers) within the Sierra Nevada sampling area compared to the sampling areas of the other two mountain ranges (Cascades $n = 254$ and Rocky Mountains $n = 41$). Additionally, the Sierra Nevada study area is considerably smaller (≈12,000 km^2) than the Cascade Mountain (≈150,000 km^2) and Rocky Mountain (≈120,000 km^2) study areas, resulting in the highest sampling spatial density of the three mountain ranges. Metamorphic geology underlays 29% of our sites, plutonic geology 49% of our sites, and volcanic geology 22% of our sites (Supporting Information S1).

2.3. Sample Collection Methods

Samples were collected from outflow streams as close to the glacier or rock glacier terminus as possible. This ranged from immediately below the ice to up to 10 m away. Each sample was collected in late summer (August–September 2012–2014) to capture the greatest contribution of ice melt and least amount of seasonal snowmelt. Many of the sites within our survey still have annual snow melting out well into June and early July. PRISM climate data show significant decreases in air temperatures starting during late September at virtually every site; thus, it is unlikely that higher contributions of glacier or rock glacier ice melt would be seen in later months for any of our sample sites (Supporting Information S1). PRISM data also show increases in monthly precipitation beginning in October at every site; thus, chances of meltwater sample dilution or hydrochemical alteration from more recent precipitation would have greatly increased if glaciers and rock glaciers had been sampled later in the year (Supporting Information S1). Meltwater temperature and specific conductance were measured in situ with a hand-held probe (Thermo Scientific Orion 3-Star). Water and stream sediment samples from terminus outflow of each glacier or rock glacier feature were collected according to standard methods (http://www.nrel.colostate.edu/projects/lvws/pages/accesstodata/fieldlabmethods.html). Samples for pH, reactive nitrogen (NH_4^+ and NO_3^-), metal cation concentrations, and SiO_2 were collected in acid-washed Nalgene® high density polyethylene (HDPE) plastic bottles, after rinsing three times with sample water. Samples collected for carbon and DOM measurement and total dissolved nitrogen (TDN) were collected in glass borosilicate bottles that had been previously sterilized in a muffle furnace (900°C for 6 h). Sediment samples collected for microbial analyses were collected in sterilized 60 mL HDPE plastic centrifuge tubes and then subsampled into 5 mL cryotubes within 6 h of collection.

Samples for reactive nitrogen, pH, and metals were filtered (0.2 μm Millipore filter) within 24 h of collection. Samples for carbon chemistry and TDN were filtered (Whatmann GF/F) then acidified to ≈pH 3 within 24 h of collection. Samples collected for fluorescence analysis were not acidified. Immediately after being subsampled, cryotube samples for microbial community analysis were flash frozen in liquid nitrogen to preserve the integrity of the nucleic acids.

2.4. Laboratory Analysis

We measured pH with a Radiometer Copenhagen TTT85 Titrator. Metals and other ions derived from weathering were measured using inductively coupled plasma optical emission spectrometry at the Environmental Sciences Research Laboratory at the University of California, Riverside. Dissolved silica (SiO_2), ammonium (NH_4^+), nitrate (NO_3^-), total inorganic nitrogen, total dissolved nitrogen (TDN), and dissolved organic carbon (DOC) were analyzed using standard methods at the EcoCore facility at Colorado State University. Fluorescence and UV scans were completed for estimates of humification index (HIX), specific ultraviolet absorption at 254 nm (SUVA254), fluorescence index (FI), and freshness index (β:α). Humification index (HIX) serves as an indicator of the humicity of organic matter [*Zsolnay et al.*, 1999] and SUVA254 as an indicator of aromaticity [*Weishaar et al.*, 2003]. Combined, HIX and SUVA254 values allow us to estimate DOM complexity. Fluorescence index (FI) is an indicator of proteineitity [*McKnight et al.*, 2001; *Cory and McKnight*, 2005] and indicative of the level of microbial processing in DOM. Freshness index (β:α) is an indicator of freshness of organic matter [*Parlanti et al.*, 2000]. Fluorescence samples were analyzed on a Horiba Scientific Aqualog.

2.5. Microbial Analysis

Samples for microbial community analysis were collected from stream sediments (approximately 10 cm depth) fed by meltwaters at the terminus of the glacier and rock glacier for 23 sites in 2012 and 2013. Stream sediments were collected within 5 m of glacial terminus. Polymerase chain reaction (PCR) amplification was performed for each DNA sample in triplicate and pooled. To facilitate multiplexed sequencing, barcoded primers with Illumina adapters and linkers were used to amplify the V4 region of bacterial 16S rRNA genes [*Caporaso et al.*, 2011, 2012]. PCR reactions were performed with KAPA2G Fast HotStart ReadyMix (KapaBiosystems, Wilmington, MA, USA). Negative controls were included to test for contamination. Amplicon concentrations were measured with a PicoGreen dsDNA assay (Life Technologies, Grand Island, NY, USA). The amplicons were cleaned with the UltraClean PCR Clean-Up Kit (MoBio Laboratories Inc., Carlsbad, CA) and sequenced on an Illumina MiSeq platform at Michigan State University. Sequences were demultiplexed, and forward and reverse 16S rRNA gene reads were merged.

2.6. Data Analysis

Data were analyzed using the R programming language, with the *t* test configured for nonparametric Welch-Satterthwaite test to compare differences in meltwater biogeochemistry between glacier types. Our use of a Welch-Satterthwaite test allowed for comparison of samples of unequal variance and distribution. The lmfit function in R was used for analysis of variance testing to compare meltwater biogeochemistry between mountain ranges. Plot function and ggplot2 package were used for figures. Humicity of organic matter was examined as humification index (HIX) and was calculated as cumulative area under 435–480 nm emission at 254 nm excitation divided by cumulative area under 300–345 nm at 254 nm excitation. DOM complexity was examined as specific ultraviolet absorption at 254 nm (SUVA254) and was calculated as UV absorbance at 254 nm divided by measured DOC concentration (mg L^{-1}). Proteineitity of organic matter was examined with fluorescence index (FI) and was calculated as emission at 470 nm divided by emission at 520 nm, both at 370 nm excitation. Freshness of DOM was examined as freshness index (β:α) and was calculated as intensity of emission at 380 nm and 310 nm excitation divided by maximum intensity of emission between 420 and 435 nm at 310 nm excitation. Bacterial diversity between glacier types as well as between mountain ranges was examined using 16S sequencing. Microbial 16S sequences were analyzed using the Mothur program (June 2015) [*Kozich et al.*, 2013]. Sequences were unified, made unique, aligned, filtered, removed of chimeras, filtered, and assigned operational taxonomic units (OTUs) using the MiSeq SOP (June 2015) [*Kozich et al.*, 2013]. Bacterial taxa were assigned to OTUs using the Silva Comprehensive Ribosomal RNA database (www.arb-silva.de). Samples were not rarefied. Alpha and beta diversity were estimated through rarefaction plots created in R. The location of data can be found within the Acknowledgments section.

3. Results

3.1. Differences in Glacier Type

Water samples from glaciers and rock glaciers differed significantly in physical and chemical characteristics. Across all three mountain ranges, rock glacier meltwaters had higher temperatures, pH, and conductivity than glacier meltwaters (Figures 3a–3c). Rock glacier meltwaters were also enriched in a range of weathering products including SiO_2, Ca^{2+}, K^+, Mg^{2+}, and Sr^{2+} but depleted in Fe^3 and Mn^{2+} relative to glaciers (Table 2). In addition, NO_3^- concentrations, and TDN, were significantly higher in meltwater samples from rock glaciers than glaciers. However, NH_4^+ concentrations were more enriched in glacier meltwaters than rock glacier meltwaters (Figures 3d–3f).

We evaluated differences in organic chemistry characteristics of the meltwaters. We found no significant difference in DOC concentrations between glacier and rock glacier meltwaters but clear differences in composition of fluorescing dissolved organic matter (FDOM) between glacier types (Table 3). Humification index (HIX) was twice as high, on average, in the meltwaters from rock glaciers than glaciers, consistent with more complex, humic-like carbon being released from rock glaciers (Table 3). However, there was no clear difference in fluorescence index (FI) or freshness index (β:α) between glacier meltwater types (Table 3). Average FI for all samples combined (1.6 ± 0.12) suggested that most DOM from both glacier meltwater types was of microbial rather than terrestrial plant origin.

Evaluation of the 16S sequences showed clear differences in the bacterial communities between glacier and rock glacier stream sediments. The microbial communities sampled from rock glacier stream sediments had higher α diversity (within sample diversity) compared to samples derived from glacial stream sediments (Figure 4a). Rock glacier stream sediments also had higher richness in microbial communities, with a total of 4408 more unique operational taxonomic units (OTUs) unique to all rock glacier stream sediments than those found in all glacier stream sediment communities (Figure 4b). Whereas there were a considerable number of shared OTUs (7673) between glacial stream sediment types, there were also a large number of OTUs that were unique to each glacial stream sediment type with variability between sites as large as variability between glacier and rock glacier stream sediments.

The most common bacterial taxa present in both glacier and rock glacier sites were also the most abundant taxa within each sample. The most abundant genus, seen in all samples, was the psychrophile, *Polaromonas* sp. Also present in all samples were the nitrite oxidizers *Nitrospira sp*. and the psychrophiles *Hymenobacter* sp., *Deinococcus* sp., and *Sulfuricurvum* sp. *Sulfuricurvum*; a sulfur oxidizer previously found in glacial-fed meltwaters of the European Alps was also present in our glacier stream sediments, but not rock glacier stream sediments [*Wilhelm et al.*, 2014]. Rock glacier stream sediments had many more unique and identifiable genera compared to glacier stream sediments, including many genera that are noted to be tolerant of warmer temperatures and common to soil microbial communities, including *Anaerolineacea* sp., *Bryobacter* sp., *Gemmatimonas* sp., *Planctomycetaceae* sp., *Sphingomodales* sp., and *Terrabacter* sp. Identifiable genera associated with rock glaciers were also more diverse than those associated with glaciers, while many of the OTUs endemic to the glacier sites did not have identified species within the Silva reference database.

3.2. Regional Differences

Beyond differences in biogeochemical characteristics between glacier meltwater types, our analyses identified characteristics that appeared to be primarily influenced by geography. It should be noted that sample sizes

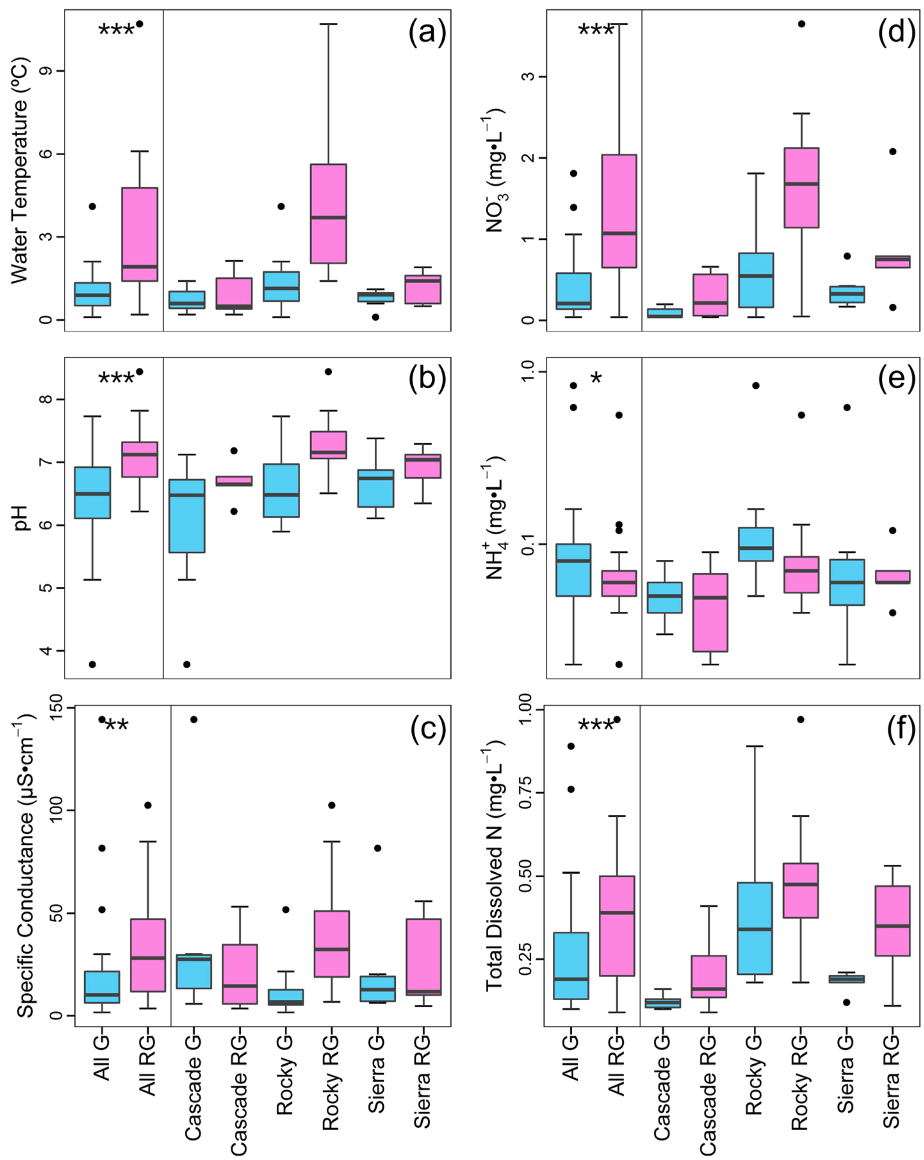

Figure 3. Physical and chemical measurements for glaciers and rock glaciers by mountain range. Glaciers are blue boxes, and rock glaciers are pink boxes. Boxes represent upper and lower quartiles, whiskers indicate range of measurement, points indicate outliers, and bold bars indicate sample mean. While fewer samples were collected within the Sierra Nevada ($n = 11$) compared to the other mountain ranges (Cascade $n = 13$ and Rocky Mountains $n = 26$), this simply reflects the much smaller total number of extant large glaciers within the Sierra Nevada sampling area compared to the sampling areas of the other two mountain ranges. The Welch-Satterthwaite T test for nonparametric samples sets accounts for this disparity between sample sizes, and * indicates significance at $p < 0.05$, ** at $p < 0.01$, and *** at $p < 0.001$.

were different between each of the mountain ranges in the study; however, variability within each range for most of the biogeochemical attributes measured was less than variability between mountain ranges (Figure 3 and Tables 2 and 3), though relative differences between meltwater types were consistent between mountain ranges. It should also be noted that differences in sample size between ranges were related to the total number of features within each mountain range (i.e., the Sierra Nevada has the smallest sample size within our study, but the Sierra Nevada also hosts the fewest number of glaciers and rock glaciers).

Meltwaters from Rocky Mountain rock glaciers were warmer than rock glacier meltwaters from the Sierra Nevada or Cascade Mountains (Figure 3a). Conductivities were higher in the Cascade Mountains compared to the other mountain ranges, though the greatest difference in conductivity between glacier meltwaters (11 $\mu S\,cm^{-1}$) and rock glacier meltwaters (37 $\mu S\,cm^{-1}$) was found in Rocky Mountain sites. Differences in metals varied with

Table 2. Metal Concentrations[a]

Sample Group	Al		Ca		Fe		K		Mg		Mn		SiO_2		Sr	
All Feature Summaries																
All glaciers	0.93	(0.73)	1.55	(1.79)	**0.21**	(**0.37**)	0.20	(0.19)	0.25	(0.35)	0.01	(0.02)	1.04	(1.71)	0.01	(0.01)
All rock glaciers	0.77	(0.74)	**3.68**	(**3.22**)	0.03	(0.05)	**0.47**	(**0.67**)	**0.75**	(**1.21**)	0.00	(0.00)	**3.04**	(**3.42**)	**0.01**	(**0.01**)
Mountain Range Summaries																
Cascade Mountain glaciers	0.84	(0.58)	2.43	(2.13)	**0.20**	(**0.13**)	0.18	(0.17)	0.31	(0.28)	0.02	(0.02)	1.30	(3.19)	0.01	(0.01)
Cascade Mountain rock glaciers	0.05	(0.01)	1.46	(1.01)	0.04	(0.00)	0.24	(0.03)	0.16	(0.10)	0.00	(0.00)	3.94	(6.40)	0.01	(0.00)
All Cascade Mountain features	0.73	(0.59)	1.98	(1.72)	0.16	(0.13)	0.21	(0.17)	0.24	(0.22)	0.01	(0.02)	2.52	(5.13)	0.01	(0.01)
Rocky Mountain glaciers	0.79	(0.70)	1.42	(1.91)	0.07	(0.13)	0.23	(0.23)	0.28	(0.42)	0.01	(0.00)	0.53	(0.56)	0.01	(0.01)
Rocky Mountain rock glaciers	0.66	(0.69)	**4.79**	(**3.09**)	0.03	(0.05)	0.56	(0.85)	**1.20**	(**1.43**)	0.00	(0.00)	**2.77**	(**2.95**)	0.02	(0.01)
All Rocky Mountain features	0.72	(0.67)	3.25	(3.08)	0.05	(0.09)	0.43	(0.28)	0.78	(1.15)	0.00	(0.00)	1.74	(2.32)	0.01	(0.01)
Sierra Nevada Glaciers	1.45	(1.09)	0.78	(0.39)	**0.54**	(**0.74**)	0.18	(0.17)	0.11	(0.15)	0.01	(0.20)	1.76	(2.77)	0.01	(0.00)
Sierra Nevada Rock Glaciers	1.20	(0.83)	3.45	(4.27)	0.05	(0.06)	0.53	(0.03)	0.30	(0.33)	0.00	(0.00)	2.70	(3.57)	0.01	(0.01)
All Sierra Nevada features	1.31	(0.87)	1.99	(3.05)	0.37	(0.63)	0.34	(0.40)	0.20	(0.25)	0.01	(0.02)	2.19	(3.03)	0.01	(0.01)

[a]Boldface indicates significance of statistical relationship at $p < 0.05$.

mountain range and appeared to be related to parent material and bedrock geology (Table 2). Rocky Mountain glacier and rock glacier meltwaters had higher NO_3^- concentrations (1.1 ± 0.92 mg L^{-1}) than Cascade Mountain or Sierra Nevada features (0.19 ± 0.22 mg L^{-1} and 0.37 ± 0.23 mg L^{-1}, respectively) (Figure 3e). Similarly, NH_4^+ concentrations were higher in the Rocky Mountain glacier sites (0.16 ± 0.07 mg L^{-1}) than both other mountain ranges. As stated above, there was no significant difference in DOC concentrations between mountain ranges; however, the fluorescence results suggested more DOM of microbial origin in the meltwaters of the Cascade Mountains and Sierra Nevada compared to the Rocky Mountains (Table 3). The Cascade Mountains had a higher mean $\beta:\alpha$ ratio than both the Sierra Nevada and Rocky Mountains, indicative of "fresher" or more recent carbon being released from the glaciers and rock glaciers of the Cascade Mountains. SUVA254 was lower in the Rocky Mountains than Sierra Nevada and Cascade Mountain sites, meaning that carbon from glacier and rock glacier effluent in the Rocky Mountains has lower aromaticity than that from the Cascade Mountains and Sierra Nevada (Table 3). The humification index (HIX) was nearly 3 times higher in rock glacier meltwaters of the Cascade Mountains and the Rocky Mountains than ice glacier meltwaters, suggestive of higher humicity and allochthonous sources of DOM in rock glacier effluent in these two mountain ranges.

We also found pronounced differences in microbial communities among mountain ranges. The microbial communities sampled in the Rocky Mountains had the highest α diversity of any region (Figure 4a), with microbial community α diversity being the lowest in the Sierra Nevada. Differences in microbial community α diversity were significant for rock glacier samples in both the Sierra Nevada and Cascade Mountains, while differences were more variable for microbial communities sampled from the Rocky Mountains (Figure 4a). The Rocky Mountains also had the greatest richness in sediments fed by meltwaters, with 12,906 OTUs in total, 6643 of

Table 3. Fluorescence Indices for Dissolved Organic Matter[a]

Sample Group	DOC (mg L^{-1})		Fluorescence Index		Freshness Index		Humification Index		SUVA254	
All Feature Summaries										
All glaciers	0.61	(0.43)	1.61	(0.12)	0.83	(0.28)	0.54	(0.44)	2.29	(1.23)
All rock glaciers	0.66	(0.43)	1.60	(0.12)	0.82	(0.25)	**1.38**	(**1.87**)*	2.21	(1.37)
Mountain Range Summaries										
Cascade Mountain glaciers	0.35	(0.12)	1.69	(0.15)	1.10	(0.44)	0.46	(0.55)	3.36	(0.93)
Cascade Mountain rock glaciers	0.72	(0.60)	1.66	(0.13)	0.92	(0.22)	**1.75**	(**3.18**)*	2.51	(1.38)
All Cascade Mountain features	0.52	(0.44)	1.68	(0.14)	**1.01**	(**0.35**)*	1.06	(2.19)	2.96	(1.19)
Rocky Mountain glaciers	0.81	(0.48)	1.56	(0.08)	0.72	(0.08)	0.66	(0.41)	1.56	(0.78)
Rocky Mountain rock glaciers	0.77	(0.38)	1.56	(0.11)	0.77	(0.11)	**1.55**	(**1.42**)*	1.65	(1.08)
All Rocky Mountain features	0.79	(0.42)	1.56	(0.10)	0.75	(0.10)	1.14	(1.15)	**1.61**	(**0.94**)*
Sierra Nevada Glaciers	0.53	(0.39)	1.64	(0.09)	0.74	(0.07)	0.41	(0.38)	2.51	(1.39)
Sierra Nevada Rock Glaciers	0.31	(0.13)	1.63	(0.10)	0.85	(0.11)	0.44	(0.64)	3.46	(1.41)
All Sierra Nevada Features	0.43	(0.31)	1.63	(0.09)	0.79	(0.10)	0.43	(0.48)	2.94	(1.41)

[a]Boldface indicates significance of statistical relationship at $p < 0.05$.
*significance at $p < 0.01$.

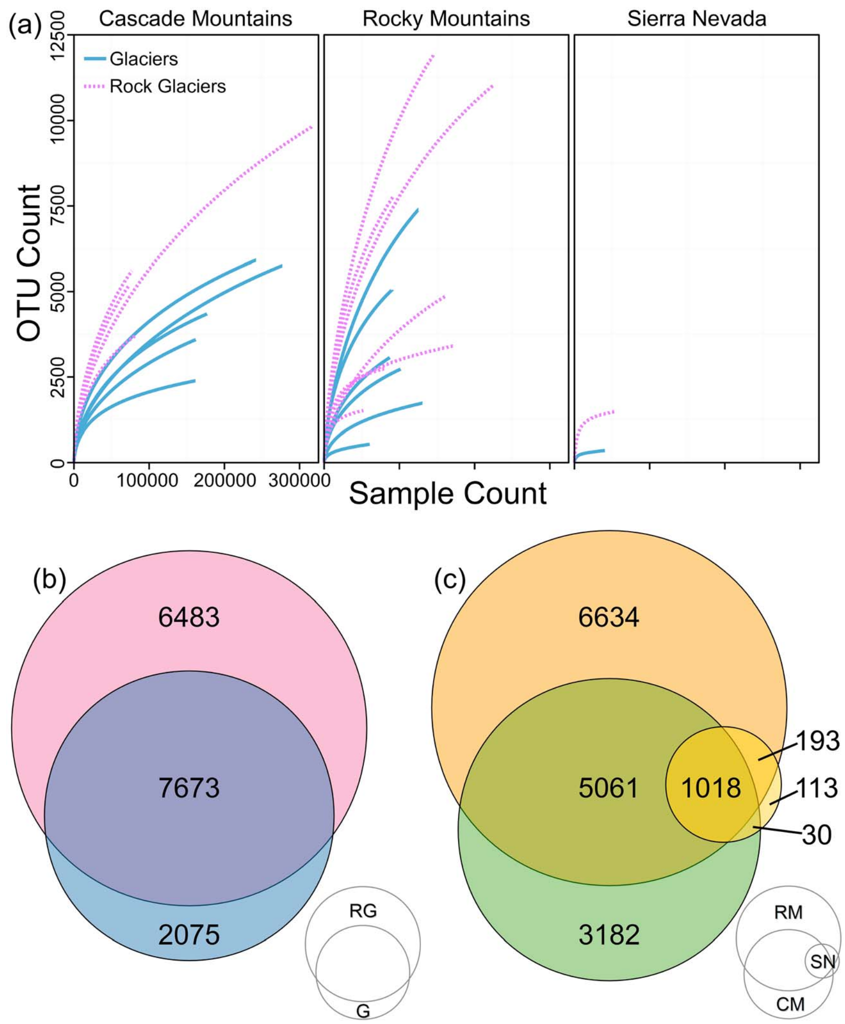

Figure 4. (a) Rarefaction curves as an estimate of α diversity for microbial communities sampled at the base of glaciers and rock glaciers in each of the surveyed mountain ranges. For each range, individual rock glaciers had higher microbial α diversity than ice glaciers. Rock glaciers also had greater overall microbial richness (overall number of OTUs) at the measured sampling depth of each sample. Venn diagrams showing overlap in membership between microbial communities sampled from (b) glaciers and rock glaciers (labeled G and RG) and (c) among Mountain Ranges (Cascade Mountains = CM, Rocky Mountains = RM, and Sierra Nevada = SN). All numbers are representative of Operational Taxonomic Units (OTUs) that are novel to their respective feature or area or are common between overlapping spheres. Rock Glaciers had a greater number of unique OTUs; however, there were a large number of cosmopolitan OTUs between feature types. The Rockies had the greatest number of OTUs and shared the most OTUs with the Cascades. The Sierra Nevada had the fewest OTUs, and the majority were shared between all three mountain ranges.

which were unique to the range (Figure 4c). The Sierra Nevada was the least diverse, with 1354 OTUs, only 113 (8%) of which were unique. Sierra Nevada sites shared very few OTUs with the other ranges, with only 30 OTUs shared between the Sierra Nevada and the Cascade Mountains and 113 OTUs shared with only the Rocky Mountains. The lower richness of the Sierra Nevada sites may partly be due to the smaller number of samples collected for the Sierra Nevada compared to the Cascade Mountains or Rocky Mountains, though individual site richness was much lower for each of the Sierra Nevada samples compared to all other individual samples from the other two mountain ranges (Figure 4a). The Cascade Mountains were intermediate in their microbial diversity, 9291 total OTUs, 3182 (34%) of which were unique. The Cascade Mountains also shared over 50% of their OTU diversity (5061 OTUs) with the Rocky Mountains (Figure 4c).

The most abundant bacterial taxa present in all ranges were the same taxa that were common between feature types, including *Gemmatimonas* sp., *Hymenobacter* sp., *Intrasporangiaceae* sp., and *Polaromonas* sp. Many unclassifiable gammaproteobacteria were found only in the Cascade Mountains and the Rocky Mountains.

Flavobacterium were exclusive to the Cascade Mountains, along with many *Acidthiobacillus* taxa, known for their metal oxidizing life strategies and tolerance of low pH environments. *Burkholderiales* sp., *Terrabacter* sp., and *Thiobacillus* sp. were the most abundant microbes exclusive to the Rocky Mountains. Nearly all the abundant taxa exclusive to the Sierra Nevada were unclassified.

4. Discussion

Glaciers and rock glaciers sit at the interface of atmospheric and terrestrial environments [*Slemmons et al*., 2013]. They integrate atmospherically deposited chemicals and weathering products, process reactive compounds through biotic and abiotic pathways, and then release the altered solutes to alpine headwaters. Our results suggest that glacier type dictates both concentration of the weathering products released and the complexity of organic matter exported via meltwaters (Tables 2 and 3), while geographic region dictates the rock type that is weathered (and thus kind of weathering products released), the rate and intensity of weathering, and the compounds that are atmospherically deposited (Figure 3b and Tables 1 and 2). The result is that some characteristics (e.g., temperature, weathering products, and complexity of DOM) appear to be driven primarily by glacier type (i.e., rock or ice glacier) while other characteristics (e.g., NH_4^+, NO_3^-, and microbial processing of DOM) appear to be more influenced by geographic characteristics.

Our survey suggests that specific characteristics of each mountain range control the amount of weathering products delivered to headwater ecosystems. For example, we found fewer differences between the weathering products of glacier and rock glacier meltwaters in the Cascade Mountains relative to the Sierra Nevada and Rocky Mountains. In contrast to the continental glaciers of the Rocky Mountains and Sierra Nevada, glaciers of the Cascade Mountains are maritime glaciers. As such, they sit at lower elevations, receive greater amounts of precipitation, and are volumetrically larger than other alpine ice features in the continental United States (Table 1 and Supporting Information S1). Glaciers in the Cascade Mountains are likely to have much higher subglacial mechanical and chemical weathering rates than other glaciers of the American West because of more persistent precipitation throughputs. Enhanced microbial respiration due to increased delivery of redox pairs in the zone of basal melting would increase CO_2 concentrations in the water, further increasing mineral dissolution through the production of carbonic acid [*Montross et al*., 2013]. The effects of this increased carbonic acid production would be further exaggerated in the Cascade Mountains, as the basaltic mineral complexes of the parent material are more readily weathered than the granitic bedrock of the Sierra Nevada and Rocky Mountains thus less likely to have pronounced differences in meltwater chemistry between glacier types.

Similarly, our results show that N concentrations in both glacial and rock glacial meltwaters appear to reflect regional atmospheric N deposition. The Rocky Mountains had NO_3^- and NH_4^+ concentrations nearly twice as high in both glacier types relative to meltwaters from the other mountain ranges (Figures 3d–3f). While there is evidence that some marine origin sedimentary rock is nitrogen bearing [*Holloway et al*., 1998], the crystalline, plutonic bedrock of the Colorado Front Range does not contain nitrogen in either the minerals nor trapped within the interstitial spaces of the lattice structure [*Mast et al*., 1990]. Atmospheric N deposition, however, is greatly elevated in the Colorado Front Range compared with other western mountains [*Fenn et al*., 2003]. This is consistent with elevated nitrogen concentrations previously observed in surface waters of Rocky Mountain watersheds fed by glaciers [*Baron et al*., 2009; *Saros et al*., 2010; *Williams et al*., 2007] (Supporting Information S1). Nitrogen deposition in the Front Range is elevated due to the prevalence of intensive industrial and agricultural activity to the east [*Baron et al*., 2000].

Glaciers in the western United States act as delayed source of reactive N and other pollutants, effectively increasing the lag time between anthropogenic stressors (atmospheric deposition) and impact on the ecosystem. Therefore, even with recent reductions of anthropogenic N pollution, there may be a delayed response in the reduction of N concentrations and ecosystem recovery in alpine headwaters [*Mast et al*., 2014]. Whether the reactive N seen in meltwaters is of recent atmospheric origin prior to in situ biological processing remains unknown. However, distillation through evaporation and sublimation on the glacial surface could concentrate atmospherically sourced compounds to enhance microbial activity during base flow conditions or “hot moments” [*Battin et al*., 2004], periods when hydrological connectivity and temperature are at optimal levels for biological processing of N and organic matter. It also appears that reactive N in the Rocky Mountains is not entering the production of organic matter within glaciers, as our results show that lower fluorescence indices values of glaciers and rock glaciers in the Rocky Mountain sites compared to the Cascade Mountains and Sierra Nevada (Table 3). These lower values suggest lower N concentrations in the DOM of glacier meltwaters. This is consistent with less tight cycling of organic nitrogen and may be further evidence of an N threshold being reached in the Rockies [*Baron et al*., 2000], as nitrogen is not being as tightly assimilated into biological DOM. This same phenomena of increasing temporal lag between atmospheric inputs and release to headwaters has been noted in other glaciated ranges including the Kenai, Chugach, and Coast Mountains of Southeast Alaska (organic matter) [*Hood et al*., 2009] and Swiss Alps (pesticides) [*Schmid et al*., 2010].

Previous research has shown that small glaciers contribute a disproportionate amount of DOM for their size and fuel heterotrophic metabolism at great distances downstream [*Hood et al*., 2015]. The DOM values we observed for glaciers and rock glaciers were low but similar to concentrations reported from large maritime glaciers [*Hood et al*., 2009]. Differences in the structure of organic matter released from glaciers and rock glaciers, as seen in our study (Table 3), could cause differences in alpine ecosystem activity through preferential lability of compounds specific to a glacial type. Previous research on glacial DOM from Southeast Alaska suggests that glacier DOM is highly labile and fuels bacterial metabolism in neighboring waters [*Hood et al*., 2009], but the lability of rock glacier DOM remains unknown. Our results show rock glaciers had higher humification, or complexity, of organic matter than glaciers. This suggests that rock glacial DOM is likely less labile than that of glaciers for two principal reasons. First, there is likely quantitatively more (and more diverse) biological activity occurring within the pore spaces, and stream sediments of the rock glacier, producing a broader range of more complex and recalcitrant DOM compounds than glaciers. Second, meltwaters of rock glaciers likely have greater amounts of complex organic compounds compared to that of glaciers due to leaching materials from plants living on the rock glacier surface that then percolate through the rock glacier and are subsequently locked into the ice matrix and eventually released into meltwaters (Table 3). Ice glaciers do not have plants growing on their surface; thus, they lack this allochthonous input of complex DOM to their ice. Both result in production of more complex metabolites in rock glacier meltwaters compared to glacier meltwaters. These hypotheses are consistent with our analyses of the bacterial communities associated with each glacial type, as we saw higher microbial diversity and DOM complexity in rock glacier stream sediments compared to glacier stream sediments (Table 3 and Figure 4). Further research should use more descriptive methods of organic matter characterization (e.g., mass spectrometry), along with direct evaluation of DOM lability to evaluate differences in lability of DOM and biological processing between meltwaters of different glacier types.

In this study the sediment-rich rock glacial environment supported more abundant and diverse microbial communities than those of glaciers (Figures 4a–4c). This is consistent with a known positive relationship between size and diversity of the microbial population present and amount of sediment in the subglacial environment [*Sharp et al*., 1999]. Significantly, warmer temperatures in rock glacier effluent compared to that glaciers also likely reduced selective pressure for psychrophiles and supported a richer and diverse bacterial community (Figures 3 and 4a–4c). Taxa only found in rock glaciers also had more bacterial species in common with known soil microbes indicating a more cosmopolitan microbial community. Biological diversity between glaciers and rock glaciers at higher trophic levels should be examined, as low temperatures and increased sediment loads have been correlated with lower diversity of invertebrates in meltwater-fed streams [*Milner et al*., 2009]. Subglacial environments are biologically active [*Simon et al*., 2009; *Wilhelm et al*., 2013, 2014], and our work shows that alpine glaciers and rock glaciers in the American West contribute biologically significant additions to alpine ecosystems. The commonality of *Polaromonas* sp. between all sites in our study, as well as cyrospheric ecosystems globally, suggests that the *Polaramonas* sp. is common to many cold environments [*Darcy et al*., 2011; *Margesin et al*., 2012; *Wilhelm et al*., 2014]. However, with abundant unclassified taxa exclusive to meltwater-fed glacial sediments, glaciers may represent areas of diversity and biological processing not shared by rock glaciers. This is supported by other studies that showed rare taxa in exclusively glacially fed streams to be disproportionately active [*Wilhelm et al*., 2014]. These unique microbial communities may be lost with the ongoing retreat of alpine glacial ice driven by climate change and may prove a ripe ground for discovery of novel bacterial taxa and unique metabolic pathways.

Over the coming century the differences in biogeochemical characteristics of headwaters fed by either glaciers or rock glaciers will become more similar along with the geomorphology of the glaciers themselves [*Clarke et al*., 2015; *Radić et al*., 2014]. Rock glaciers are predicted to melt slower than alpine glaciers, but eventually, even rock glacier ice will likely be lost. Continued ablation of ice can decrease ice fractions relative to rock and turn some glaciers into rock glaciers [*Outcalt and Benedict*, 1965; *White*, 1971; *Krainer and Mostler*, 2000]. For these cases, we can apply a space-for-time substitution by comparing differences between glaciers and rock glaciers within each range. This substitution allows for examination of potential future meltwater biogeochemical scenarios for presently glacial-fed headwater ecosystems experiencing warming alpine climates. During the current stage of global glacial recession, the higher geochemical and microbial contributions of rock glaciers compared to glaciers suggest that rock glaciers will have a pronounced impact on the biogeochemical processes of many alpine headwaters.

The results presented here combined with previous research suggest that rock glacier meltwaters may be representative of what future biogeochemical inputs will be in currently ice-glaciated watersheds. With increasing air temperatures, the elevated biogeochemical and microbial characteristics of rock glaciers compared to glaciers will likely dominate meltwaters that reach sensitive headwater ecosystems. Further, some glaciers are likely to become more rock glacier like in the biogeochemistry of their meltwaters and increase the biogeochemical signal of rock glaciers on the alpine headwaters they feed. Our results suggest that both feature-specific and range-specific biogeochemical characteristic may place bottom up controls on ecosystem function. Understanding which biogeochemical characteristics will be a function of glacier type and which will be driven by region allows for better implementation of management strategies to protect and adapt to these changing headwater ecosystems.

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