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Alpine glaciers have receded substantially over the last century in many regions of the world. Resulting changes in glacial runoff not only affect the hydrological cycle, but can also alter the physical (i.e., turbidity from glacial flour) and biogeochemical properties of downstream ecosystems. Here we compare nutrient concentrations, transparency gradients, algal biomass, and fossil diatom species richness in two sets of high-elevation lakes: those fed by snowpack melt alone (SF lakes) and those fed by both glacial and snowpack meltwaters (GSF lakes). We found that nitrate (NO_3^-) concentrations in the GSF lakes were 1–2 orders of magnitude higher than in SF lakes. Although nitrogen (N) limitation is common in alpine lakes, algal biomass was lower in highly N-enriched GSF lakes than in the N-poor SF lakes. Contrary to expectations, GSF lakes were more transparent than SF lakes to ultraviolet and equally transparent to photosynthetically active radiation. Sediment diatom assemblages had lower taxonomic richness in the GSF lakes, a feature that has persisted over the last century. Our results demonstrate that the presence of glaciers on alpine watersheds more strongly influences NO_3^- concentrations in high-elevation lake ecosystems than any other geomorphic or biogeographic characteristic.

Introduction

Changes in the volume of glacial runoff have been observed in alpine regions around the world (*1–4*). These changes have important implications for solute flux to stream ecosystems (*5–7*) as well as the supply of freshwater to human populations (*8–10*). Less is known, however, about how changes in the influx of glacial meltwater affect the chemistry (*11*) and biota of lake ecosystems. In the Canadian Rockies, melting alpine glaciers release concentrated organic pesticides into lake ecosystems and contribute 50–97% of the organochlorine inputs to these systems, resulting in higher concentrations relative to nonglacial lakes (*12*). In the southern Rocky Mountains of North America, an area with relatively high atmospheric reactive N (Nr) deposition (4–8 kg N ha^{-1} yr^{-1}), meltwaters from ice and rock glaciers have elevated nitrate concentrations (*13*). Lake-water NO_3^- concentrations are also high in this area, but because of relatively high Nr deposition (*7, 14*), the extent to which meltwater from ice and rock glaciers contribute Nr remains unclear. Nitrogen is a key limiting nutrient in alpine lake ecosystems (*15, 16*), hence an influx of nitrate-rich glacial meltwater could have profound effects on productivity and species diversity in historically N-limited alpine lakes. Here we focus on NO_3^- concentrations in glacial meltwater and its effects on high-elevation lake ecosystems in two low N deposition areas of the U.S. Rocky Mountains: the Greater Yellowstone Ecosystem (central Rockies) and Glacier National Park (northern Rockies) (Figure 1). The selected sites in the central Rockies have a combined rate of NO_3^- and ammonium (NH_4^+) deposition between 1.4–2.5 kg Nr ha^{-1} year^{-1}, while those in the northern Rockies are between 2.0–3.4 kg Nr ha^{-1} year^{-1} (*17*). Alpine glaciers receded substantially in both regions over the course of the 20th century (*18–20*).

Experimental Procedures

Watershed land cover classes were delineated for 26 watersheds across the two study areas using the Northwest GAP Analysis classes (*21*), which included perennial ice and snow (denoted North American Alpine Ice Field in the Northwest GAP classes), bedrock, talus, and 18 types of vegetation (Supporting Information (SI) Table S-1 provides a complete list of the 21 land cover classes). A geographic information system (GIS) was used to delineate watersheds using a 30 m digital elevation model, and to calculate basin and climatic predictor variables using various GIS techniques for each of the watersheds. Predictor variables included mean nitrate deposition, watershed area, land use, and precipitation derived from multiple data sources (*17, 21–23*). Perennial ice and snow cover was present on 14 watersheds. Of these, 12 had named (seven watersheds) or unnamed (five watersheds) glaciers delineated on U.S. Geological Survey base maps (from 1956 for Beartooth region, 1968 for Glacier National Park); the 12 lakes in this group were denoted as GSF. During our fieldwork, we were able to confirm the presence of glacial ice for nine of these; we were unable to reach the locations for the remaining three. We note here that the GIS analysis does not distinguish active glaciers from ice that has become stagnant. Assuming that new glaciers have not formed in the last 50 years, we inferred that, for the remaining two (Two Medicine and Beauty) of 14 watersheds with perennial ice and snow cover, they have perennial snow. These two lakes were thus categorized as SF systems along with those situated on the remaining 12 watersheds without any perennial ice and snow cover.

We sampled the dissolved nutrient chemistry of the 14 SF and 12 GSF lakes along with as many accessible inlet streams as possible entering these lakes. Lake water samples were collected from the pelagic zone using a van Dorn bottle deployed from a rubber raft. All 26 lakes were sampled in mid- to late July; a subset of six lakes (two GSF, four SF) was

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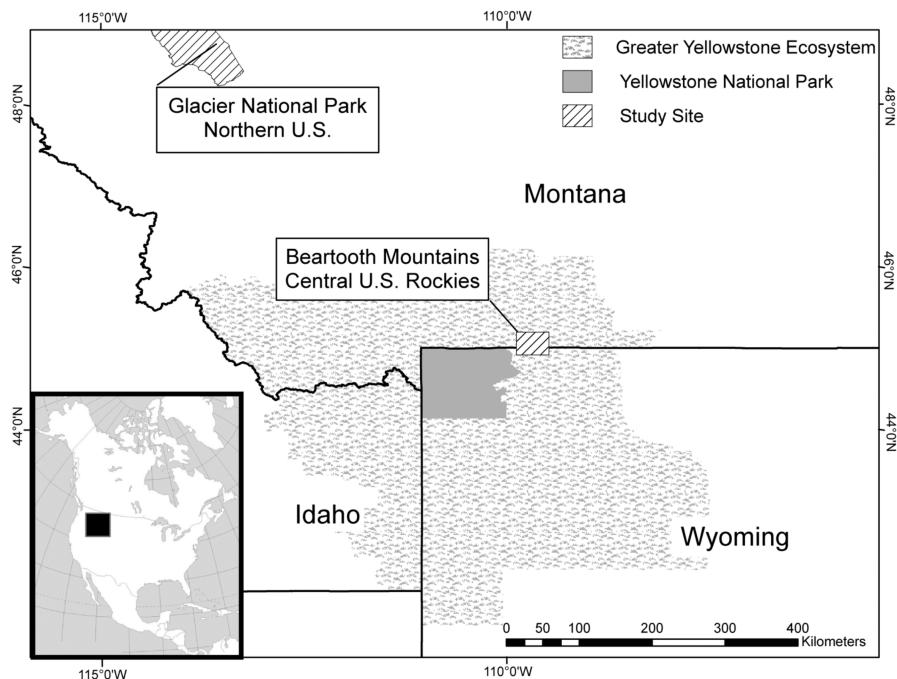 [⊥] University of Alberta.

FIGURE 1. Map of the study region in the U.S. Rocky Mountains. Lakes in the central Rockies are located in the Beartooth Mountain Range, which is part of the Greater Yellowstone Ecosystem. Lakes in the northern Rockies are located in Glacier National Park, which is part of the Crown of the Continent Ecosystem.

resampled during the last half of August. Inlet stream and glacial meltwater samples were collected by submerging an HCl acid-washed bottle (prerinsed three times with sample water) into the lake or stream. All water samples for nutrient analyses were filtered through 0.4 μm polycarbonate membranes prerinsed with deionized water. NO_3^--N was quantified using the cadmium reduction method on a Lachat QuikChem 8500 flow injection analyzer with a limit of quantification of 1 μg N L^{-1}. Matrix interferences were tested by spiking an aliquot of sample from each lake with 50 μg NO_3^--N L^{-1}; percent recovery ranged from 78 to 98% across samples. Soluble reactive phosphorus (SRP) was measured using the ascorbic acid method with a limit of quantification of 1 μg P L^{-1}. Dissolved silica was measured with the heteropoly blue method.

NO_3^- concentrations in the ice and surface meltwater of Sundance Glacier, situated near one of the GSF lakes in the central Rockies, were also measured. Ice from Sundance Glacier was collected by first scraping away a thin layer of surface debris with acid-washed polycarbonate spatulas, then using a hammer and acid-washed chisel to remove a piece of ice, which was then allowed to melt in an acid-washed bottle.

For a subset of lakes ($n = 9$ for each lake type), we examined key physical and biological metrics. Total algal biomass was measured as chlorophyll a; samples were collected onto Whatman GF/F filters, frozen, extracted in acetone, and measured with a Turner Designs Trilogy fluorometer. Material retained on polycarbonate filters was analyzed for particulate P by persulfate digestion followed by measurement of SRP as above. A conservative estimate of total P was obtained by summing these fractions (as in ref 16). Water-column transparency to ultraviolet radiation (UVR, measured at 320 nm) and photosynthetically active radiation (PAR, 400−700 nm) were quantified with a Biospherical Instruments Cosine (BIC) submersible radiometer and 1% depths estimated from diffuse attenuation coefficients (24). Logistical constraints resulted in $n = 8$ per lake type for the light profiles. We also determined concentrations of dissolved organic carbon (DOC), as this material can play an important role in attenuating light in lake ecosystems (25). Epilimnetic

(2−3 m depth) water samples for DOC were filtered through precombusted Whatman GF/F filters and stored in the cold and dark until analysis with a Shimadzu TOC-V$_{CPH}$ Total Organic Carbon Analyzer (as in ref 26).

Diatoms (Bacillariophyceae) are unicellular photoautotrophic algae that are highly sensitive to changes in nutrient concentrations, and often dominate primary production in oligotrophic lakes (27, 28). We determined diatom community structure in surface sediments of the subset of 18 lakes as well as down-core assemblages in six lakes (three GSF, three SF). Surface sediment samples were collected in 2007; long cores were collected in 2001 or 2007. Methods for the collection and dating of sediment cores are previously described (16, 29). Taxonomic richness of diatom communities in the surface sediments and down-core assemblages was calculated by rarefaction analysis of species-level data (30). The dominant pattern of down-core assemblage variability was also quantified with the leading axis of detrended correspondence analyses (DCA (31)) for each cored lake. DCA was conducted on the relative frequencies (% of sum counted) of all diatoms >1% in any one sample.

One-way analysis of variance (ANOVA) tests were used to compare various characteristics of GSF versus SF lakes; Levene's test for homogeneity was used in all cases. Data that were not normally distributed were log transformed; if this failed to improve normality, we conducted nonparametric one-way ANOVA using Wilcoxon (Kruskal−Wallis) scores. Spearman's rank correlation analysis was used to examine the relationships between lake water nitrate concentrations and the 21 watershed characteristics, with a Bonferroni correction applied ($p = 0.05/21 = 0.002$).

Results and Discussion

A summary of select watershed features of the GSF and SF lakes reveals that lakes in the two categories have similar ranges in elevation and position with respect to treeline (Table 1, with the full data set in SI Table S-2). Compared to watersheds of SF lakes, GSF watersheds have a higher percent cover by perennial ice and snow ($p < 0.001$) as well as by bedrock and talus ($p = 0.06$).

TABLE 1. Select Watershed Characteristics of the Study Lakes. Average Values for Elevation and Percent Watershed Coverage by Perennial Ice and Snow As Well As Bedrock and Talus Are Indicated, with the Range of Data Provided in Parentheses[a]

				treeline		
lake type	elevation (m a.s.l.)	% perennial ice and snow	% bedrock and talus	Be	Tr	Ab
GSF	2047 (1191−3094)	2.25 (0.01−10.1)	13.1 (5.9−26.2)	8	2	2
SF	2574 (1576-3144)	0.008 (0−0.1)	6.8 (0−28.4)	7	3	4

[a] Position of lakes with respect to treeline is indicated as number below (Be), at (Tr), or above (Ab). A full table of these values, as well as lake water chemistry, is provided in SI Table S-2.
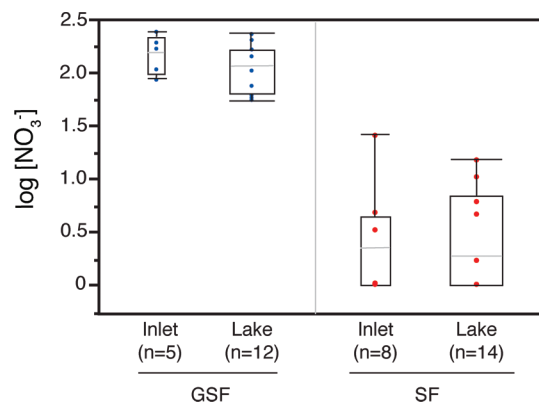

FIGURE 2. Comparison of log[NO_3^-] between GSF lakes and inlet streams and SF counterparts. Boxes represent the lower and upper quartiles, whiskers indicate the range of measurements, and gray bars indicate the mean in each category. Values below the detection limit of 1 μg NO_3^--N L^{-1} were entered as 1 μg N L^{-1}. Note that some points plot on top of each other.

FIGURE 3. Comparison of lake water log[NO_3^-] to total wet inorganic nitrogen deposition calculated for each site. Data for GSF lakes are blue squares, while those for SF lakes are red diamonds.

TABLE 2. Comparison of July and August NO_3^- Values (in μg NO_3^--N L^{-1}) for Two GSF and Four SF lakes in the Beartooth Mountains

lake type	Lake	July	August
GSF	Rainbow	139	121
	Glacier	90	84
	Beartooth	2	2
SF	Beauty	1	<1
	Island	4	<1
	Fossil	1	<1

Across the 26 lakes in this study, NO_3^- concentrations were higher in the GSF compared to the SF lakes (nonparametric one-way ANOVA, $p < 0.0001$; Figure 2). The average NO_3^- concentration of the GSF lakes was 114 ± 17 μg N L^{-1} (range: 52−236 μg NO_3^--N L^{-1}), while the average of the SF lakes was very low at 4 ± 1 μg N L^{-1} (range: <1−14 μg NO_3^--N L^{-1}). NO_3^- concentrations were also higher in the inlet streams of the GSF lakes (i.e., streams draining from alpine glaciers) compared to those of SF lakes ($p < 0.0001$; Figure 2). The average NO_3^- concentration of the GSF inlets was 158 ± 30 μg N L^{-1} (range: 82−250 μg NO_3^--N L^{-1}), while the average of the SF inlets was 5 ± 3 μg N L^{-1} (range: <1−26 μg NO_3^--N L^{-1}). SRP concentrations were below detection (<1 μg PO_4^{-3}-P L^{-1}) in all streams and lakes, except in one SF lake (Heart, SRP = 1 μg P L^{-1}). Silica concentrations did not differ between the two lake types (GSF lakes: 1794 ± 176 μg Si L^{-1}, SF lakes: 1511 ± 198 μg Si L^{-1}; $p = 0.30$). July and August lake water NO_3^- concentrations were similar in the subset examined (Table 2), suggesting that later snowmelt did not account for the higher NO_3^- concentrations in GSF lakes in July.

Out of 21 types of land cover quantified for each watershed in this study, only percent perennial ice and snow cover correlated significantly with lake water NO_3^- concentrations
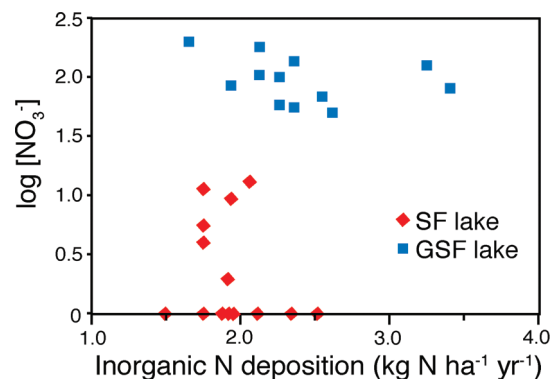
(Spearman's $\rho = 0.63$, $p = 0.001$). A linear relationship between percent perennial ice and snow cover and lake water NO_3^- concentrations was not apparent (data shown in SI Table S-2); rather it is the presence-absence of alpine glaciers that is associated with high versus low nitrate concentrations, respectively. While the percent of remaining perennial ice and snow cover is lower in the central Rockies relative to sites to the north, NO_3^- concentrations in GSF lakes were comparable in both areas. Rather than the percent of watershed covered by perennial ice and snow, NO_3^- concentrations in GSF lakes may relate more strongly to metrics such as the current mass of perennial ice on each watershed, the current rate of perennial ice retreat on each watershed, as well as the percent contribution of glacial runoff to the total hydrological budget of each lake; determining values for these metrics was beyond the scope of this study. While lichen communities that can fix nitrogen frequently dominate bedrock and talus habitat, the percent watershed cover by this habitat was not significantly correlated with lake water NO_3^- concentrations (Spearman's $\rho = 0.43$, $p = 0.03$) after applying the Bonferroni correction. We note that three of the SF lakes with undetectable NO_3^- concentrations had watersheds with more than 15% coverage by bedrock and talus, whereas nine of the GSF lakes had watersheds with less than 15% coverage by this habitat.

Estimated rates of current Nr deposition were not correlated with lake water NO_3^- in either region investigated (Figure 3). Although the central Rockies have a lower range of combined $NO_3^- + NH_4^+$ deposition rates than the northern Rockies, lake water NO_3^- concentrations were not different between the two areas. Previous work in the SF lakes of the central Rockies revealed that enhanced atmospheric Nr deposition has altered diatom community structure in some lakes over recent decades, even though measurable changes in NO_3^- concentrations in these SF lakes are not yet apparent (16). While approximately half of the lakes in Glacier National Park receive glacial meltwater, we estimate that only about 10−20% of those in the central Rockies receive these inputs, hence the majority of lakes in this region are SF, likely have
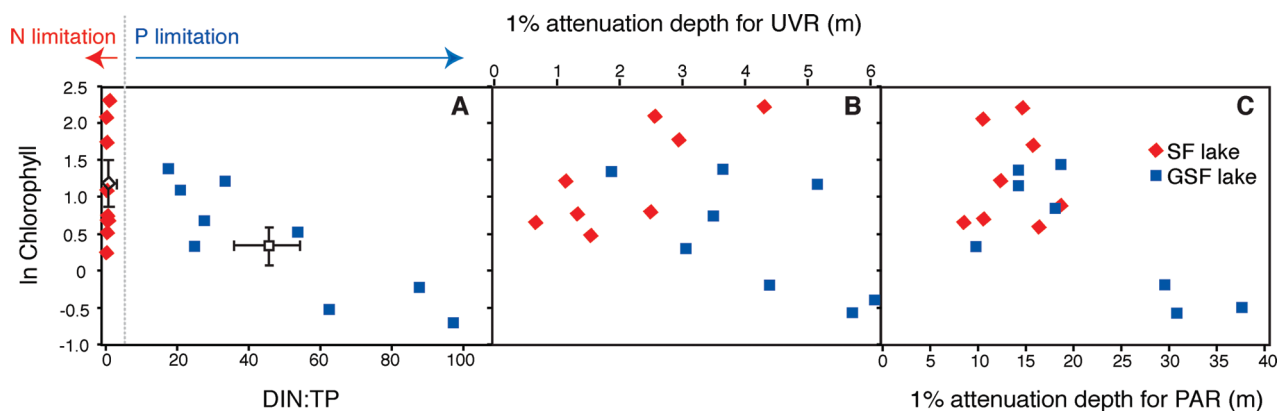
FIGURE 4. Relationships between algal biomass (as ln[chlorophyll]) and selected lake characteristics. (*A*) dissolved inorganic nitrogen: total phosphorus (DIN:TP) ratio; (*B*) the 1% attenuation depth for ultraviolet radiation (UVR, measured at 320 nm); and (*C*) the 1% attenuation depth for photosynthetically active radiation (PAR; 380−700 nm). Data for GSF lakes are blue squares, while those for SF lakes are red diamonds. The mean ± one standard error are indicated with an open symbol for each group in Panel A.

low NO_3^- concentrations, and thus remain susceptible to enhanced atmospheric Nr deposition.

The influx of N-rich glacial meltwater affects the structure and function of high-elevation lake ecosystems in several ways. Although algal growth is often N-limited in alpine lakes (*15, 16*), algal biomass was lower in the N-rich GSF lakes than in the N-poor SF lakes (*p* = 0.06; Figure 4a). The ratio of dissolved inorganic N: total phosphorus (DIN:TP (*32*)) suggests that SF lakes are N-limited, while GSF lakes are P-limited (Figure 4a). Chlorophyll levels declined in GSF lakes as the DIN:TP ratio increased (r^2 = 0.75, *p* < 0.001).

Lowered algal biomass can result from light limitation in lakes receiving high inputs of glacial flour. However, this was not the case in the investigated lakes, which are not in direct contact with glaciers but rather situated some distance from receding termini, thereby allowing for upstream trapping of minerogenic glacial sediment. Rather, we found the opposite: GSF lakes were more transparent than SF lakes to UVR (*p* = 0.02), and equally transparent to PAR (*p* = 0.07). Furthermore, chlorophyll *a* concentrations were lower in the more transparent GSF lakes (Figure 4b and c). Average DOC concentrations were low in all lakes (SF lakes: mean ± SE = 0.9 ± 0.2 mg L^{-1}; GSF lakes: 0.6 ± 0.1 mg L^{-1}); these differences were not statistically significant (*p* = 0.07).

Diatom species richness in surface-sediment samples from GSF lakes was lower than in the SF lakes (one-way ANOVA *p* = 0.008; Figure 5a). Diatom taxonomic richness in down-core sediment records from GSF lakes was consistently low over the last century, ranging from 12 to 26 taxa (example from Rainbow Lake, Figure 5d). In contrast, species richness ranged from 35 to 54 in cores from SF lakes over the same interval (example from Beauty Lake, Figure 5b). While richness differed between Rainbow and Beauty, DCA scores reveal a similar degree of diatom community turnover in both lakes over the last century (Figure 5b and d). However, abrupt declines in diatom richness and higher rates of community turnover are observed in SF lakes influenced by elevated Nr deposition (e.g., Emerald Lake, Figure 5c) (*16*). Emerald Lake, located in the Beartooth Wilderness, has among the highest NO_3^- concentrations recorded from any SF lake sampled: 10 μg N L^{-1}. Diatom communities from this lake had initially high richness in the early 20th century, similar to other SF lakes, but then progressively declined as atmospheric Nr subsidies became pronounced (Figure 5c). The analysis of diatom richness across both spatial and temporal scales indicates that species richness is lower in GSF lakes, and these lakes have experienced this effect for over a century.

It is not unexpected that alpine glacial meltwater contains NO_3^-, as glaciers accumulate a range of atmospherically

delivered chemicals (*12, 33*). NO_3^- is also among the first ions to elute from melting glacier ice (*34*). The key question, however, is why glacial meltwaters in the central and northern Rockies are so enriched in NO_3^-. The limited data available on ice cores in this region are consistent with our observations. For example, ice from the Upper Fremont Glacier in the central Rocky Mountains (Wind River Range) contains variable amounts of NO_3^- over time, with concentrations occasionally above 10 μg L^{-1} between 1717 and 1985, and then in excess of 100 μg L^{-1} after 1985 (*35*). Samples that we collected from the Sundance Glacier revealed NO_3^- concentrations of 11 μg N L^{-1} in the ice, 28 μg N L^{-1} in a meltwater stream on the surface of the glacier, and 158 μg N L^{-1} in a pond situated on the surface of the glacier, receiving the surface meltwater stream. Similar glacier ice NO_3^- concentrations occur at Taylor Glacier in the Colorado Front Range (*7*). Processes including the alpine distillery (*36*) as well as relatively high sublimation and evaporation rates on glaciers in alpine regions appear to concentrate NO_3^- in these environments, prior to delivering high NO_3^- meltwaters to downstream aquatic ecosystems. Evaporative concentration may explain the high NO_3^- concentration observed in ponded water on the Sundance Glacier.

The higher NO_3^- concentration of glacial meltwater relative to seasonal snowpack melt may also be due, in part, to its reduced contact with watershed soils where microbial communities may rapidly assimilate any available Nr (*37*). Channelization of supraglacial runoff implies that the bulk of solutes, whether preconcentrated or not, will be disseminated to meltwater streams with minimal intervening biological uptake. This contrasts to SF watersheds, where snowmelt percolates through soils before reaching streams. Additionally, nitrification of snow and icemelt NH_4^+ in subglacial environments is a mechanism for NO_3^- production. Isotopic studies of aqueous NO_3^- in an Arctic glacier system on Svalbard revealed that this mechanism explained more than 80% of the increase in NO_3^- concentrations observed between supra- and subglacial streams, whereas contributions from rock-derived NH_4^+ appeared minimal (*38*). Additional hypotheses, including those involving rock glaciers and landscape development, are discussed elsewhere (*7, 13, 39, 40*), although we note that our analysis of watershed characteristics did not reveal significantly different NO_3^- contributions associated with the extent of talus or vegetation types across GSF versus SF watersheds. Determining the age of talus (Pleistocene versus Holocene neoglacial) across these watersheds may provide additional insight; studies in a high N deposition region of the southern Rocky Mountains suggest that talus age contributes, in part, to differences in watershed retention of N (*13, 41*).
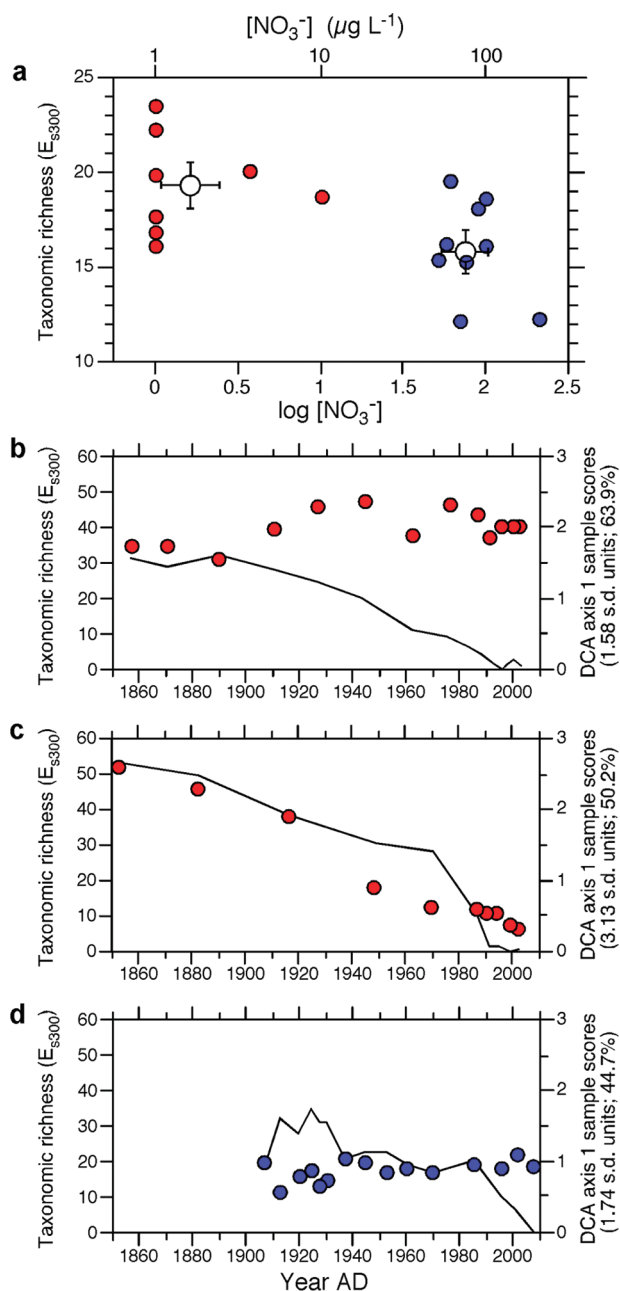
FIGURE 5. Taxonomic richness of sediment diatom assemblages based on rarefaction analysis (based on *n* = 300 (*E*$_{S300}$) for every sample). (*A*) species richness versus log[NO$_3^-$] across surface sediment samples from GSF (blue) and SF (red) lakes, with the mean ± one standard error indicated with an open symbol for each group. Additional plots portray the temporal evolution of diatom taxonomic richness (circles) and detrended correspondence analysis (DCA) first-axis sample scores (line) gleaned from ^{210}Pb-dated sediment cores from (*B*) Beauty Lake (SF); (*C*) Emerald Lake (SF lake with pronounced late 20th-century nitrogen deposition); and (*D*) Rainbow Lake (GSF).

Our results demonstrate that the presence of glacier ice in alpine watersheds of the American Rocky Mountains more strongly influences NO$_3^-$ concentrations in high-elevation lake ecosystems than any other geomorphic or biogeographic characteristic. Several key ecological features, including nutrient limitation patterns and species richness of a major algal group, differ between glacially influenced and snowpack-fed lakes. The mosaic of remaining glaciers in the central and northern Rockies therefore creates complex and heterogeneous geographic patterns of nutrient limitation and

biogeochemical processes. Given predictions that alpine glaciers will disappear from the U.S. Rockies by 2030 (*20*), these observations raise serious questions concerning the future biogeochemical and ecological trajectories of hundreds of lake ecosystems within this vast region.

Supporting Information Available

Comprehensive tables of the 21 land cover classes delineated in this study as well as lake name, elevation, watershed area, lake area, nutrient chemistry, percent watershed coverage by perennial ice and talus, and named glaciers for each lake are provided. This material is available free of charge via the Internet at http://pubs.acs.org.

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