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Stream Chemistry Responses to Bark Beetle Disturbance and Changing Atmospheric Deposition in Alpine and Forest Headwater Catchments

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ABSTRACT

The extent of alpine land cover influences the chemistry of streams draining mountain catchments and may determine how they respond to ecosystem change. During the first two decades of the 2000s, the Southern Rockies, USA, experienced both severe bark beetle infestation and significant decreases in atmospheric nitrogen (N) and sulfur (S) deposition. To evaluate the consequences of these events, we compared the chemistry of samples collected during 2004–2006 and 2017–2019 in streams draining 18 headwater catchments comprised of mixtures of forest and alpine land cover. Stream total dissolved N, nitrate, and sulfate concentrations increased linearly with the proportion of alpine cover within the study catchments. Consistent with regional patterns in atmospheric deposition, stream nitrate decreased and ammonium increased, though stream sulfate was unchanged. Differences in solute concentrations between the sampling periods were greatest in catchments with the highest proportion of alpine cover and were minimal in fully forested catchments. This relationship demonstrates the sensitivity of catchments with alpine headwaters to changing nutrient deposition and, conversely, the capacity for nutrient retention by non-host vegetation to buffer the impacts of beetle-related tree mortality in fully forested catchments.

1 | Introduction

The chemical composition of streams draining high-elevation watersheds is a sensitive indicator of climate-related change and ecosystem perturbation (Moser et al. 2019; Rock et al. 2024; Knapp et al. 2026). Upper elevation treeline partitions headwater catchments into zones with distinct biogeochemical influences on surface water quality. For example, the sparse alpine vegetation above treeline, coupled with poorly developed, coarse-textured soils, exposed rock, and short-growing seasons (Retzer 1962; Clow and Sueker 2000) limit nutrient retention and promote downslope N export (Ballantyne et al. 2011; Mast et al. 2011). Precipitation amount and atmospheric deposition load increase with elevation (Clow et al. 2015), and the N contained in alpine snowpack and soil water N are higher than in subalpine forests (Stottlemyer et al. 1997). In contrast, water and nutrient demand by forest vegetation limits nutrient losses from subalpine watersheds (Stottlemyer and Troendle 1992). The mixture of tree species, multi-layered canopy and uneven age structure contribute to the resilience of subalpine forests and facilitate their post-disturbance recovery (Rhoades et al. 2013, 2017). Better understanding of what regulates water quality in headwater catchments will help refine expectations about how changing conditions influence the sustained supply of clean water (Clark et al. 2021).

Forest mortality caused by insect outbreaks has been shown to increase nutrient leaching (Kana et al. 2013; Zhu et al. 2025) and threaten surface water quality (Huber 2005). Severe drought conditions in the early 2000s triggered epidemic level mountain pine bark beetle (*Dendroctonus ponderosae*) activity across western North America (Raffa et al. 2008; Meddens and Hicke 2014). In Colorado, the outbreak killed 40%–70% of mature trees in many lodgepole pine-dominated forests (Chapman et al. 2012; Collins et al. 2011). Bark beetles introduce fungi to the host's vascular system, and expanding fungal hyphae block water uptake within weeks of infestation (Hubbard et al. 2013). As a result of reduced plant demand, soil water and nutrient availability increase beneath beetle-killed trees (Clow et al. 2011). In Bavarian spruce forests, nitrate leaching from the rooting zone began the year following bark beetle attack and peaked after 3–5 years (Huber et al. 2004; Huber 2005). Similar to other disturbances, the ecological consequences of insect outbreaks generally track the level of insect activity and tree mortality. However, variability in tree species composition, stand structure and site and climatic conditions influences both tree mortality and non-host compensatory growth to influence catchment-scale responses (Rhoades et al. 2017). For example, in spite of increased soil water and N following the Colorado outbreak (Clow et al. 2011), nutrient uptake and growth responses of residual live vegetation restricted streamwater N losses to levels far below those after forest harvesting or wildfire (Rhoades et al. 2013).

As a consequence of air quality regulations, (i.e., Clean Air Act 2025) widespread, significant reductions in nitrate (NO_3-N) and sulfate (SO_4^{2-}) deposition occurred during the early 2000s across the continental US (Lehmann et al. 2005; Li et al. 2016; Lloret and Valiela 2016). At high-elevation sites (~2500–3500 m) in central Colorado for example, SO_4^{2-} and NO_3-N deposition declined by 53% and 46% during the early 2000s (Figure 1; National Atmospheric Deposition Program (NADP) 2022). Ammonium (NH_4-N) deposition remained relatively constant during the time period (Du 2016). Surface water chemistry shows evidence of changing deposition inputs, though local physical and biological factors have been shown to complicate the responses (Clark et al. 2021; Burpee et al. 2022).

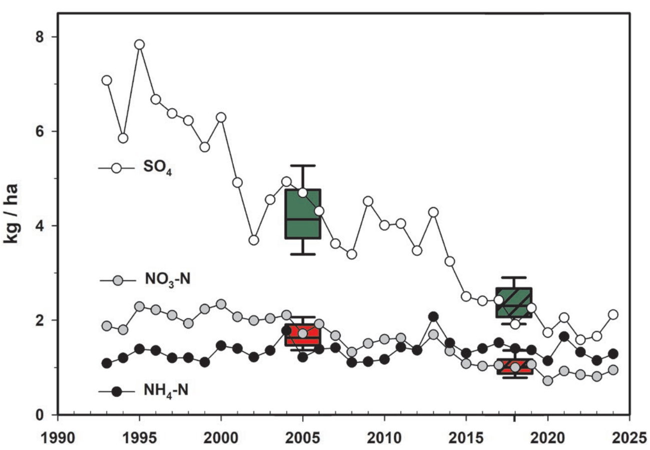

FIGURE 1 | Annual wet N and S deposition in the Colorado Front Range. Lines denote values averaged from six sites (2477–3520 m elevation; National Atmospheric Deposition Program (NADP) 2022), and boxplots represent two sites at the Fraser Experimental Forest (2736 and 3227 m elevation). Fraser SO_4^{2-} (green) and NO_3-N (red) deposition were averaged for the 2004–2006 (hollow) and 2017–2019 (hatched) stream sampling periods. Box plots show median line, 25th and 75th (box limits) and 10th and 90th percentiles (whiskers) for SO_4^{2-} and NO_3-N. Both SO_4 and NO_3-N loads differ statistically ($p < 0.001$) between sampling periods. For clarity, Fraser NH_4-N deposition was not plotted.

Concurrent bark-beetle related forest disturbance and decreased N and S deposition during the early 2000s provides an opportunity to evaluate the relative consequences of biotic and abiotic change on stream water chemistry. We analysed stream chemistry and nutrients in 18 tributaries draining adjacent catchments (Figure 2), first during the peak of local bark beetle activity and relatively high N and S deposition (2004–2006) and again after the outbreak had ended and N and S deposition declined (2017–2019; Figure 1). The study catchments spanned a range of physical attributes (e.g., area, elevation; Table 1) and cover (i.e., proportion of a catchment in subalpine forest and alpine zones). Our overall study objectives were to characterize the relation between catchment conditions and stream water chemistry and subsequently determine if those conditions influenced changes in stream water between the two periods. This analysis focused on biologically reactive ions (NO_3-N, NH_4-N, total dissolved N and SO_4^{2-}) that are sensitive both to ecosystem disturbance and regional atmospheric deposition patterns. We also considered dissolved C, as well as cations and anions that are released from forest soils and weatherable minerals that often vary with catchment lithology.

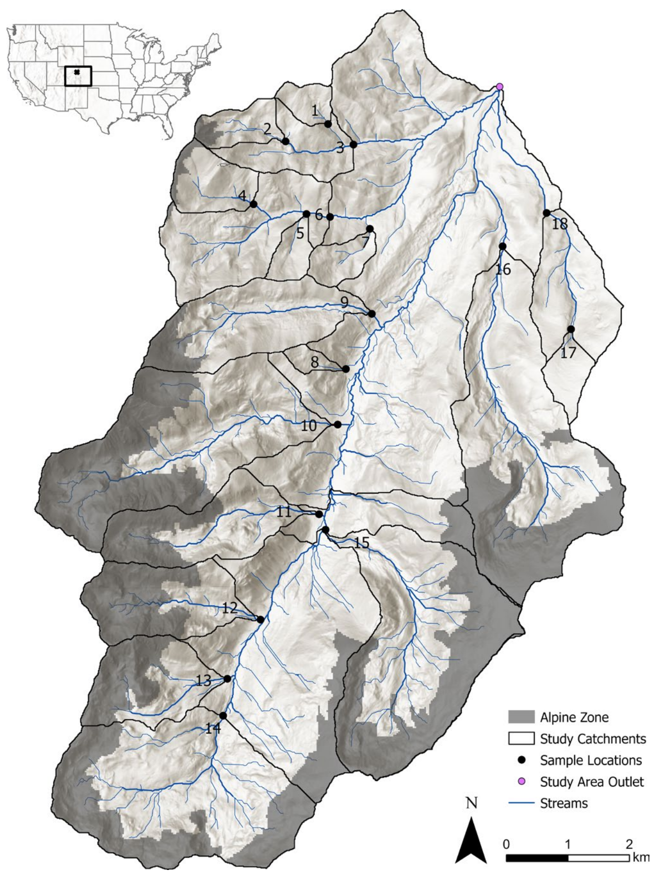

FIGURE 2 | The Saint Louis Creek drainage and study tributaries at the Fraser Experimental Forest, Colorado, USA. Inset map shows the site location (X symbol) within the continental USA, the state of Colorado (bolded outline), and other state outlines. Hillslope shade denotes the Rocky Mountains. The elevation of treeline ranges from 3245 to 3644 m above sea level (average: 3475 m) at the study site. See Table 1 for sample tributary names and attributes.

TABLE 1 | Characteristics and cover of study catchments at the Fraser Experimental Forest, Colorado.

		Area	Elevation			Slope	Alpine		Alpine cover			
			Min	Mean	Max				Alp Veg of Catchment	No-Veg of Catchment	Alp Veg of Alpine	No-Veg of Alpine
Catchment	ID	ha	m above sea level			%	ha	%	%			
Deadhorse N.	1	46.9	2993	3142	3277	30.7	0.0	0.0	0.0	0.0		
Deadhorse S.	2	79.5	3056	3261	3534	39.3	13.9	17.6	8.0	9.6	45.5	54.5
Deadhorse Main	3	272.8	2867	3142	3534	37.3	13.9	5.1	2.3	2.8	45.5	54.5
Lexen	4	119.7	3024	3278	3535	40.2	14.4	11.9	3.8	8.0	32.4	67.6
Wyssen	5	51.0	2918	3115	3286	40.5	0.0	0.0	0.0	0.0		
W. St. Louis	6	496.0	2897	3181	3535	38.4	16.5	3.3	1.0	2.3	31.1	68.9
Short	7	63.5	2895	3042	3236	33.8	0.0	0.0	0.0	0.0		
Byers	9	341.9	2903	3292	3812	38.9	52.9	15.4	13.2	2.3	85.2	14.8
Alder	8	32.4	2862	3171	3419	36.9	0.0	0.0	0.0	0.0		
Iron	10	762.7	2903	3432	3902	49.2	387.5	50.7	27.2	23.5	53.7	46.3
Lunch	11	291.4	2926	3414	3866	46.2	119.8	40.9	19.5	21.4	47.7	52.3
Gordon	12	274.3	3030	3467	3867	50.1	174.1	63.2	30.3	32.8	48.0	52.0
Mine	13	237.8	3090	3451	3786	43.4	126.2	52.9	37.7	15.2	71.2	28.8
Upper St. Louis	14	791.8	3118	3468	3806	32.3	298.1	37.6	30.7	6.9	81.7	18.3
Range	15	771.4	2924	3505	3890	39.1	362.6	47.1	35.4	11.7	75.1	24.9
E. St. Louis	16	867.1	2897	3399	3857	32.5	289.7	33.4	28.5	4.9	85.2	14.8
Upper Fool	17	65.5	3207	3399	3508	18.3	0.0	0.0	0.0	0.0		
Lower Fool	18	300.3	2915	3210	3508	25.6	0.0	0.0	0.0	0.0		
Study area	FEF	8521.0	2739	3273	3902	36.2	1976.6	23.3	16.3	7.0	69.9	30.1

Note: See Figure 2 for sample locations and catchment delineations.

Since tree mortality reduces plant nutrient demand and may promote N leaching and stream N export (Huber 2005; Zhu et al. 2025), we expected the greatest NO_3-N responses in fully forested catchments. Conversely, we expected the effect of decreased N and S deposition to be most evident in catchments with extensive alpine headwaters, where limited plant cover and biotic retention do little to filter deposition inputs. Both forest disturbance and deposition patterns have the potential to alter soil nutrients, though their net effects on streamwater chemistry likely vary with headwater land cover. Together, we expect these findings to help inform expectations about the water quality of high-elevation watersheds as they respond to disturbance and adjust to changing climatic conditions.

2 | Methods

2.1 | Study Area Description

The US Forest Service Fraser Experimental Forest (FEF) is located 137 km west of Denver on the western edge of the Front Range of the Southern Rocky Mountains in Colorado, USA, and was established in 1937 to study the links between forest vegetation and water supply in high-elevation catchments (Figure 2). Saint Louis Creek drains the 93 km^2 research area and joins the Fraser River, a major headwater tributary to the Colorado River. Land cover at FEF consists primarily of old-growth subalpine forests and alpine ecosystems. There are also relatively young forests (< 100 years) that regenerated after research-related harvesting in two catchments (Fool Creek and Deadhorse). The climate at FEF is temperate and continental with long cold winters and short cool summers. Annual temperature and precipitation at 2740 m elevation average 1.0°C and 769 mm/yr. (Elder 2005, 2006); January and July temperatures average −10°C and 13°C. Annual precipitation varies from 456 to 1200 mm/yr. at five long-term monitoring sites (elevation range: 2875–3385 m). Sulfate, NO_3-N and NH_4-N in wet deposition at Fraser average 4.2, 1.7 and 1.2 kg/ha/yr. (1990–2019; Figure 1). Since the early 2000s, SO_4^{2-} and NO_3-N deposition loads have decreased by 44% and 38% ($p < 0.001$), due to lower concentration of those solutes in precipitation (National Atmospheric Deposition Program (NADP) 2022). In contrast, NH_4-N loads have remained unchanged.

We sampled 18 tributaries of Saint Louis Creek in adjacent catchments within FEF (Figure 2). The study catchments spanned from 2862 to 3902 m above sea level (Table 1). At FEF, the elevation of treeline ranges from 3245 to 3644 m. The area above treeline (i.e., alpine zone), represents 23% of the entire 8521 ha study area (USGS station # 09026500; 39°54′36″ N, 105°52′40″ W). The proportion of catchments located in the alpine zone span from 0% to 63%. Catchment areas range from 32 to 867 ha (median 274 ha). The alpine zone at FEF supports a variety of vegetation assemblages, including grass, sedge and forb-dominated meadows, fellfields, fens and willow carrs (Popovich et al. 1993) that cover 60% of the alpine zone. Bare soil, unconsolidated rock (i.e., talus) and rock outcrops comprising the remaining 40% of the zone. Below treeline, the subalpine forests at FEF contain a mixture of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*) and lodgepole pine (*Pinus contorta*). Overall, the soils at FEF are poorly developed, coarse-textured Inceptisols formed from igneous and metamorphic rock (Alstatt and Miles 1983; Bergstrom et al. 2018). Soils in the alpine zone are Pergelic Cryumbrepts, with very gravelly or cobbly sandy loam horizons extending to 84–162 cm depths. Subalpine forest soils are predominantly Dystric Cryochrepts with sandy loam texture and high cobble fraction throughout 114–152 cm profiles. Soils in isolated depressional or alluvial areas in both zones may be poorly drained and accumulate surface organic matter layers.

Like much of Colorado's Front Range, metamorphosed lithology is widespread at FEF (49% of study area; Table 2); biotite gneiss is the most extensive rock type (Kellogg et al. 2008; Shroba et al. 2010). Igneous rocks cover 6% of the study site; granite (Silver Plume) and various mixtures of granodiorite are extensive (up to 52%) in a subset of catchments. Geologic faulting in the tributaries draining from the west of St. Louis Creek in the northern portion of the study area thrust Jurassic and Cretaceous strata upon the matrix of Precambrian, crystalline rock. These sedimentary strata include interbedded shale, claystone, and fine-grained sandstone and siltstone formations (Eppinger et al. 1985). A variety of unconsolidated materials cover 42% of the study area and up to 82% of some catchments. Pleistocene-age glacial till is the most common depositional class.

2.2 | Streamwater Analysis

Tributary sampling occurred monthly during 2004, 2005, and 2006 and roughly a decade later (2017, 2018, and 2019). Stream water was collected after triple-rinsing bottles in sample water. Samples for anion and cation analyses were collected in opaque HDPE plastic bottles; those for dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) analyses were collected in amber borosilicate glass bottles. Prior to use, plastic sample bottles were triple washed with de-ionized water (Specific conductivity (SC) < 1.0 µS cm^{-1}), and glass bottles were combusted for 1 h at 500°C in a muffle furnace. Samples were refrigerated after collection; then ion chemistry samples were filtered through 0.45 µm mesh membrane filters (Durapore PVDF, Millipore Corporation, Billerica, MA, USA), and DOC and TDN samples were filtered through 0.7 µm mesh glass fibre pre-filters (Millipore Corporation, Billerica, MA, USA).

Anion and cation concentrations were determined by ion chromatography and conductivity detection with electrolytic suppression (U.S. Environmental Protection Agency 1997) with a Dionex AS12A Anion-Exchange column, an AG12A guard column (Thermo Fisher, Waltham, MA, USA), and a Waters IC-Pak Cation M/D column (Waters Co., Milford, MA, USA) using EZChrom Elite Software (Scientific Software Inc., Pleasanton, CA, USA). Samples were analysed within 72 h of collection. Detection limits were 0.01 mg L^{-1} for K^+, Na^+, NH_4-N, Cl^-, and NO_3-N, and 0.02 mg L^{-1} for Ca^{2+}, SO_4^{2-}, and Mg^{2+}. Acid neutralizing capacity (ANC) was measured on unfiltered subsamples by Gran titration. Specific conductivity and pH were analysed automatically with PC Titrate sensors (Man-Tech Co., Guelph, ONT, CA). Dissolved organic carbon and TDN concentrations were quantitated using high-temperature combustion catalytic oxidation on a total organic C/N analyser after 2 M HCl treatment to remove mineral C (TOC-V_{CPN} Shimazdu Corporation,

TABLE 2 | Stream chemistry in tributaries of Saint Louis Creek at the Fraser Experimental Forest, Colorado.

		pH		ANC		SC		Ca^{2+}		Mg^{2+}		Na^{+}	
Catchment	**ID**	**Mean**	**Max**	**Mean**	**Max**	**Mean**	**Max**	**Mean**	**Max**	**Mean**	**Max**	**Mean**	**Max**
Deadhorse N.	1	8.1	8.4	1721	2674	171	238	27.9	42.2	3.6	5.0	2.4	3.3
Deadhorse S.	2	8.0	8.3	1408	1834	137	169	22.7	32.3	2.7	4.2	1.5	2.6
Deadhorse main	3	8.0	8.3	1338	1864	134	169	21.5	28.8	2.7	3.9	1.9	2.6
Lexen	4	7.8	8.3	793	1183	81	117	12.6	20.5	1.8	2.4	1.6	3.0
Wyssen	5	7.8	8.1	947	1287	98	123	13.2	17.2	3.3	4.4	1.8	2.1
W. St. Louis	6	7.9	8.2	1037	1418	106	128	15.4	19.5	2.6	3.6	1.7	2.3
Short	7	7.8	8.1	978	1283	105	126	14.1	17.8	3.5	4.8	2.1	2.7
Byers	8	7.7	7.9	625	883	74	93	10.9	16.3	1.6	2.5	1.4	2.1
Alder	9	7.9	8.1	1008	1529	108	155	14.7	30.1	3.4	4.4	2.5	3.3
Iron	10	7.7	8.0	666	998	92	114	13.8	19.8	1.7	2.2	1.2	1.7
Lunch	11	7.7	8.1	700	912	97	128	14.2	22.6	2.1	2.8	1.2	2.4
Gordon	12	7.8	8.1	932	1417	121	172	17.7	33.3	3.4	6.9	1.3	1.6
Mine	13	7.7	8.1	689	910	81	107	10.8	16.0	3.0	4.1	1.1	1.9
Upper St. Louis	14	7.4	7.8	401	606	54	69	7.3	9.6	1.2	1.5	1.7	2.5
Range	15	7.4	7.8	354	521	47	64	6.4	10.9	1.0	2.4	2.1	2.9
E. St. Louis	16	7.4	8.0	343	794	40	59	4.7	7.0	1.0	1.9	2.0	3.0
Upper Fool	17	7.3	7.8	319	481	36	48	3.8	6.3	0.9	1.3	2.4	3.3
Lower Fool	18	7.5	8.0	536	844	58	77	6.8	12.7	1.5	2.1	2.7	5.2
All tributaries		**7.7**	**8.4**	**895**	**2674**	**94**	**238**	**14.1**	**42.2**	**2.1**	**6.9**	**2.0**	**5.2**
St. Louis creek	FEF	**7.8**	**8.1**	**802**	**1119**	**94**	**113**	**13.0**	**16.4**	**2.5**	**3.1**	**2.3**	**3.3**
		SO_4^{2-}		Cl^{-}		DOC		TDN		NO_3-N		NH_4-N	
Catchment	**ID**	**Mean**	**Max**	**Mean**	**Max**	**Mean**	**Max**	**Mean**	**Max**	**Mean**	**Max**	**Mean**	**Max**
Deadhorse N.	1	3.2	4.8	0.2	0.7	2.5	11.8	0.10	0.34	0.02	0.12	0.013	0.09
Deadhorse S.	2	1.8	3.5	0.2	0.5	0.9	2.8	0.08	0.21	0.03	0.08	0.011	0.10
Deadhorse main	3	2.6	4.0	0.2	0.6	1.5	5.5	0.08	0.19	0.02	0.08	0.012	0.09
Lexen	4	1.7	2.7	0.2	0.6	1.3	3.7	0.08	0.24	0.02	0.08	0.011	0.06
Wyssen	5	2.9	3.6	0.3	0.8	2.0	5.7	0.06	0.14	0.01	0.12	0.014	0.07
W. St. Louis	6	2.7	3.6	0.2	0.5	1.7	5.5	0.08	0.20	0.02	0.08	0.009	0.07
Short	7	3.5	4.7	0.2	0.6	2.0	6.1	0.09	0.20	0.02	0.09	0.014	0.08
Byers	8	4.4	6.2	0.2	0.3	1.2	3.4	0.12	0.21	0.09	0.24	0.009	0.04
Alder	9	4.5	7.0	0.3	0.5	1.5	6.0	0.07	0.20	0.02	0.12	0.008	0.07
Iron	10	10.1	15.4	0.1	0.3	1.2	3.3	0.22	0.33	0.19	0.32	0.009	0.06
Lunch	11	11.1	19.2	0.1	0.3	1.2	3.2	0.23	0.37	0.19	0.32	0.006	0.03
Gordon	12	12.5	17.0	0.1	0.4	0.8	2.8	0.25	0.42	0.24	0.47	0.008	0.04
Mine	13	5.1	7.0	0.1	0.4	1.4	5.4	0.16	0.25	0.11	0.23	0.011	0.20

(Continues)

TABLE 2 | (Continued)

Catchment	ID	SO_4^{2-} Mean	SO_4^{2-} Max	Cl^- Mean	Cl^- Max	DOC Mean	DOC Max	TDN Mean	TDN Max	NO_3-N Mean	NO_3-N Max	NH_4-N Mean	NH_4-N Max
Upper St. Louis	14	5.1	8.0	0.1	0.5	2.2	7.2	0.21	0.37	0.12	0.21	0.007	0.04
Range	15	3.3	5.0	0.2	0.4	1.5	5.0	0.24	0.34	0.16	0.25	0.008	0.06
E. St. Louis	16	2.2	3.8	0.2	0.5	2.1	7.3	0.13	0.36	0.05	0.16	0.012	0.18
Upper Fool	17	1.6	2.6	0.1	0.8	2.4	9.5	0.10	0.34	0.02	0.09	0.010	0.07
Lower Fool	18	2.2	3.4	0.2	0.7	2.9	10.1	0.10	0.28	0.01	0.13	0.011	0.07
All tributaries		**3.1**	**19.2**	**0.2**	**0.8**	**1.8**	**11.8**	**0.11**	**0.42**	**0.04**	**0.47**	**0.011**	**0.20**
St. Louis creek	**FEF**	**5.3**	**6.8**	**0.2**	**0.4**	**1.6**	**5.3**	**0.12**	**0.21**	**0.06**	**0.12**	**0.010**	**0.07**

Note: Data are mean and maximum concentrations for samples collected monthly during 2004–2006 and 2017–2019. Units are mg/L for all by pH (unitless), ANC (μeq/L), and SC (μS/cm). Saint Louis Creek site is the outlet of the study area. Bold values denote the mean and maximum values for all tributaries and for the main stem of Saint Louis Creek where it exits FEF. Refer to Figure 2 for sampling locations.

Columbia, MD). Detection limits for DOC and TDN were 0.04 and 0.01 mg L^{-1}, respectively.

2.3 | Statistical and Geospatial Analyses

We used Pearson's correlations to identify relations and then least-squares regression to evaluate how stream solute levels responded to catchment vegetation cover and physical attributes (IBM SPSS Inc., Chicago, IL, NY, V. 29). Solute concentrations were compared between the active bark beetle, high-N deposition era (2004–2006) and about a decade later (2017–2019) using mixed effects analysis of variance with catchments and time periods as the random and fixed effects, respectively. Throughout the text, differences among means were assigned and reported for p values $\alpha \leq 0.05$.

We characterized land cover and conditions within the contributing area of each study catchment. Watersheds were delineated on a 3DEP 10-m DEM (U.S. Geological Survey (USGS) 2023) and elevation, slope, and terrain ruggedness were calculated using WhiteboxTools (Lindsay 2020; R Core Team 2025). Terrain ruggedness estimates topographic variability based on elevation differences between an individual pixel and its eight neighbouring pixels (Riley et al. 1999). The alpine zone was delineated with high-resolution photography (U.S. Department of Agriculture Farm Service Agency (USDA FSA) 2024), during September–November NDVI < 0.6 (U.S. Geological Survey (USGS) 2024), and canopy cover < 20% (LANDFIRE 2021). Alpine vegetation and non-vegetated areas (i.e., bare ground and rock) were differentiated based on a peak summer vegetation NDVI threshold of 0.35.

3 | Results

3.1 | General Spatial Patterns

Solute concentrations varied widely among the tributaries at FEF (2 to 26-fold differences), though there were similarities among some neighbouring catchments (Table 2). For example, pH, ANC, SC, and Ca^{2+} were highest in catchments containing sedimentary rock (catchments 1–3; Figure 2, Table S1) and generally lowest in tributaries draining the eastern half of the study area (catchments 14–18). The highest mean values of TDN, NO_3-N, and SO_4^{2-} occurred in upper elevation catchments at the southern end of the St. Louis Creek (SLC) drainage (catchments 10–15). In those catchments, mean NO_3-N comprised 78% of TDN compared to 31% in all the other catchments that were located lower in the drainage (Table 2). Concentrations of biologically conservative solutes derived from weathering generally increased downstream along the mainstem of SLC. For example, SC, ANC, and the dominant cation concentrations were 1.4 to 2.1 times higher downstream and pH was 0.4 units higher (Table 2). In contrast, concentrations of the biologically reactive solutes DOC, TDN, and NO_3-N were 27%, 40%, and 50% lower at the downstream SLC sample site (ID = FEF) compared to upper SLC sampling location (catchment 14).

3.2 | Catchment Characteristics

For the study tributaries, concentrations of many solutes were significantly correlated ($p < 0.05$) with total catchment area and the absolute and proportional extent of the alpine and subalpine zones (Table 3). For example, pH, ANC, SC, and Mg^{2+} all decreased with catchment area and for most of these analytes with alpine area. In contrast, TDN and NO_3-N increased both with catchment size and the areal extent of alpine area. Stream TDN, NO_3-N, and SO_4^{2-} concentrations were positively related to the percent alpine cover (Table 3), and reciprocally with subalpine cover (not shown). In contrast, DOC, NH_4-N, Na^+, and Cl^- concentrations were negatively related to the percent alpine cover. Relations between solute concentrations and mean or maximum catchment elevations were generally similar to those reported for alpine cover (Table 3). Neither K^+ nor Ca^{2+} concentrations were significantly related to total catchment or alpine extent, though they were both negatively related to mean catchment elevation. Mean catchment slope and an index of ruggedness were related to fewer analytes and equally split between positive (NO_3-N, SO_4^{2-}) and negative (DOC, Na) relations. With a few notable exceptions (i.e., slope and ruggedness), TDN and NO_3-N were the solutes most closely related to catchment characteristics (Table 3).

TABLE 3 | Correlations between stream chemistry and characteristics of 18 headwater tributaries at the Fraser Experimental Forest.

		Catchment area				Elevation			
		Total	Alpine	Subalpine	Alpine	Mean	Max	Slope	Ruggedness
		ha			%	m		%	
TDN	*r*	**0.60****	**0.81****	0.34	**0.90****	**0.83****	**0.82****	0.46	**0.52***
	p	**0.01**	**0.00**	0.17	**0.00**	**0.00**	**0.00**	0.05	**0.03**
NO_3-N	*r*	**0.49***	**0.73****	0.23	**0.92****	**0.77****	**0.82****	**0.65****	**0.70****
	p	**0.04**	**0.00**	0.37	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
NH_4-N	*r*	−0.42	−0.44	−0.33	**−0.51***	**−0.63****	**−0.68****	−0.28	−0.33
	p	0.09	0.07	0.18	**0.03**	**0.01**	**0.00**	0.27	0.18
DOC	*r*	−0.02	−0.21	0.13	**−0.54***	−0.31	**−0.47***	**−0.84****	**−0.85****
	p	0.93	0.40	0.62	**0.02**	0.21	**0.05**	**0.00**	**0.00**
pH	*r*	**−0.53***	**−0.49***	**−0.47***	−0.25	**−0.61****	−0.46	0.41	0.39
	p	**0.02**	**0.04**	**0.05**	0.31	**0.01**	0.05	0.09	0.11
ANC	*r*	**−0.57***	**−0.54***	**−0.50***	−0.38	**−0.65****	**−0.58***	0.18	0.15
	p	**0.01**	**0.02**	**0.03**	0.12	**0.00**	**0.01**	0.48	0.54
SC	*r*	**−0.52***	−0.43	**−0.50***	−0.20	**−0.53***	−0.44	0.34	0.33
	p	**0.03**	0.08	**0.03**	0.42	**0.02**	0.06	0.16	0.18
Na^+	*r*	−0.19	−0.33	−0.05	**−0.66****	−0.43	**−0.57***	**−0.80****	**−0.82****
	p	0.46	0.18	0.85	**0.00**	0.07	**0.01**	**0.00**	**0.00**
K^+	*r*	−0.39	−0.34	−0.36	−0.34	**−0.58***	−0.38	0.30	0.29
	p	0.11	0.17	0.14	0.17	**0.01**	0.12	0.22	0.24
Mg^{2+}	*r*	**−0.64****	**−0.49***	**−0.65****	−0.19	**−0.58***	**−0.55***	0.34	0.33
	p	**0.00**	**0.04**	**0.00**	0.44	**0.01**	**0.02**	0.16	0.19
Ca^{2+}	*r*	−0.46	−0.38	−0.45	−0.18	**−0.48***	−0.39	0.34	0.33
	p	0.05	0.12	0.06	0.47	**0.04**	0.11	0.17	0.19
SO_4^{2-}	*r*	0.19	0.44	−0.03	**0.71****	**0.47***	**0.56***	**0.68****	**0.74****
	p	0.44	0.07	0.92	**0.00**	**0.05**	**0.02**	**0.00**	**0.00**
Cl^-	*r*	−0.42	**−0.53***	−0.26	**−0.72****	**−0.83****	**−0.77****	−0.14	−0.20
	p	0.09	**0.02**	0.29	**0.00**	**0.00**	**0.00**	0.58	0.42

Note: Pearson's correlation coefficient (*r*) and two-tailed significance level (*p*) for mean catchment solute concentrations. Bolded values refer to 2-tailed correlations at 0.05 (*) and 0.01 (**) significance levels.

The proportion of alpine cover within a catchment explained 83% of the variability in stream NO_3-N concentrations of the study tributaries ($p < 0.001$; Figure 3), and TDN concentrations followed a similar pattern. Mean NO_3-N concentration increased from 0 to 0.24 mg N/L across the range in alpine cover (Table 1). Catchments with > 30% alpine cover had roughly 6-times higher NO_3-N concentrations than those with < 20% cover. Similarly, five catchments with > 10% unvegetated alpine cover (12%–33%) had 5-times more NO_3-N than those with less. Stream NO_3-N decreased sharply across the range of average canopy cover and NDVI in the study catchments ($p < 0.001$; Figure 3). The proportion of stream TDN comprised of NO_3-N was also closely related to alpine cover ($r^2 = 0.79$). For example, NO_3-N was 78% of TDN in catchments with the highest levels of alpine cover and as low as 10% in the other catchments.

Stream solute composition also reflected the lithology of individual catchments (Table S1). Stream Ca^{2+}, Mg^{2+}, ANC, and SC concentrations were all positively related to the extent of shale and granodiorites in FEF catchments (Pearson's *r* values 0.64–0.84; $p < 0.001$). Cover of shale explained 73% of the linear increase in Ca and ANC concentrations, 68% of SC and 49% of stream pH across study catchments ($p < 0.001$ for each reported relation). Mean stream pH differed by 0.6 units across the lithologic groups with highest values on shale and lowest in catchments containing granite, though individual pH values spanned nearly 2 units. Catchments dominated by biotite gneiss (> 75%

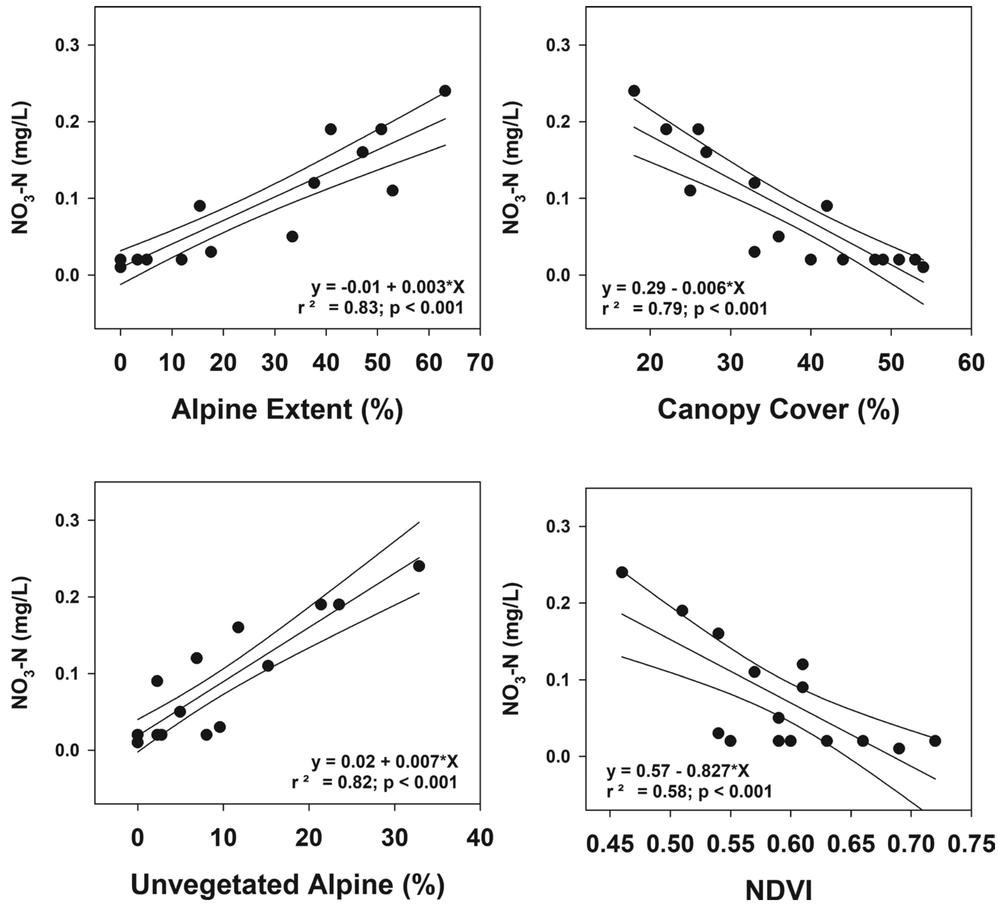

FIGURE 3 | Linear relations bracketed by 95th percentile confidence intervals for catchment characteristics and stream nitrate concentrations in 18 headwater tributaries at the Fraser Experimental Forest, Colorado. Nitrate concentrations are catchment means for samples collected between 2004 and 2017. Canopy cover and summer NDVI (Normalized Difference Vegetation Index) were derived from 2020 and 2024 Landsat images, respectively.

cover) had the highest levels of Mg^{2+}, K^+, and Cl^- of any rock group and higher Na^+ than those containing shale. The highest Na^+ and DOC occurred in catchments containing granite combined with gneiss.

3.3 | Response to Change

There were significant changes ($p < 0.05$) in most solutes between the early-2000s period of high MPB and N deposition and 2010s post-MPB period of decreased N deposition (Table 4). Stream pH, Na^+, K^+, and NO_3-N all declined ($p < 0.01$), and SC, ANC, Ca^{2+}, Mg^{2+}, and NH_4-N all increased. The greatest changes were for the inorganic N forms. Nitrate decreased by 0.01 mg N/L on average, representing a 22% change ($p < 0.001$). Conversely, the 0.01 mg N/L increase in NH_4-N was > 3-fold increase over the earlier period ($p < 0.001$). It is notable that in spite of the large decrease in S deposition, stream SO_4^{2-} did not differ between the two periods.

Stream NO_3-N was lowest in completely forested catchments and had fairly similar concentrations during the peak and post-MPB periods (Figure 4). Though differences between the periods were small, NO_3-N concentrations were generally higher during the post-MPB period in fully forested catchments. Conversely, there were consistent decreases in NO_3-N concentration in catchments with at least 30% alpine cover. The extent of alpine cover explained a similar amount of variability in stream NO_3-N concentrations (i.e., $r^2 = 0.84$) during both periods (Figure 4), though the slope of the relation was 1.6 times higher during peak-MPB period. Though NH_4-N increased in the later study period, concentrations of that solute were unrelated to the extent of alpine cover. Conversely, though stream SO_4^{2-} concentrations increased with alpine cover, they did not differ among the study periods (Figure 4).

4 | Discussion

4.1 | Stream Water Relation to Land Cover

Land cover and underlying catchment properties regulated the chemistry of streams draining high-elevation catchments at FEF (Tables 1 and 2). Land cover effects were exemplified by chemical differences between catchments with high amounts of alpine and those that were fully forested. Gordon Creek, the catchment with both the highest amount of alpine (63%) and unvegetated cover (33%) (Table 1), had the highest TDN, NO_3-N, and SO_4^{2-} and the lowest DOC concentration (Table 2). Overall, six catchments with the highest alpine cover (37%–63%) had

TABLE 4 | Comparison of solutes in 18 tributaries of Saint Louis Creek during a period of high bark beetle and high N deposition (2004–2006) and about a decade after bark beetle activity and *N* deposition had declined.

	Sample era	Mean	SE	Min	Max	
pH	2004–2006	7.8	0.01	6.7	8.3	***
	2017–2019	7.7	0.01	6.6	8.4	
ANC	2004–2006	793.2	16.4	157.4	1977.9	***
	2017–2019	928.0	16.7	173.7	2674.2	
SC	2004–2006	90.5	1.6	21.4	204.0	*
	2017–2019	95.9	1.5	23.1	225.0	
Ca^{2+}	2004–2006	13.4	0.3	2.0	40.2	**
	2017–2019	14.6	0.3	2.4	39.2	
Mg^{2+}	2004–2006	2.1	0.03	0.4	4.6	***
	2017–2019	2.3	0.04	0.4	6.9	
Na^{+}	2004–2006	2.0	0.02	0.8	5.2	**
	2017–2019	1.9	0.02	0.7	3.3	
K^{+}	2004–2006	1.0	0.01	0.2	2.7	***
	2017–2019	0.9	0.01	0.3	2.0	
SO_4^{2-}	2004–2006	3.4	0.10	1.4	15.1	NS
	2017–2019	3.4	0.09	1.0	19.2	
Cl^{-}	2004–2006	0.2	0.003	0.1	0.8	NS
	2017–2019	0.2	0.003	0.0	0.7	
NO_3-N	2004–2006	0.06	0.003	0.00	0.47	***
	2017–2019	0.05	0.002	0.00	0.36	
NH_4-N	2004–2006	0.00	0.000	0.00	0.10	***
	2017–2019	0.01	0.001	0.00	0.20	

Note: Units are mg/L for all by pH (unitless), ANC (μeq/L) and SC (μS/cm). Significant difference (*p* values: *0.05-0.01; **0.01-0.001; ***< 0.001) among sample eras in mixed effects analysis of variance. DOC and TDN were not analysed during the early period.

2.3-, 10.5-, and 3.1-times higher TDN, NO_3-N, and SO_4^{2-} compared to six fully forested catchments. One of the fully forested catchments (Fool Creek) had both the highest mean DOC and the lowest NO_3-N concentrations. On average, stream DOC and NH_4-N concentrations were 1.8- and 1.4-times higher in the six fully forested catchments compared to the six with the highest alpine cover.

These patterns reflect lower nutrient uptake and soil development in catchments with higher alpine cover. Early research in FEF's Lexen Creek documented 2–10 times higher NO_3-N concentrations in stream water draining the alpine portion of the catchment compared to the subalpine zone where NO_3-N leaching in the subalpine forest was also much lower (Stottlemyer and Troendle 1992; Stottlemyer et al. 1997). Sparse vegetation, coupled with the high elevation, steep slopes and ruggedness of the alpine zone results in limited nutrient uptake, soil formation and soil C accumulation and contribute to the high N and low DOC export we observed in catchments with higher alpine cover (Tables 2 and 3). Like most terrestrial ecosystems, subalpine forests are limited by N supply (Fahey et al. 1985), and lodgepole forests at FEF are known to retain nearly all of atmospheric N inputs (i.e., $>90\%$; Stottlemyer et al. 1997; Rhoades et al. 2017). In contrast, the continuous surface organic horizons and deeper soils typical of subalpine forests (Alstatt and Miles 1983) generate soluble C that elevates DOC released from fully forested catchments (Fegel et al. 2021). The strong relationship between streamwater NO_3-N, TDN and DOC and alpine land cover demonstrates the relative importance of alpine biogeochemistry on watershed exports and surface water quality (Seastedt et al. 2004).

We recognized that nested within the general effects of land cover, landscape features such as inclusions of weatherable bedrock, headwater seeps, and wetlands can have disproportionate effects on catchment-scale stream water (McClain et al. 2003; Soulsby et al. 2007). For example, at a nearby site, weathering of calcite from isolated outcrops generated most of the Ca measured in streams draining alpine catchments comprised primarily of granitic and metamorphic bedrock (Clow et al. 1997). At FEF, a small band of shale and granodiorite (Eppinger et al. 1985) was sufficient to elevate stream

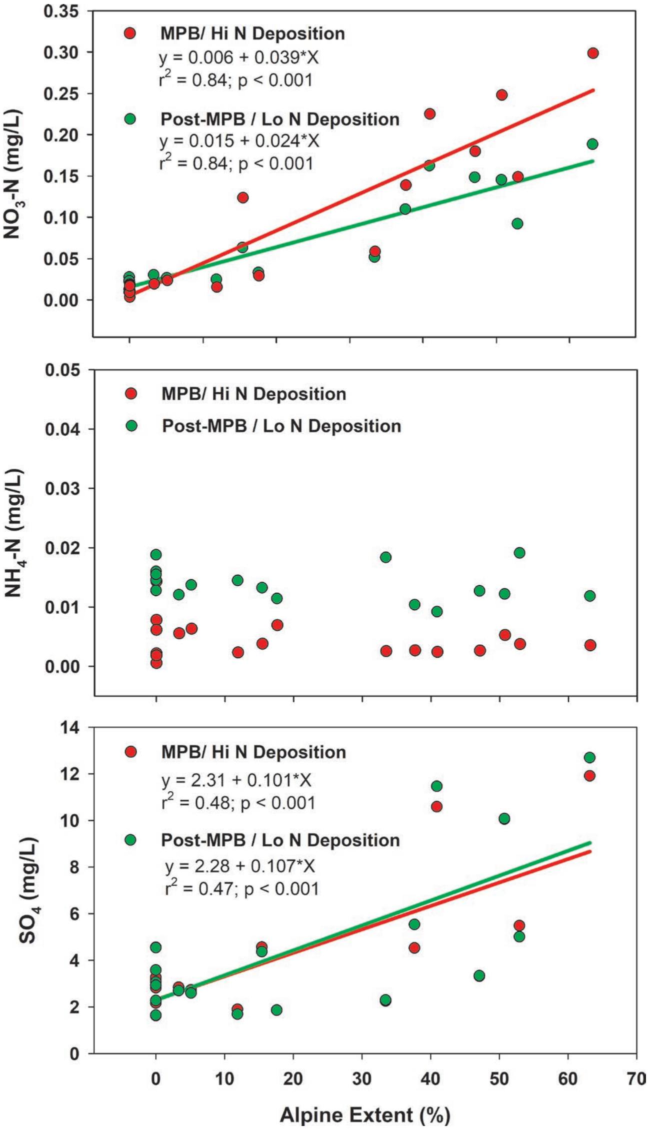

FIGURE 4 | Relations between stream nitrate (NO_3-N), ammonium (NH_4-N) and sulfate (SO_4) and the extent of alpine cover in study catchments during the period of high bark beetle (MPB) activity and high N deposition (2004–2006; red symbols) and about a decade after the bark beetle outbreak when regional and local N deposition had declined significantly (2017–2019; green symbols). Regression lines shown for significant linear relations ($p < 0.05$).

pH, ANC, Ca^{2+} and Mg^{2+} (Tables 2 and S1) relative to streams draining the metamorphic rock that dominates the area (Kellogg et al. 2008). Elsewhere in Colorado, alpine wetlands associated with periglacial solifluction lobes released much higher SO_4^{2-} than either snow-fed or forested wetlands (Rea et al. 2025). That study found that the higher C of the subalpine forest wetlands supported microbially mediated sulfate reduction, resulting in decreased stream SO_4^{2-} export. We also found that SO_4^{2-} was higher and DOC lower in FEF catchments with greatest extent of alpine cover though our sampling did not capture the influence of individual landscape features. Though the biogeochemical effects of local features are well known, they are rarely mapped at scales relevant to surface water chemistry (Olson and Hawkins 2012).

4.2 | Stream Water Responses After Bark Beetle Attack

Bark beetles killed ~80% of lodgepole pine trees in the overstory of mature forests at FEF during the early 2000s (Collins et al. 2011; Rhoades et al. 2017). Assuming that reduced nutrient demand following tree mortality would elevate stream NO_3-N during the MPB outbreak, we expected the greatest increase in catchments with the highest forest cover and a decline once beetle activity subsided. We observed the opposite pattern (Figure 4). In fully forested catchments, NO_3-N concentrations were low during both periods, and the significantly higher post-MPB period concentration (0.005 mg N/L) was near our analytical detection limit (0.002 mg N/L).

The patterns we observed were consistent with the minimal increases in stream NO_3-N reported during the outbreak and the decade following it at FEF (Rhoades et al. 2017) and sites across Colorado (Rhoades et al. 2013). The low NO_3-N concentrations in fully forested catchments (Figures 3 and 4) provide evidence of strong terrestrial N limitation and resilience of subalpine forests following insect outbreaks. Enhanced growth and nutrient uptake are known to minimize leaching following beetle-related tree mortality (Rhoades et al. 2013) and other disturbances (Vitousek et al. 1979). Previous work at FEF showed that pine mortality stimulated both diameter growth of overstory spruce trees and height growth of understory conifers (Rhoades et al. 2017). Elsewhere, the extent of gaps caused by dying trees (Parsons et al. 1994) and the pace of recovery (Huber 2005) determined the magnitude and persistence of post-bark-beetle NO_3-N losses. The response we observed in the fully forested watersheds at FEF (Figure 4) suggests that compensatory growth and nutrient uptake by > 1500 t/ha of live overstory and understory trees (Rhoades et al. 2017) was adequate to prevent excess nutrients from elevating stream NO_3-N losses.

Though earlier work at FEF demonstrate that the post-MPB increase in N export was minimal, equivalent to a small fraction of N inputs (i.e., < 2% of 2.6 kg N/ha/yr. inorganic deposition; Rhoades et al. 2017), insect-related mortality can cause large NO_3-N losses in forests that receive higher N deposition. For example, NO_3-N leaching exceeded European drinking water thresholds (i.e., 11 mg NO_3-N/L) after a spruce bark beetle outbreak (Huber 2005) in forests that received 12 to 16 kg N/ha/yr.; responses were greatest where understory vegetation was sparse. At another high N deposition site (7–14 kg N/ha/yr), stream NO_3-N concentrations increased from < 0.2 to 1.3 mg NO_3-N/L within 1–3 years of pine mortality (Zhu et al. 2025). The combination of low N deposition and relatively high density of non-host trees and understory vegetation at FEF (Rhoades et al. 2017) likely limited N losses. It is unknown how these findings relate to a beetle outbreak underway in forests near a densely populated urban area that receives higher N deposition (Burns 2004; Heindel et al. 2022).

4.3 | Changing Deposition at High Elevation

Differences in stream N concentrations between the two sampling periods (Table 4) tracked changes in deposition at FEF and surrounding areas (Figure 1). Overall, stream NO_3-N decreased by 22% and NH_4-N increased 3.5-fold. However, stream SO_4^{2-} did not differ between the sampling periods. We predicted that if solute concentrations responded primarily to declining deposition inputs (Figure 1) that changes would be most evident in higher elevation catchments and those with the greatest extent above treeline. Our stream N data supported this expectation (Figure 4). Stream NO_3-N decreased from 18% to 42% (31% average) in the six catchments with highest (i.e., $\geq 38\%$) alpine cover. Conversely, the solute increased up to 3-fold in the six fully forested catchments. Stream NH_4-N increased in every study stream, though the magnitude of change was unrelated to land cover or elevation.

At FEF, stream SO_4^{2-} was unchanged over the course of the study in spite of the 53% decrease in SO_4^{2-} deposition observed both locally and at regional monitoring sites. Though SO_4^{2-} responded to alpine cover and elevation like NO_3-N and TDN, it remained relatively constant during this period of significant forest disturbance and changing atmospheric deposition. Elsewhere in Colorado, stream SO_4^{2-} export from high-elevation catchments more than doubled from the mid-1980s through the early 2000s, during a period of decreased SO_4^{2-} deposition (Crawford et al. 2019). Similar increases in SO_4^{2-} have been observed in alpine streams globally and have been linked to permafrost thaw and elevated sulfide weathering (Crawford et al. 2019; Manning et al. 2024; Colombo et al. 2025). It is possible that our study commenced after significant warming or atmospheric deposition-related changes had occurred. However, there has been no general increase or decrease in SO_4^{2-} concentrations in four long-term research catchments at FEF (Fool, E. St Louis, Deadhorse Main, Lexen) since 1990 (FEF, unpublished data). In contrast to other locations in Colorado (Crawford et al. 2019; Manning et al. 2024), the absence of mining and sulfide bearing minerals and limited occurrence of periglacial features (Retzer 1962) likely explains why stream SO_4^{2-} remained relatively constant at FEF.

Though we attributed temporal patterns in stream solutes to changing N and S deposition, headwater catchments are exposed to numerous other inputs including dust (Ballantyne et al. 2011), microplastics (Brahney et al. 2020), and other compounds (Arienzo et al. 2025). There is growing awareness that deposition of dust derived from distant sources alters snowpack albedo and snowmelt timing (Painter et al. 2007), and snowpack and alkalinity (Rhoades et al. 2010; Clow et al. 2016) in high-elevation forest and alpine ecosystems. Rates of dust deposition have increased due to regional drying and land-use change (Neff et al. 2008), though aeolian inputs and depositional soil layers have been documented in alpine areas at FEF (Retzer 1962) and in mountainous catchments elsewhere (Litaor 1987; Schwikowski et al. 1995; Muhs and Benedict 2006). Wildfire smoke has been shown to impact the chemistry of streams and lakes across western North America (Farruggia et al. 2024; Fernandez et al. 2024). Uncertainty about the consequences of these and other poorly studied inputs justifies monitoring to assess changes from expected and unknown future changes in deposition and disturbance in high-elevation catchments. Alpine ecosystems are susceptible to changes associated with climate warming and atmospheric deposition (Litaor 2022), though our study demonstrates that surface water responses differ among analytes.

4.4 | Management Implications and Conclusions

High-elevation land cover regulates stream solute concentrations as well as catchment-scale responses to changing atmospheric deposition. Overall, FEF streams were sensitive to decreased atmospheric N inputs though the magnitude of solute-specific responses varied between catchments with forest and alpine headwaters (Figure 3). The general decrease in stream N was consistent with widespread changes attributed to Clean Air Act implementation (Lehmann et al. 2005; Du 2016). Our findings show the value of considering forest and alpine land cover when evaluating the biogeochemical consequences of air quality regulation (Lassiter et al. 2026).

It is hard to generalize between forest disturbance events, since outcomes vary with disturbance types and severity and are further modified by ecosystem and site conditions. For the FEF region where atmospheric nutrient deposition is low, the post-bark beetle decrease in tree nutrient uptake had little effect on N export, since compensatory uptake by residual vegetation absorbed any soil nutrient surplus (Rhoades et al. 2013). These findings and early studies concluded that beetle-related tree mortality had much less impact on stream nutrients than either wildfire or forest harvesting (Clow et al. 2011). In high N-deposition environments, where residual vegetation was sparse, excess post-disturbance soil nutrients overwhelmed the vegetation uptake capacity and resulted in N leaching and water quality concerns (Huber 2005; Zhu et al. 2025). As a whole, these findings demonstrate the importance of maintaining live vegetation and promoting vegetation recovery to mitigate nutrient losses following tree mortality.

This study shows the biogeochemical influence of land cover, especially in the uppermost portions of high-elevation catchments (Li et al. 2024). Headwater stream reaches comprise most of the length in river networks (MacDonald and Coe 2007), and land cover is a key determinant of nutrient retention and loss from those areas (Yang et al. 2021). Upland and riparian forest cover are known to improve the water quality of catchments dominated by urban and agricultural land uses (Dodds and Oakes 2008; Djodjic et al. 2021). In this study, we found that nutrient retention in fully forested catchments buffered biogeochemical perturbation associated with high levels of tree mortality. Catchments with extensive alpine cover, in contrast, were more responsive to temporal deposition patterns than those with forested headwaters.

High elevation land cover is sensitive to climatic conditions (Andrus et al. 2021; Pederson et al. 2025). For example, alpine treeline has moved up by 0.4 m/yr. globally since 1900 (Lu et al. 2025). Increased temperatures and drought stress have increased tree mortality and reduced seedling establishment for subalpine forest species across the western US (Hoecker et al. 2026). In the Colorado Front Range, the bioclimatic area suitable for lodgepole pine is predicted to decrease by > 75% by 2060 (Crookston 2009; Fornwalt et al. 2024). Bark beetle outbreaks have likely complicated patterns at FEF and throughout Colorado (Maher et al. 2021; Siegert et al. 2024). Temperature warming in alpine ecosystems has been linked to higher subsurface transport of weatherable minerals and increased surface water concentrations (Manning et al. 2013; Crawford et al. 2019; Barnes et al. 2014; Knapp et al. 2026), though the implications of climate-related land cover change for clean water delivery will require continued monitoring and further study.

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Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Dominant lithology underlying catchments at the Fraser Experimental Forest, Colorado. Data is cover (%) by rock types within individual catchments and the entire study area above the historic gauging station (Figure 2). See text for geologic mapping citations.