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RESEARCH ARTICLE

Experimental evidence of dust-driven shifts in production, chlorophyll *a*, and community composition in mountain lakes

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Abstract

Drought and human land use have increased dust emissions in the western United States. However, the ecological sensitivity of remote lakes to dust deposition is not well understood and to date has largely been assessed through spatial and temporal correlations. Using in situ bioassays, we investigated the effects of dust enrichment on the production, chlorophyll *a* (Chl *a*) concentration, and taxonomic composition of phytoplankton and microbial communities in three western US mountain lakes. We found that dust-derived nutrients increased Chl *a* concentration in all three lakes, but the magnitude of the effect varied from 32% to 226%. This variation was related to pre-existing lake conditions, such as trophic status, pH, and nutrient limitation. In Castle Lake, co-limited by N and P, dust bioassays showed an increase in Chl *a* content per cell but suppressed primary production and increased dark ^{14}C uptake. In contrast, both Flathead Lake and The Loch were primarily P-limited and exhibited increases in Chl *a* concentration. The contrasting Chl *a* and primary production results from Castle Lake are consistent with the alleviation of nitrogen limitation where energy Adenosine triphosphate (ATP) is used for nutrient assimilation instead of carbon fixation. Dust additions also altered the algal and microbial communities. The latter included the addition of new phyla (e.g., *Deinococcota*), indicating that dust-delivered microbes have the potential to thrive in receiving lakes. Our study provides the first short-term experimental in situ evidence of rapid ecosystem effects in mountain lakes following dust exposure. The results emphasize the need for continued research in this area to understand interactions of both the short- and long-term consequences of dust-induced perturbations in remote lakes in the context of global changes.

Human activities, such as land use, energy production, and agricultural activities, coupled with climate change events including wildfires and drought, have dramatically disrupted the global nitrogen (N) and phosphorus (P) cycles, leading to cross-ecosystem fertilization through atmospheric nutrient transport (Baron et al. 2000; Wolfe et al. 2001; Brahney, Mahowald, et al. 2015). Whereas human activities within catchments can affect downstream freshwater nutrient concentrations, dust transport carries nutrients and organisms to remote ecosystems that would otherwise be free from direct human impact (Morales-Baquero et al. 2006; Brahney et al. 2014; Brahney, Mahowald, et al. 2015). Dust deposition has increased by 5–7 fold in the western United States in recent centuries and again in the last few decades (Neff et al. 2008; Brahney et al. 2013; Tong et al. 2017), raising questions as to whether atmospheric dust transport is contributing to eutrophication (Stoddard et al. 2016) and even harmful cyanobacteria blooms in these systems (WDEQ 2023, Gonzalez-Olalla and Brahney 2025). Similar

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increases in dust deposition have been observed in other parts of the world, such as the Tibetan Plateau in China (Wan et al. 2016; Wei et al. 2021), Japan (Tsugeki et al. 2012), Spain (Jiménez et al. 2018), Australia and New Zealand (Hooper and Marx 2018; Brahney et al. 2019), South America (Li et al. 2008), and Africa (Mulitza et al. 2010; Evan et al. 2016).

Dust can carry substantial amounts of N and P to ecosystems, but the composition and bioavailability of these nutrients vary with biogeography and land use (Neff et al. 2002; Lawrence and Neff 2009; Zhang et al. 2018; Scholz and Brahney 2022). As a result of human modification of the landscape, atmospheric particulate-P concentrations have increased by approximately 40% from pre-industrial times to now (Brahney, Mahowald, et al. 2015) as dust is increasingly generated from organic-rich substrates such as dry lakebeds, urban environments, wildfires and affected landscapes, agricultural soils, and emerging landscapes through the loss of the cryosphere (Brahney et al. 2024). Organic content within US dust is relatively high compared to the global average, ranging from 15% to 67% by weight (Dahms and Rawlins 1996; Malm et al. 2004; Lawrence and Neff 2009). Biomass burning and wildfires also contribute to high soluble P concentrations in dust, depending on the degree of pyrolyzation (Boy et al. 2008; Bigio and Angert 2019), and thus, have the potential to influence aquatic ecosystems (Goldman et al. 1990; Mackey et al. 2013; Olson et al. 2023). Similarly, dust from urban pollution, wildfires, and biomass burning, and receding glaciers may contain significant amounts of soluble and bioavailable organic P species (Zhai et al. 2009; Brahney 2019; Goodman et al. 2019; Koffman et al. 2021).

Nitrogen concentration and speciation in dust reflect variation in soil content, agricultural activities, and biomass burning as well as atmospheric interactions where atmospheric gases may adsorb to particulates in the atmosphere (Mace et al. 2003; Lawrence and Neff 2009; Brahney et al. 2022). With increasing regional dust deposition and decreasing nitrate emissions, dust-N might play an increasingly important role compared to N deposition from rain and gaseous aerosols. With respect to nitrogen, it has been estimated that the flux of organic N may contribute 25% of the total N deposition flux globally (Jickells et al. 2013). In North America, the water-soluble organic N in dust can contribute up to 66% of total atmospheric N deposition (Neff et al. 2002), although this fraction of dry deposition is rarely measured.

The effects of dust-derived nutrients on freshwater ecosystems are still poorly understood and likely underestimated, but have gained recent interest due to the spatial and temporal relationships between dust deposition rates and phosphorus, dissolved organic carbon (DOC), nutrient limitation, and ecosystem processes (Morales-Baquero et al. 2006; Mladenov et al. 2012; Catalan and Camarero 2014; Brahney et al. 2014; Brahney, Ballantyne, et al. 2015). Because dust has the potential to stimulate both primary production and heterotrophic respiration, the ecological response of dust deposition may vary based on dust composition and the chemical and biological condition of the recipient lake. Organic carbon in dust has the potential to alter freshwater species assemblages by stimulating heterotrophic bacteria and increasing C transfer through the microbial loop (Fig. 1a). Under nutrient-limited conditions, bacteria have a competitive advantage over algae in scavenging nutrients (Currie and Kalff 1984). Thus, increases in dust-derived DOC can lead to intensified competition between bacteria and phytoplankton for inorganic nutrients (Carney et al. 2016). Several studies have found that DOC inputs from dust stimulated microbial growth in water bodies in the Mediterranean area (Pulido-Villena, Reche, and Morales-Baquero 2008; Pulido-Villena, Wagener, and Guieu 2008; Reche et al. 2009), and high microbial diversity has been reported in dust samples from across the United States (Barberán et al. 2015). However, it is not yet fully understood whether dust carries new taxa into receiving waters or how the characteristics of receiving water bodies may ultimately affect the establishment of dust-borne bacteria and fungi, and/or stimulate resident microbes.

Given the potential for dust to provide nutrients that stimulate primary production and microbial respiration in freshwater systems (González-Olalla et al. 2024), it stands to reason that elevated dust emissions can affect mountain lake ecosystems, most of which are oligotrophic with nutrient-limited primary producers (Moser et al. 2019). However, direct field experimental evidence is still lacking, especially for regions such as the western United States where dust has been proposed as a mechanism driving eutrophication. Our central hypothesis is that dust deposition influences mountain lake ecosystems through the supplementation of bioavailable phosphorus, nitrogen, as well as other micronutrients (Fig. 1a). However, we expect that the response of mountain lakes will likely depend on dust P speciation and its relative bioavailability to phytoplankton. Inorganic exchangeable P in dust is easily leached and available for algae after deposition into the water column. Whereas organic P compounds can be used after enzymatic hydrolysis, the efficiency of which is dependent upon organic P concentration and speciation, pH, and specific phytoplanktonic composition (Boström et al. 1988). However, these impacts may be modulated by the biogeochemical status of the receiving waters. Here we quantify the bioavailable content of dust collected from remote locations of the western United States and perform in situ bioassays in three mountain lake systems to evaluate ecological responses to short-term dust additions.

Materials and methods

To evaluate the potential effect of dust on aquatic ecosystems, we conducted in situ bioassay experiments in three mountain lake systems in the western United States. Mountain systems were chosen as they are ideal study locations for assessing the effects of dust deposition due to their natural oligotrophic status, limited anthropogenic disturbance, as well as

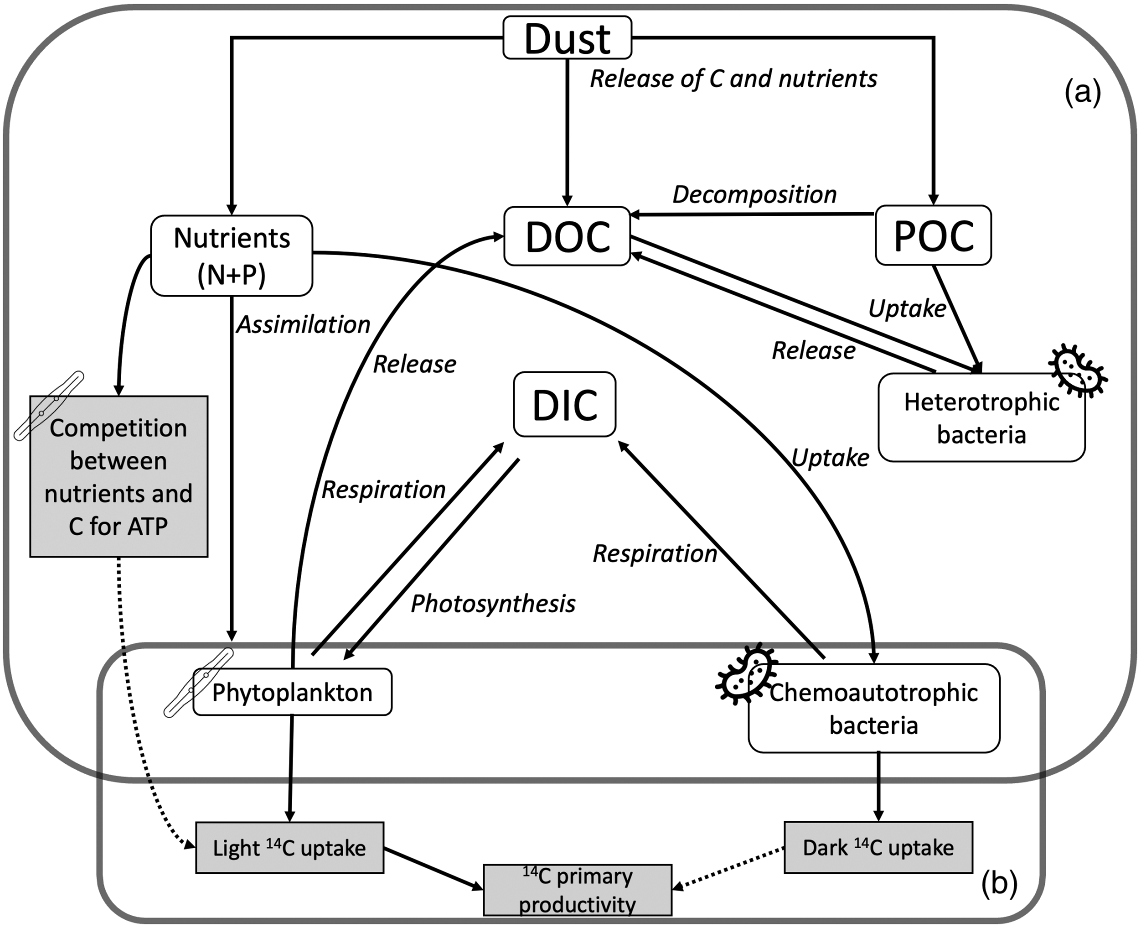

Fig. 1. Conceptual model for the influences of dust inputs on (**a**) nutrients and carbon paths and biological activities and (**b**) ^{14}C primary productivity. Dotted lines indicate negative effects.

their high airshed to watershed ratios (Brahney et al. 2014, 2021, 2022; Catalan et al. 2017; Moser et al. 2019). Additionally, mountains can intercept dust that is usually mixed and transported higher in the atmospheric column, resulting in higher rates of dust deposition to mountain lakes (Catalan et al. 2017). The sizeable proportion of their bare rock watersheds results in poor soil development, but these same steep slopes can increase dust-nutrient transport to lakes from atmospheric deposition (Kopáček et al. 2005; Brahney et al. 2014; Nielson and Brahney 2024). However, mountain catchments pose challenges for experimental research due to their inherent remoteness. The lakes we studied are Castle Lake, CA, Flathead Lake, MT, and The Loch, CO. An on-site laboratory at Castle Lake allowed us to perform time-dependent bioassay trials as well as quantify production using the ^{14}C technique (Goldman 1964).

Study sites

Castle Lake (41′13″N, 122′22″W) is located in the Trinity Mountains (Northern California) at an elevation of 1660 m above sea level (m asl) and is ice-free for an average of 135 d. This lake is a slightly alkaline meso-oligotrophic lake with the phytoplankton community typically expressing co-limitation of nitrogen and phosphorus and other trace elements such as molybdenum (Mo) (Elser et al. 1995; Park et al. 2003). The Loch (40′17″N, 105′39″W), situated in Rocky Mountain National Park (Colorado) at an elevation of 3109 m asl, is ice-covered from October to April. It is a slightly acidic oligotrophic lake that is typically P limited due to high historical N deposition and limited weathering of monazite, a P-bearing mineral (Baron et al. 1991; Nydick et al. 2003; Price et al. 2022). Flathead Lake (47′53″N, 114′04″W) is located between Mission Mountains and Salish Mountains in northwestern Montana at an elevation of 881 m asl. It is a large, deep, slightly alkaline, oligotrophic lake with serial N & P limitation, with P as the primary limiting nutrient (Ellis et al. 2015; Elser et al. 2022). As nutrient limitations can frequently shift between seasons and locations, we performed nutrient limitation assays concurrently with the dust addition assays at all lakes. Table 1 provides detailed lake characteristics. The average dust deposition rates at three lake sites

Table 1. Characteristic of three studied mountain lakes. SA: surface area. MD: mean depth. Avg temp: average temperature of surface water during experimental trials. Chl *a*: initial Chl *a* concentration. CA : LA, catchment area to lake area ratio.

Lake	SA (km^2)	MD (m)	CA : LA	Elevation (m)	pH	Avg temp (°C)	Chl *a* ($\mu g\ L^{-1}$)	Mean dust dep. rate ($mg\ m^{-2}\ d^{-1}$)	Max monthly dust dep. rate ($mg\ m^{-2}\ d^{-1}$)
Castle Lake	0.2	11.4	4.2	1660	8.5	22.1	1.3	25	297
Flathead Lake	510	39	43.6	881	8	21.8	0.9	15.8	50
The Loch	0.05	1.5	132	3109	6.5	10.3	3.5	10.7	74

(estimated from nearby National Atmospheric Deposition Program [NADP] sites) ranged from 11 to 25 $mg\ m^2\ d^{-1}$, though several monthly average deposition rates reached as high as 300 $mg\ m^2\ d^{-1}$, highlighting the episodic nature of dust. Total phosphorus (TP) concentrations in dust varied from 1.1 to 5.4 $mg\ g^{-1}$ (Brahney et al. 2020).

Dust collection and determination of bioavailable nutrients

To collect dust samples, we employed Dry Sampling Units in tandem with the National Atmospheric Deposition Program, as outlined by Brahney et al. (2020). These Dry Sampling Units capture the dry gravitational flux of dust to ecosystems while eliminating contamination (Brahney et al. 2020). Dusts used in this experiment were collected from 11 sites across the western United States (Supporting Information Fig. S1) between 2019 and 2020 using the methods described in Brahney et al. (2020) and frozen until further analyses. In the experimental trials, we elected to use a mixed dust sample collected from various sites throughout the western United States for all three lakes to separate the biological response in the three lakes from differences due to site-specific dust composition.

To determine the amount of bioavailable P in dust materials, we used a sequential extraction procedure modeled after Moir and Tiessen (2007) and Ruttenberg (1992). Previous dust studies have used modified versions of either the soil method (Scholz and Brahney 2022) or sediment method (Zhang et al. 2018), but our goals were to assess both the immediately bioavailable nutrients (minutes to hours) and those that would become available through microbial degradation over days to weeks (Supporting Information Fig. S2). Our sequential P extraction procedure quantified five P pools based on increasing bioavailability (Supporting Information Fig. S2): (1) readily soluble and freely exchangeable inorganic P (P_i) extracted with KCl, (2) labile P_i and organic P (P_o) extracted with $NaHCO_3$, (3) Al and Fe associated P_i and Labile P_o extracted with NaOH, (4) authigenic and biogenic apatite and Ca-associated P_i and stable P_o extracted with acetic buffer at pH 4, and (5) residual P. The detailed procedures are provided in the Supporting Information. We used a ratio of two parts dust to one part solution for all extractions, and between each step, we rinsed and dried the dust overnight. P_i was measured using the standard molybdate blue method (Murphy and Riley 1962) and TP was measured similarly after the extraction was digested with potassium persulfate and autoclaved. P_o was obtained by subtracting P_i from TP. The residual in the last step was analyzed for total TP only. We conducted P measurements on a SpectraMax® M2 spectrometer (Supporting Information Fig. S2).

Lake bioassay experiments

We used the sequential leaching data described above to estimate the amount of P released in each experimental trial in the absence of biological activity, similar to González-Olalla et al. (2024). In this study, we define bioavailable P as the combination of P extracted with KCl and $NaHCO_3$, as well as NaOH extracted P_o (Sonszogni et al. 1982; Pu et al. 2023). Based on our assessments, we found that every 1 mg of the mixed dust material releases 0.1 μg of KCl-extracted P (the most bioavailable P) and 0.75 μg of total bioavailable ($P_i + P_o$; Supporting Information Fig. S2).

To determine the dust addition levels, we used recorded western dust deposition rates (Brahney et al. 2020) and estimated dust loading to the water surface, assuming that 30% of the catchment deposition reaches the lake (Brahney, Ballantyne, et al. 2015; Scholz and Brahney 2022). Note that the physics of particle sedimentation is beyond the scope of the study. However, in an ideal non-turbulent system, Stokes Law dictates that the average dust particle would only sink 1 m per day. Given the turbulence of natural lake systems, it stands to reason that dust would remain suspended in the epilimnion for at least the duration of the experiment, and more likely much longer. The low dust addition (12 $mg\ L^{-1}$) simulated 2–10 dust events in the lake, while the medium dust addition (24 $mg\ L^{-1}$) simulated dust accumulation over a 3-month growing period, and the high dust addition (40 $mg\ L^{-1}$) simulated accumulation of winter deposition, which may reach the lake in a pulse during melt. Because Flathead Lake is considerably larger and deeper, with a greater epilimnion volume to dilute dust inputs, lower concentrations were used (5, 10, and 20 $mg\ L^{-1}$; Supporting Information Fig. S2). We recognize that these concentrations are estimates, as it is not possible to directly determine prospective dust concentrations given the episodic nature of dust inputs. However, for example, in The Loch (0.05 km^2 surface area, average depth 1.5 m), if we assume dust accumulates over 6 months of winter (5 months at an average deposition rate of 10.7 mg m^{-2} d^{-1} and 1 month at a maximum of 74 mg m^{-2} d^{-1}), and that 30% of the catchment deposition enters the lake as a pulse during snowmelt, dust concentrations could reach as high as 100 mg L^{-1}. Thus, our high dust concentration of 40 mg L^{-1} is likely conservative and appropriate for the smaller mountain lakes.

In July and August 2021, in situ bioassay experiments were conducted using a buoy-frame-anchor system. We used slightly different methods at each site based on available facilities and distinct lake morphologies. At all sites, we collected lake water using an integrated water sampler (one 2.5-m clear polyvinyl chloride (PVC) tube with two rubber stoppers) and removed large zooplankton with a 180-μm mesh. We dispensed the mixed lake water into 250-mL clear incubation bottles. Both the dust and control treatments had three replicates. We added pre-mixed and pre-weighed dust materials into filled bottles and shook them. All bottles were then attached to a floating frame attached to an anchored buoy. All the bottles were suspended and incubated for 96 h in the epilimnion. Because the Loch has a shallow depth (mean 1.5 m, maximum 4.7 m), we opted to incubate bottles at 2 m below the surface in this lake. However, in the other two lakes, we incubated at 5 m to mitigate the risk of potential photoinhibition. We rotated and shook the bottles at least once every day during the bioassay. Note that the dust additions were not sufficient to influence light characteristics within the bottles. In addition, we simultaneously determined nutrient limitation of phytoplankton through additional incubations with +N, +P, and +N & +P addition treatments. Nutrients were added as KNO_3 and KH_2PO_4 to reach a final concentration of 448 μg L^{-1} N and/or 62 μg L^{-1} P (Supporting Information Fig. S2). Along with controls, all experiment assays (dust, nutrients) were performed in triplicate.

Determination of chlorophyll *a* and primary production

Chlorophyll *a* (Chl *a*) was determined by filtering the sample on pre-ashed (450°C, 4 h) acid-rinsed ADVANTEC 0.3-μm glass fiber filters. The resulting filters were then wrapped in tinfoil and kept frozen until analysis. Chlorophyll *a* analysis followed the fluorometric method (Welschmeyer 1994). Due to the presence of an on-site laboratory at Castle Lake, the onsite Turner Designs 10-AU fluorometer allowed us to determine daily chlorophyll variation through the experiment by examining the relative fluorescence units (RFUs) measured at 44, 68, 78, and 96 h. In addition, at Castle Lake we conducted primary production rates (PPRs) measurements in parallel with the bioassay. We labeled three light samples and one dark bottle sample from each dust treatment and the control with inorganic ^{14}C in the form of $NaHCO_3$ and then incubated in 150-mL glass bottles at the same depth as our primary bioassay experiment (5 m). We also measured PPR at 48 and 96 h of the primary bioassay to determine temporal trends of primary production (Goldman 1988). At the end of the bioassay, we separated water into subsamples for the following analyses. We filtered water samples with MF-Millipore 0.45-μm MCE membrane filters (HAWP02500), which were dried for 24 h and counted on a pico-counter (IPC-650, Protean Instrument Corporation). We calculated net PPR by subtracting dark bottle PPR from light bottle PPR, and bacterial productivity was indexed by ^{14}C dark uptake rates (*see* Statistical analyses section). It was impractical to conduct these additional analyses at the other two lakes given their remote nature.

Determination of nutrients and phytoplankton community

Filtered samples were analyzed for C, N, and P constituents at Utah State University. Filtrates were acidified with trace metal grade HCl to pH 2. Total dissolved P and soluble reactive phosphorus (SRP) concentrations were determined using the ascorbic acid method and persulfate digestion method on a SpectraMax® M2 spectrometer (Baird et al. 2017). Organic P concentrations were calculated from the difference of Total dissolved P and soluble reactive phosphorus. Total dissolved nitrogen, total dissolved carbon, and inorganic carbon were determined with a Skalar C/N analyzer directly at Utah State University. We estimated DOC from total dissolved carbon and inorganic carbon, and measured the fluorescence index to determine the source of DOC (derived from extracellular release and leachate from bacteria and algae vs. terrestrially terrestrial plant and soil organic matter) in the dust treatments (Fellman et al. 2010). Unfiltered water subsamples were preserved with 50% glutaraldehyde to a final concentration of 2% for phytoplankton community analysis. Samples were stored in dark bottles, cooled, and immediately sent to BSA Environmental Services, Inc. (Beachwood, OH) for community composition and biovolume quantification.

Determination of microbial community composition

We performed 16S amplicon DNA sequencing to characterize bacterioplankton communities. To collect bacterial biomass, we filtered 500 mL of pooled water from treatments through 0.2-μm pore size filters (Supor PES membrane, Pall Life Sciences, Port Washington, NY, USA) and extracted genomic DNA directly from the filters using the DNEasy PowerWater Kit (Qiagen, Valencia, CA, USA). We used Polymerase Chain Reaction (PCR) -amplification of the V4 region of the bacterioplankton 16S rRNA gene with the primer set 515F and 806R (Caporaso et al. 2011) using dual indices developed by (Kozich et al. 2013). Following PCR, we normalized the samples using SequalPrep Normalization Plate Kits (Applied Biosystems, Waltham, MA) and pooled them at equimolar concentrations. We submitted the samples for 2 × 250 bp paired-end sequencing on the Illumina MiSeq System at the Utah State University Center for Integrated Biosystems (https://caas.usu.edu/biosystems/). We processed the sequences using the QIIME 22021.2 bioinformatics pipeline (Bolyen et al. 2019). Briefly, we demultiplexed samples and denoised with DADA2 via the q2-dada2 plugin, and phylogeny was constructed with fasttree2 (Price et al. 2010) via q2-phylogeny using aligned amplicon sequence variants that were aligned with MAFFT (Katoh and Standley 2013) (via q2-alignment).

Statistical analyses

To examine potential differences in Chl *a* concentrations across the control, dust, and nutrient treatments for each lake, we conducted a one-way ANOVA (ANOVA, *aov* function, base R package). In addition, we used natural log response ratios (LRR) as an effect size metric (Cabrerizo et al. 2020) to assess the impacts of dust and nutrient treatments on Chl *a* concentrations in the three lakes as:

$$\mathrm{LRR}_{\mathrm{treatment}} = \mathrm{Ln}\frac{\mathrm{Chl}\,a_{\mathrm{treatment}}}{\mathrm{Chl}\,a_{\mathrm{control}}} \tag{1}$$

To determine the daily Chl *a* increase rates across dust addition gradients, we conducted a linear regression analysis of daily RFU in dust treatments at Castle Lake and the control and compared slopes of regression lines using a post hoc test after one-way ANOVA. The final Chl *a* concentrations from the nutrient addition bioassays in each lake were used to determine the type of nutrient limitation using a five-category classification system proposed by Elser et al. (2009): single N or P limitation, synergistic N–P co-limitation, strict N–P co-limitation, sequential co-limitation by N or P, and dual limitation. Net PPRs were examined for differences across the control and dust treatments using one-way ANOVA and a post hoc test. We also obtained *F* and *p* values from two-way ANOVAs (*aov* function, base R package) to examine the effects of dust treatment, lakes, and their interaction on biological response variables (Chl *a*, RFU, and PPR).

To characterize the effects of dust treatments on phytoplankton and bacterioplankton communities, we first estimated the relative abundance of mixotrophs to the total phytoplankton. We then used nonmetric multidimensional scaling (NMDS) with the “vegan” package (Dixon 2003) in R and “q2-diversity” plugin in QIIME 2 to visualize differences in community composition in each lake based on a Bray–Curtis distance matrix. Bray–Curtis distance is a measure of community composition similarity or dissimilarity (Bray and Curtis 1957). We applied the Hellinger transformation to relative count data prior to performing nonmetric multidimensional scaling. This transformation minimizes distortion due to many zero values for species (Legendre and Gallagher 2001). We assigned taxonomy of microbial communities to amplicon sequence variants using the q2-feature-classifier plugin (Bokulich et al. 2018) and classify-sklearn Naive Bayes Classifier against the Silva 138 99% operational taxonomic unit (OTUs) reference sequences (McDonald et al. 2012). We used ANCOM (Mandal et al. 2015) at the genus level (via q2-composition) to evaluate the differential abundance of bacterioplankton. The effects of dust treatments and locations on microbial and phytoplankton community composition were examined using two-way PERMANOVAs (*adonis2* function, vegan package) with dust treatment and location as the main factors. To test for differences in the abundance of specific taxa across treatments and locations, we conducted multiple comparisons with False Discovery Rate (FDR)-adjusted *p*-values. To quantify the effects of dust treatments on phytoplankton size variations, we classified size structure from biovolume based on equivalent spherical diameter (Finkel et al. 2010) and calculated biomass for diatoms and other cells using regression Eqs. 2 and 3 according to Strickland (1970) based on laboratory data (Soria-Píriz et al. 2017). To visualize how dust additions influence the size structures in three lakes, we normalized biomass to describe the trend only. All analyses and figures were conducted in R version 4.1.3 (R Development Core Team 2021).

$$\mathrm{Log}\,C = 0.76\,\mathrm{Log}\,V - 0.29 \tag{2}$$

$$\mathrm{Log}\,C = 0.94\,\mathrm{Log}\,V - 0.60 \tag{3}$$

where C is carbon mass (pg cell^{-1}) and V is cell volume (μm^3 cell^{-1}).

To estimate the contribution of bacterial productivity between treatments, we assumed that ^{14}C dark uptake rate represents the chemoautotrophic bacteria productivity because chemoautotrophic microorganisms contribute a large fraction of ^{14}C uptake in the dark (Swan et al. 2011; Callieri et al. 2014). We also calculated the percentages of ^{14}C dark uptake rate (one replicate) to light uptake (three replicates) after 48 and 96 h at Castle Lake.

Results

Nutrient limitation and chlorophyll *a* concentrations

During our experimental period, algal production in the three mountain lakes was limited by different nutrients, specifically nitrogen and phosphorus (Fig. 2a). Castle Lake’s algal growth was co-limited, with the addition of N + P increasing Chl *a* by 151% relative to the control treatment. At Flathead Lake, P addition dramatically increased Chl *a* concentrations by 243% while N + P additions had a super-additive effect (341%), indicating sequential co-limitation by N. At The Loch, only P significantly increased Chl *a* concentrations (by an average of 72%), suggesting that The Loch was limited by P alone (Fig. 2a). Comparing the effect sizes of nutrient additions on Chl *a*, we found that N addition had a negative influence on Chl *a* concentration at The Loch and a weak positive influence at the other two lakes ($\mathrm{LRR_N} < 0.3$). P addition had the largest effect at Flathead Lake ($\mathrm{LRR_p} = 1.23$) and the smallest at Castle Lake ($\mathrm{LRR_p} = 0.07$). N + P addition influenced Flathead Lake substantially ($\mathrm{LRR_{NP}} = 1.48$) while affecting The Loch the least ($\mathrm{LRR_{NP}} = 0.46$) (Fig. 2b).

Dust additions also increased Chl *a*. At the end of the bioassay experiments, dust addition increased Chl *a* concentrations at the three lakes by 1.32 to 3.26-fold, but the magnitude of

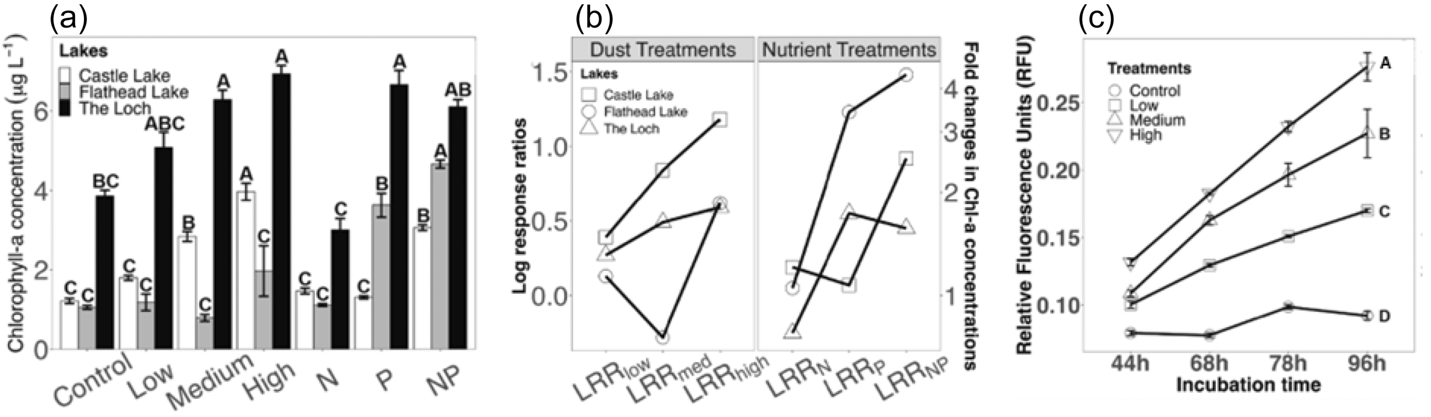

Fig. 2. (**a**) Chlorophyll *a* concentrations at the end of bioassay in controls, dust, and nutrient treatments in three mountain lakes. Significant differences between treatments for each lake are indicated by different letters. (**b**) Log response ratios (LRRs, effect sizes, left y-axis) and fold changes (right y-axis) for Chl *a* concentration in dust and nutrient treatments over the control in three lakes. (**c**) Relative fluorescence unit variations during the incubation at Castle Lake. Statistical differences in slopes between treatments are indicated by different letters.

response differed by lake (Fig. 2a; Table 2). Low dust treatments increased Chl *a* concentrations at Castle Lake and The Loch by 1.48-fold and 1.32-fold, respectively, but had no clear relationship at Flathead Lake (Fig. 2a,b). Medium and high dust treatments stimulated Chl *a* by 2.33 and 3.26-fold (Castle Lake), 1.63 and 1.8-fold (The Loch), respectively (Fig. 2a,b). Log response ratios revealed that Castle Lake had the largest responses for all dust treatments with the highest LRR values, and The Loch had the lowest increase of Chl *a* from low to high dust treatments (Fig. 2b). The high dust treatment at Flathead Lake had substantially elevated LRR values relative to $\mathrm{LRR}_{\mathrm{low}}$ and $\mathrm{LRR}_{\mathrm{med}}$ (Fig. 2b).

During the bioassay at Castle Lake, we observed a consistent increase in relative fluorescence units (RFUs) during the incubation period for all dust treatments (Fig. 2c; ANOVA: df = 3, $F = 5.6$, $p = 0.01$). Over the course of 44–96 h, the RFU increased 1.69, 2.08, and 2.12-fold in the low, medium, and high dust treatments, respectively. Conversely, in the control group, RFU decreased at 68 and 96 h and peaked at 78 h. When compared to the control treatment, we observed a significant increase in RFU in the low, medium, and high dust treatments at various time intervals. Specifically, at 44 h, RFU increased by 1.27, 1.38, and 1.67-fold; at 68 h, by 1.67, 2.11, and 2.36-fold; at 78 h, by 1.53, 1.99, and 2.35-fold; and at 96 h, by 1.85, 2.47, and 3.01-fold, respectively (Fig. 2c).

Table 2. Two-way ANOVA summary of the effects of dust treatments and lakes on Chl *a* concentration.

Source	df	*F*	*p*
Treatment	3	22.5	< 0.001
Lake	2	160.8	< 0.001
Treatment × Lake	6	3.4	0.01
Residuals	24		

^{14}C primary production

Our ^{14}C experiment in Castle Lake revealed that PPR only increased with low dust addition and successively decreased in the medium and high dust treatments (ANOVA: df = 3, $F = 7.6$, $p < 0.01$). Specifically, the low dust treatment had the highest PPR (29 mg C m^{-3} h^{-1}), which was different from the PPR in the high dust treatment (18 mg C m^{-3} h^{-1}) and the control (22 mg C m^{-3} h^{-1}). Primary production rate in the medium dust treatment (26 mg C m^{-3} h^{-1}) was higher than PPR in the high dust treatment (Fig. 3a).

After 48 h, we observed an increase in the percentages of dark ^{14}C uptake to light ^{14}C uptake (%) from the control (3.4%), low (6.2%), medium (10.48%) to high (17.14%) dust treatments, which were directly correlated with dust addition levels ($r^2 = 0.99$, $p < 0.01$). After 96 h, the percentages of dark ^{14}C uptake to light ^{14}C uptake (%) increased from the control (2.2%), low (4.7%), medium (5.7%) to high (10.9%) dust treatments after 96 h (Fig. 3b; df = 3, $F = 46.3$, $p < 0.001$).

Phytoplankton community composition

The community composition, as indicated by the relative abundance of the main phytoplankton genera, differed significantly across the three lakes (two-way ANOVA: $F = 17.2$, $R^2 = 0.51$, $p < 0.001$, df = 2). The impacts of dust treatment on phytoplankton community composition depended on lake identity ($F = 3.95$, $R^2 = 0.64$, $p < 0.001$, df = 11), suggesting that compositional responses to dust were mediated by site-specific context, such as the taxonomic structure of the communities or their degree of nutrient limitation.

Cyanobacteria were the most abundant group in all lakes. In Castle Lake, chlorophyta and chrysophyta were also abundant; Flathead Lake was characterized by higher abundances of chrysophyta and diatoms; and The Loch contained higher abundances of chlorophytes and diatoms (Supporting Information Table S1). Euglenophyta and haptophyta were the

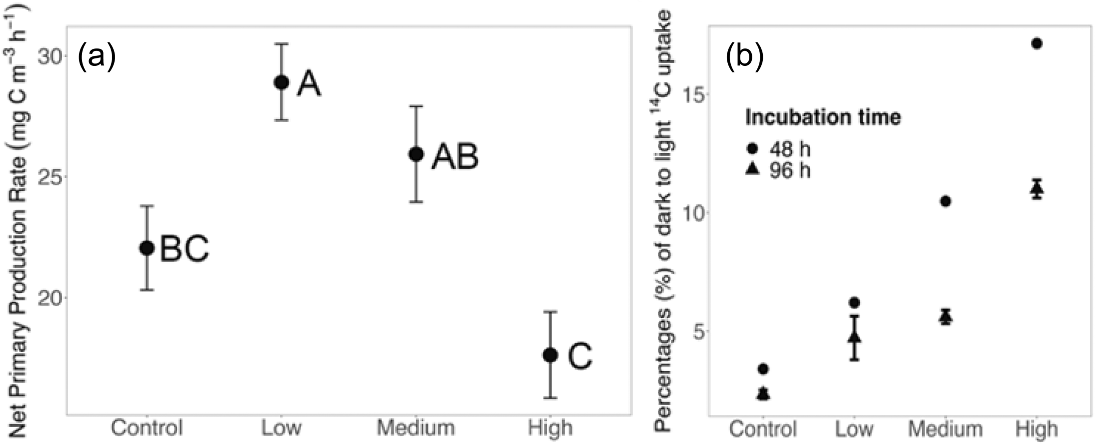

Fig. 3. (**a**) Net primary production rates (PPRs) (mean ± SE) at the end of bioassay experiment at Castle Lake. Statistical differences in PPR between treatments are indicated by letters. (**b**) The percentage of dark ^{14}C uptake to light ^{14}C uptake in ^{14}C experiment.

only groups consistently greater in number in the dust treatments compared to the control (Supporting Information Tables S1, S2). At the genus level, *Chlamydomonas* sp. and *Chrysochromulina* sp. showed statistically significant responses to dust treatments within specific lakes (Supporting Information Tables S3, S4). Although False Discovery Rate correction reduced the number of statistically significant responses, patterns in mean relative abundance suggest potential shifts in the abundance of specific taxa in response to dust treatments, particularly within individual lakes (Fig. 4). For example, in Flathead Lake, all treatments were distinct from the control; in Castle Lake, the low dust treatment was most distinct, and in The Loch most dust treatments were distinct with minor overlap with the control. Stress values were below 0.1 for individual lakes and for 0.107 for the combined lake analyses, indicating a good representation of the communities. Finally, we examined the abundance of mixotrophs relative to photoautotrophs, and although there were directional trends, none of the treatments were statistically different.

Bacterioplankton community composition

Lake bacterioplankton were unique in each lake and were affected in a consistent manner by all three dust treatments in all lakes. The communities present in the three lakes most notably separated along nonmetric multidimensional scaling axis 1 and axis 2 (Fig. 5). PERMANOVA results supported these interpretations, as communities were distinct among the three lakes and influenced by the dust treatments ($F = 6.1$, $R^2 = 0.07$, $p < 0.001$, df = 6).

Differences among the lakes and the dust addition treatments promoted taxonomic shifts in bacterial abundance in 16 genera across 11 phyla. Among the lakes, taxa within the Verrucomicrobiota, specifically *Luteolibacter*, *Prosthecobacter*, and several uncultured genera, constituted upwards of 10% of the relative abundance of the community and contributed to taxonomic shifts (Fig. 5b,c). Additionally, lake differences included a relatively reduced level of Actinobacteriota (genera *Sporichthyaceae*, *Curtobacterium*, and *Cellulomonas*) in Flathead Lake (2.8% ± 0.9) relative to the two other lakes, an elevated level of Bacillocota (genera *Bacillus* and *Exiguobacterium*) in Castle Lake (4.9% ± 2.0), and a complete lack of Bdellovibrionota and Armatimonadota in The Loch despite the presence of these two phyla in both Castle and Flathead lakes (Fig. 5b,c). The impact of the dust treatments was most pronounced due to the increased presence of the Bacillocota and Deinococcota in all dust treatments across all lakes while Bacillocota had very low relative abundance and Deinococcota was not present at all in the control treatment, nor nutrient treatment (Fig. 5b,c). Further, the abundance of several genera differed due to dust treatment, including increases in *Stenotrophomonas* (Pseudomonadota) and decreases in *Rhodococcus* (Actinobacteriota), *Geobacillus* (Bacillocota), and *Acidibacter* (Pseudomonadota). These changes were apparent across all samples treated with any amount of dust (i.e., treatment groups low, medium, and high). Additionally, the impact of dust additions on the microbes at Flathead Lake differed from that of nutrient additions alone. Specifically, instead of stimulating the occurrence of new and more diverse species, nutrient additions alone led to an increase in the abundance of residence species as compared to the control group (Fig. 5b,c).

Discussion

The objective of this study was to investigate the impact of dust on mountain freshwater ecosystems using Chl *a*, primary production, and phytoplankton and bacterial community composition as indicator metrics. Castle Lake, Flathead Lake, and The Loch provided a wide range of initial lake conditions to explore both general and site-dependent relationships between dust deposition and lake responses. Dust additions increased Chl *a* concentration in all three lakes but to different extents, while in Castle Lake, only low dust inputs enhanced ^{14}C primary productivity. The addition of dust also

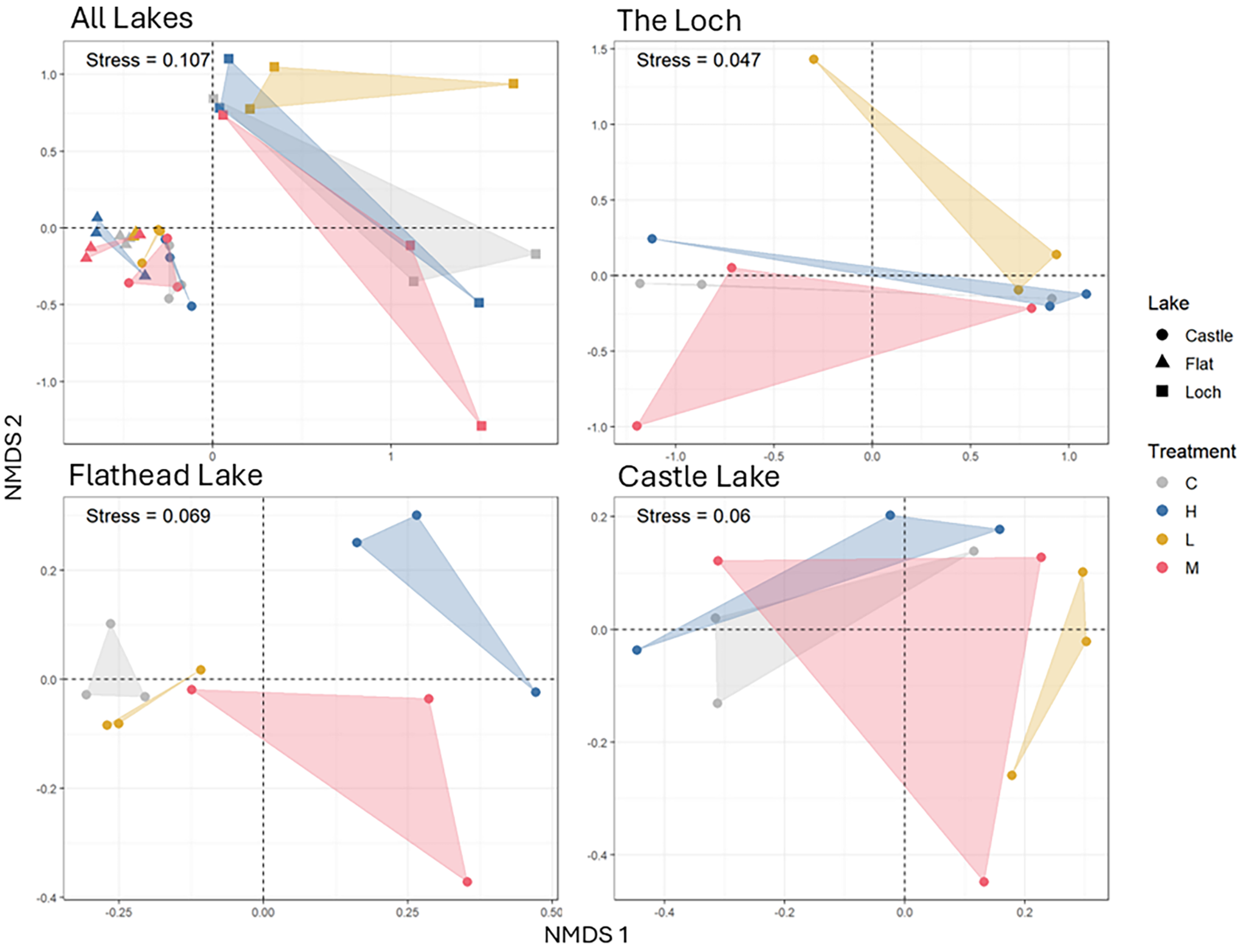

Fig. 4. Results of a nonmetric multidimensional scaling (NMDS) ordination (stress = 0.05) performed on a Bray–Curtis dissimilarity matrix of total phytoplankton community composition across three lakes.

altered microbial communities and phytoplankton community composition. Thus, bioavailable nutrients and viable microbiota available within dust can affect planktonic ecosystems (microorganism biomass, composition, production) in remote mountain lakes, but these impacts appear to vary in magnitude depending on the state of the ecosystem at the time that dust is added to the lakes.

Dust deposition effects are moderated by initial lake conditions

Our results suggest that pre-existing nutrient deficiencies in the lakes influenced the effect of dust on the community response. Because dust additions include both labile N and P as well as other macro- and micronutrients, dust has the potential to produce a larger effect than nutrient additions alone. We observed this effect at the N & P co-limited Castle Lake, where Chl *a* concentrations in dust treatments were higher than in both the +P and +N & +P treatments (Fig. 2a; Table 2). In fact, the response ratios for Castle Lake were the highest among the lakes for the dust treatments but the lowest for nutrient addition alone. This result is consistent with previous research highlighting multi-element nutrient limitation in Castle Lake, in particular work showing a role for molybdenum (Mo) (Axler et al. 1980; Glass et al. 2012). Glass et al. 2012 measured a maximum concentration of 0.38 μg L^{-1} in Castle Lake; if 100% of the Mo contained in dust is bioavailable, dust would increase Mo availability in Castle Lake by 50% (+ 0.2 μg L^{-1}). Maximum potential contributions of trace nutrients and toxins from dust are provided in Supporting Information Table S5. The importance of dust-derived N was also evident in medium and high dust treatments after 96 h in that N concentrations were lower than in

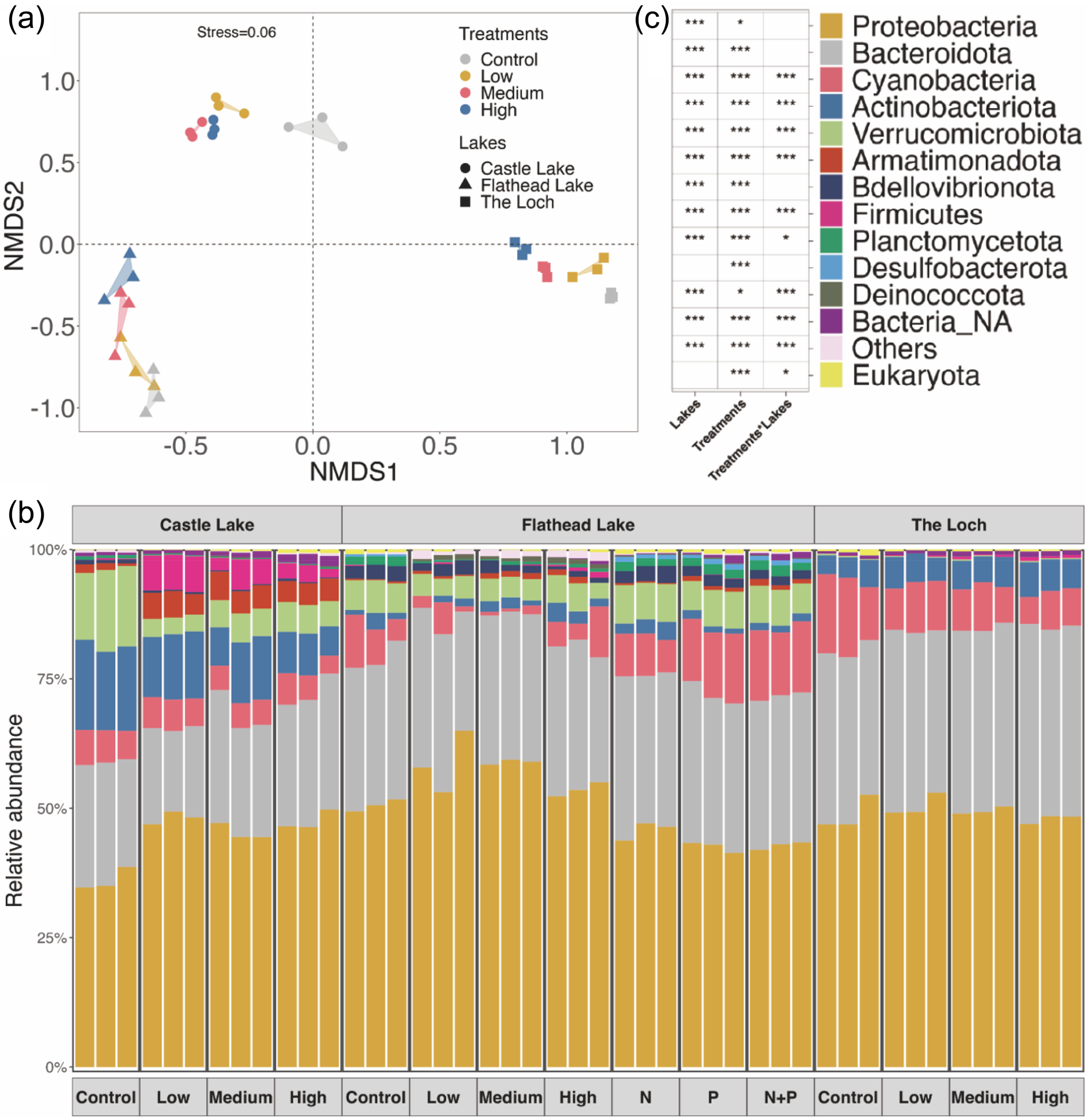

Fig. 5. (**a**) Nonmetric multidimensional scaling (NMDS) ordination (stress = 0.06) performed on a Bray–Curtis dissimilarity matrix of total bacterioplankton community composition across three lakes. (**b**) Taxa bar plot showing the effects of dust addition on bacterioplankton communities. (**c**) Statistical comparisons of the effects of dust addition on the abundance of specific bacterioplankton taxa as indicated by Bonferroni corrected *p*-values (*$p < 0.0036$; ***$p < 0.0001$).

the control and low dust treatments, indicating uptake by autotrophs. In contrast, in the strictly P-limited Loch, N concentrations remained higher in dust treatments as compared to the control (Supporting Information Table S6). Evaluating which micronutrients in dust may stimulate algal productivity in lakes would be an interesting follow-up study, shedding additional light on these results.

The finding that Chl *a* increased while PPR decreased in Castle Lake experiments was unexpected. We investigated several possible explanations. First, because changes in total productivity are often enhanced by large-sized phytoplankton (Malone 1980), we hypothesized that the low dust treatment stimulated larger algae while the high dust treatment favored smaller-sized cells. We tested this hypothesis by examining the size distribution of the plankton in each treatment (Supporting Information Fig. S3). However, we found no evidence supporting this explanation at Castle Lake (Supporting Information Fig. S3). Second, we hypothesized that dust may release toxic materials such as As, Pb, Sb, Cr, Cu, and Cd (Brahney et al. 2014) and could thus suppress algal growth and production (Paytan et al. 2009). To examine this hypothesis, we estimated the potential for metal toxicity assuming 100% of the dust metal content in the high dust treatment was soluble. However, concentrations of all toxic metals (As:

1.68 μg L^{-1}; Pb: 2.9 μg L^{-1}; Sb: 0.18 μg L^{-1}; Cr: 2.7 μg L^{-1}; Cu: 6.5 μg L^{-1}; Cd: 0.02 μg L^{-1}) were below the acute (short-term) criterion for metal toxicity for algae according to the US Environmental Protection Agency (EPA). Dust metal toxicity may be more likely when dust is anthropogenic in origin, as such dust often includes high metal concentrations from industry and transportation (Marín et al. 2017).

A third possible explanation for the observed Chl *a* increase with a simultaneous reduction in PPR is that dust inputs may have stimulated chemoautotrophic bacterial production, resulting in enhanced dark ^{14}C uptake (carbon dioxide fixation that occurs in the dark). However, while the metagenomic data show the presence of chemoautotrophs in all treatments, we did not find enrichments of chemoautotrophs related to nitrogen, sulfur, or iron oxidation in dust treatments compared to the controls. Finally, a fourth possibility regarding the discrepancy of Chl *a* and PPR was that under nutrient-limited conditions, phytoplankton might allocate energy (ATP) from photosynthesis to assimilate nutrients in the short term rather than using that ATP to fix carbon (Fig. 1). This result, including enhanced dark uptake and respiration, has been observed experimentally upon alleviation of nitrogen limitation in assays using chlorophytes (*Selenastrum minutum*, *Chlorella pyrenoldosa*, *Scenedesmus quadricauda*) (Pickett 1975; Healey 1979; Elrifi and Turpin 1986) and the diatom (*Skeletonema costatum*) as well as field studies of phytoplankton communities (Morris et al. 1971; Falkowski and Stone 1975; Rahav et al. 2018). Falkowski and Stone 1975 further note a concurrent increase in the chlorophyll content per cell during suppression of carbon fixation under the presence of light. At Castle Lake, we observed a near doubling of the Chl *a* concentration per cell biovolume with decreasing PPR (Supporting Information Table S8). This transient response is due to the use of ATP, derived from photosystem I, to assimilate nitrogen (Falkowski and Stone 1975) while reducing energy allocation to C fixation (Healey 1979; Beardall et al. 2001). Additionally, nutrient-limited phytoplankton are generally rich in carbohydrates and lipids and therefore do not “need” to increase C capture. Presumably, the most direct inference under this hypothesis is that short-term nutrient spikes would suppress C fixation for nitrogen-limited phytoplankton.

In general, the elevated DOC contributions from dust could lead to a competitive advantage for heterotrophic bacteria over phytoplankton (Fig. 1a) (Bigelow et al. 2020). In a similar marine bioassay experiment, Marañón et al. (2010) found that Saharan dust additions stimulated bacterial production while suppressing primary production. As the experimental time frames were short, as typical for nutrient assays in lakes (Elser et al. 2007), it is unlikely that elevated photosynthetic-derived DOC in comparison to dust-derived DOC would influence our experimental results. However, to evaluate this potential artifact, we measured the fluorescence index (McKnight et al. 2001). We did not find elevated concentrations of photosynthetic carbon in the Castle Lake dust treatments (Supporting Information Table S7).

Spatial and temporal observational studies that represent longer-term dust-algal relationships have suggested strong positive associations between elevated dust inputs and primary production. For example, a 10-year observational study found that Saharan dust inputs stimulated primary production but not bacterial production in mountain lakes in the Sierra Nevada of Spain (González-Olalla et al. 2018). Other observational studies have shown dust loads are correlated with both primary and secondary production in freshwater and marine systems (Cabrerizo et al. 2016; Morales-Baquero et al. 2006; Pulido-Villena, Reche, and Morales-Baquero 2008; Pulido-Villena, Wagener, and Guieu 2008; Reche et al. 2009; Tsugeki et al. 2012; Brahney et al. 2014; Brahney, Ballantyne, et al. 2015; Yoon et al. 2017; Gazeau et al. 2021). The inconsistency with our results from Castle Lake could reflect differences in observation time frames. While dust may stimulate bacterial activities and suppress production in N-limited systems at the outset, increasing nutrient availability from dust over the long term may lead to greater algal production.

Dust stimulates resident microbes and introduces new taxa

In situ observations have suggested that dust deposition may modify bacterioplankton and phytoplankton communities (Hervàs et al. 2009). Here, we provide experimental evidence supporting this hypothesis, showing that the abundance of the main microbial taxa differed in dust treatments relative to the controls (Fig. 5). The occurrence of new species or disappearance of previously present species in dust treatments contributed substantially to the separation between treatments and indicates that dust additions indeed shift community composition in ways that were different from the responses to nutrient addition alone. Specifically, the presence of new phyla (e.g., Deinococcota) and shifts in abundance of phyla such as Bacillota and Actinobacteriota indicate an influence of dust deposition on the lake microbiome. The Deinococcota genera observed were almost certainly seeded from dust as it is an extremophile that typically lives in organic-rich soil, not water, and this organism can withstand high levels of ionization energy/light intensity from solar radiation by repairing DNA following UV damage (Seck et al. 2022). Though Bacillota and Actinobacteriota are found in both aquatic and terrestrial systems, the abundance shifts and additional genera from these phyla suggest potential airborne seeding from the dust or stimulation of resident communities (Barberán et al. 2014; Barka et al. 2016), although further experimental studies are required to confirm seeding of these taxonomic groups. The increase in Bacillota is concordant with research emphasizing the resilience of this phylum, which would be required to survive wind erosion and subsequent transport processes including solar radiation prior to deposition (Filippidou et al. 2016; Makarova et al. 2001).

The impacts of dust at a larger scale

While our study has provided valuable insights, it is essential to acknowledge certain limitations that may influence the interpretation of our results. The number of study sites is restricted due to limited supplies of dust materials, reducing the generalizability of our findings. However, it is worth noting that this study marks an early effort in conducting in situ experiments in lakes, leveraging the collection of deposited dust over broad areas for a long period. Thus, this study not only demonstrates that dust deposition can impact freshwater ecosystems but also paves the way for future studies, including additional experimental evidence on micronutrient limitation alleviated by dust, the role of different dust compositions on lake responses, the seeding of lake microbiota from exogenous locations, and the specific lacustrine conditions that may modulate nutrient release from dust (e.g., pH, temperature, water composition, etc.).

The diverse responses observed in lakes following dust additions in our study likely reflect that the magnitude and nature of dust impact on lake ecosystems are contingent upon the spatial and temporal heterogeneity of freshwater conditions. For example, other observational studies have highlighted that dust can stimulate primary production and phytoplankton growth or alter community composition by modifying N:P ratios in freshwater ecosystems of the western United States (Brahney et al. 2014), southern Europe (Catalan and Camarero 2014; González-Olalla et al. 2018), and globally (Mladenov et al. 2011; Brahney, Mahowald, et al. 2015). However, the strength of dust impact may be inconsistent due to differences in the status of receiving waters, such as the nature of lake nutrient limitation (Gazeau et al. 2021), the trophic status of the lake (Marañón et al. 2010), the amount and composition of dust (Gonzalez-Olalla and Brahney 2025), and catchment properties. Indeed, a recent study incorporating controlled experiments and mechanistic models has demonstrated that geospatial location, which has major impacts on the natural conditions of lakes, plays a crucial role in determining the strength of dust effects on lakes (González-Olalla et al. 2024).

Conclusion

Our experiments support previous observational studies and controlled laboratory experiments to show that dust inputs can influence community composition and production in mountain lake ecosystems. However, in natural lake ecosystems, the manifestation of these effects appears to rely on the attendant nutrient limitation. Our data suggest that,

1. Nutrients derived from dust stimulate algal production when nitrogen is not limiting.
2. The alleviation of nitrogen-limitation from dust additions shifts the allocation of energy toward nutrient acquisition at the expense of carbon fixation.
3. Dust influences the microbial community composition through the addition of resources (nutrients, DOC) but also through the transport of viable taxa.

Our experimental field study offers a snapshot of immediate responses, capturing rapid changes in the ecological dynamics of plankton following dust exposure. While responses to long-term dust nutrient additions may differ, our findings provide a more nuanced and mechanistic understanding of how dust effects influence the ecology of mountain lakes.

Author Contributions

Janice Brahney conceived of the research, conducted the research, analyzed the data, and wrote manuscript drafts. Jiahao Wen conducted research, analyzed data, and wrote manuscript drafts. Sarah C. P. Chan and Zachary T. Aanderud generated and analyzed microbial data, and wrote and reviewed the manuscript. Jill S. Baron, Sudeep Chandra, and James J. Elser assisted with experimental design and conduction, the analysis of data, and writing and reviewing the manuscript. DeTiare L. Leifi and Erin Suenaga field assistance, data generation, writing, and reviewing of manuscript. Bonnie G. Waring conceptualization of research, writing, and reviewing of manuscript.

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Conflicts of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

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