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RESEARCH ARTICLE

Moisture and temperature controls on nitrification differ among ammonia oxidizer communities from three alpine soil habitats

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Abstract Climate change is altering the timing and magnitude of biogeochemical fluxes in many high-elevation ecosystems. The consequent changes in alpine nitrification rates have the potential to influence ecosystem scale responses. In order to better understand how changing temperature and moisture conditions may influence ammonia oxidizers and nitrification activity, we conducted laboratory incubations on soils collected in a Colorado watershed from three alpine habitats (glacial outwash, talus, and meadow). We found that bacteria, not archaea, dominated all ammonia oxidizer communities. Nitrification increased with moisture in all soils and under all temperature treatments. However, temperature was not correlated with nitrification rates in all soils. Site-specific temperature trends suggest the development of generalist ammonia oxidzer communities in soils with greater *in situ* temperature fluctuations and specialists in soils with more steady temperature regimes. Rapidly increasing temperatures and changing soil moisture conditions could explain recent observations of increased nitrate production in some alpine soils.

Keywords ammonia-oxidizing archaea (AOA), ammonia-oxidizing bacteria (AOB), global change, Loch Vale watershed, nitrification, thermal adaptation

1 Introduction

In alpine ecosystems, low primary productivity limits nitrogen (N) uptake and poorly developed soils have a limited capacity to retain N (Baron et al., 2000; Seastedt et al., 2004; Elser et al., 2009). As a result, mobile forms of N, such as nitrate (NO_3^-), are highly susceptible to leaching. Thus, the rate at which NO_3^- is formed through nitrification is a critical control on N losses from these ecosystems. Isotopic signatures of lake and stream water NO_3^- from alpine systems indicate that $>50\%$ of NO_3^- is nitrified prior to being flushed from seasonal snow, soil, and mountain features such as talus and scree (Campbell et al., 2002; Sickman et al., 2003).

Two major controls of nitrification rates are temperature and moisture; both of which are being altered in alpine ecosystems by climate change (Firestone and Davidson, 1989; Parton et al., 1996). Climate warming is likely to increase nitrification rates directly due to increased metabolic activity of nitrifiers. It is also likely to indirectly elevate nitrification as a result of changes in high-elevation hydrological cycling. Since the year 2000, increasingly high annual and seasonal temperatures in mountains of the western US and Europe have resulted in an increased proportion of precipitation falling as rain instead of snow as well as glacier ablation and the earlier onset of spring snow melt. These changes may be altering the timing of nitrification and NO_3^- loading to streams and lakes (Cannone et al., 2008; Clow, 2010; Fountain et al., 2012). In the Colorado Rocky Mountains, long-term studies have already correlated increasing summer temperatures and stream flow with increased NO_3^- concentrations in lakes and streams (Baron et al., 2009). The influence of climate change on nitrification is likely compounded by the co-occurrence of another form of global change: atmospheric N deposition. Inorganic N enrichment via deposition has been increasing in high altitude regions of the western US since the mid-twentieth century (Baron et al., 2000; Elser et al., 2009).

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Prior to 2005, the oxidation of ammonium (NH_4^+) to nitrite, which is widely considered to be the rate-limiting step in nitrification, was thought to be carried out in soil exclusively by ammonia-oxidizing bacteria (AOB) (Firestone and Davidson, 1989). However, ammonia-oxidizing archaea (AOA) with substantially different physiological properties have been discovered in diverse habitats (Francis et al., 2005; Leininger et al., 2006; Erguder et al., 2009). Ammonia-oxidizing archaea appear to be more tolerant of acute environmental conditions than AOB, including low substrate availability, low pH, and extreme temperatures (Valentine, 2007; Gubry-rangin et al., 2011; Yao et al., 2011; Hatzenpichler, 2012). Alpine ecosystems exhibit a high degree of spatial variability in microclimate conditions. These include areas of low humidity, high solar radiation, and the shading and exposure caused by topographic complexity, which may favor nitrifier communities with variable ammonia oxidation kinetics. Thus, nitrification dynamics in extreme environments like the alpine need to be revisited, along with the relative importance of these two groups of ammonia oxidizers.

We explored whether variations in temperature and soil moisture stimulated or depressed AOA and AOB abundance and NO_3^- production using soils from a high-elevation watershed in Colorado. Laboratory incubations were used to explore the effects of temperature and moisture on ammonia oxidizer abundance and net and gross rates of nitrification, as well as net N mineralization, microbial biomass, and soil respiration. We hypothesized that ammonia oxidizer communities would be dominated by AOA, not AOB. Additionally we predicted that, in all soils, net nitrification rates would increase with temperature and moisture availability.

2 Methods and materials

2.1 Site description

The Loch Vale Watershed is a northeast-facing alpine/subalpine catchment in Rocky Mountain National Park (40°17′17″; 105°39′43″) (Fig. 1). It has been the location of continuous ecological research and monitoring since the early 1980s. The catchment spans 660 ha and ranges in elevation from 3,110 m to 4,009 m above sea level. The climate is high-mountain continental with an average of 105 cm of precipitation falling each year (1984 – 2012), about 20 cm of which fall during the summer months (June, July, and August). Mean annual temperature (1984 – 2012) is 1.4°C and summer temperatures average 11.6°C (http://www.nrel.colostate.edu/projects/lvws/data.html). Bedrock material is biotite gneiss and schist (Baron, 1992).

Wet atmospheric deposition has been measured in the Loch Vale watershed since 1984 as part of the National Atmospheric Deposition Program/National Trends Network (http://nadp.sws.uiuc.edu/sites/siteinfo.asp?id = CO98). Precipitation has a mean pH of 5.2. Wet inorganic N deposition averages 2.9 kg $N \cdot ha^{-1} \cdot yr^{-1}$, roughly half of which is currently deposited as NH_4^+ -N. Wet N deposition comprises about three fourths of total (wet plus dry) N deposition (Baron et al., 2011). From 1984 to 1997, the five-year rolling mean wet inorganic N deposition increased from 2.4 kg $N \cdot ha^{-1} \cdot yr^{-1}$ to 3.7 kg $N \cdot ha^{-1} \cdot yr^{-1}$. Wet N deposition has remained relatively stable since then, with a five-year rolling mean of 2.9 kg $N \cdot ha^{-1} \cdot yr^{-1}$ from 1999 – 2012 (Morris et al., 2012).

2.2 Soil sampling and characterization

In August 2010 we sampled three different soils characteristic of alpine environments: newly exposed outwash sediment located at the base of Andrew's Glacier, soil from a poorly vegetated talus field, and soil from a densely vegetated wet sedge meadow (Fig. 1). These soils are referenced as "outwash," "talus", and "meadow" throughout the manuscript.

Using sterilized trowels, we collected approximately 5 kg of soil at each site. We sampled outwash and talus to depths of 7 cm, however a layer of dense gravel impeded us from sampling meadow soils below a depth of 3.5 cm. We transported the samples on ice in polyethylene bags to the EcoCore Analytical Services facility at Colorado State University. Upon arrival, samples were sieved to 4 mm and manually homogenized. We then removed 5 g subsamples for moisture measurements and stored the remaining soil at − 80°C for subsequent work, including microbial analyses.

Thermochron iButton™ temperature sensors buried to ~5 cm recorded soil temperature in talus and meadow soils every 30 minutes from July 14, 2010 to August 10, 2010. They were not implanted in outwash because outwash soil was inaccessible at the time of installation. We used these 21-day temperature records along with % water-holding capacity (WHC) of each soil at the time of collection to select temperature and moisture treatments for our experimental incubation.

We calculated WHC as the volume of water retained by 5 g subsamples after being saturated and allowed to drain overnight through filter funnels in a sealed cooler. Field % WHC was calculated as water content divided by WHC, expressed as a percentage.

In each soil, we evaluated pH (VWR Model 8000 pH meter) and C:N (LECO Tru-SPEC elemental analyzer, St. Joseph, MO) and applied the Bouyoucos Hydrometer method to determine soil texture (Gee and Bauder, 1986). We measured NH_4^+ -N and NO_3^- -N on an Alpkem Flow Solution IV Automated wet chemistry system (O.I. Analytical, College Station, TX). Using a chloroform slurry technique (Fierer et al., 2003), we extracted dissolved organic carbon (DOC) and dissolved organic nitrogen (DON), as well as soil microbial biomass carbon and nitrogen concentrations (MBC and MBN, respec-

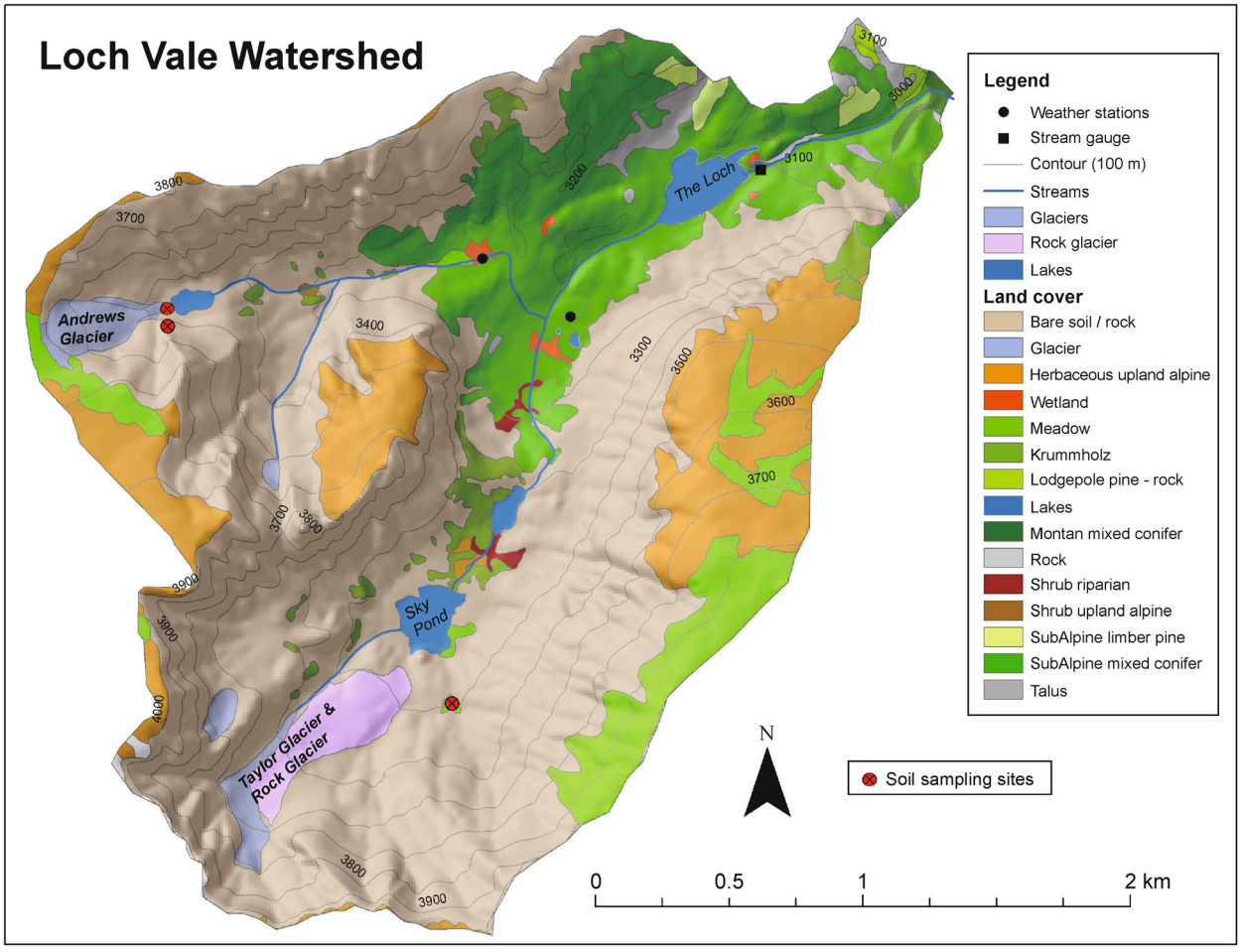

Fig. 1 Annotated map of the Loch Vale watershed, Rocky Mountain National Park, CO, USA. Soil sampling sites are indicated with red circles.

tively). A continuous flow autoanalyzer (Shimadzu, Columbia, TN) was used to analyze our extracts. Flushed MBC and MBN were calculated as the difference between control and chloroform-treated sample carbon (C) and N concentrations.

2.3 Laboratory incubations

To evaluate the effects of temperature and moisture on net nitrification, net N mineralization, and ammonia oxidizer abundance, we carried out a 45-day laboratory incubation. The incubation was preceded by a seven-day pre-incubation under temperature and moisture conditions identical to the incubation itself. In triplicate, we subjected the soils to three temperature and two moisture treatments using a full factorial design. Temperature treatments included 4°C, 12°C and 25°C. We selected these temperatures to span the range that we measured in talus and meadow during the 21 days prior to sample collection (5°C to 26°C in talus and 1°C to 8°C in meadow) (Fig. 2). We presumed an outwash temperature of ~1°C because the soil was frozen underwater until < 21 days prior to sample collection. This presumption was supported by temperature data collected the following year (EK Hall, personal communication, 2012). We selected substrate-specific moisture treatments based on each soil's % WHC in the field. These included 50% and 100% for outwash, 25% and 50% for talus and 25% and 75% for meadow. In order to create the desired moisture conditions, we air-died subsamples of each soil to 20% WHC and re-wetted them. We then transferred the wetted samples into sealed 0.24 L acid-washed Mason jars equipped with septa for taking respiration measurements.

During the seven-day pre-incubation and 45-day incubation soil CO_2 concentrations were measured daily with a LI-COR infrared gas analyzer (IRGA) (LI-COR Biosciences, Lincoln, NE). When CO_2 levels approached 3%, we flushed the jars with compressed tank breaking air for 15 minutes (Airgas, Radford, VA). We calculated rates of MBC-specific respiration by dividing total respiration rates by the initial concentrations of MBC quantified in each sample.

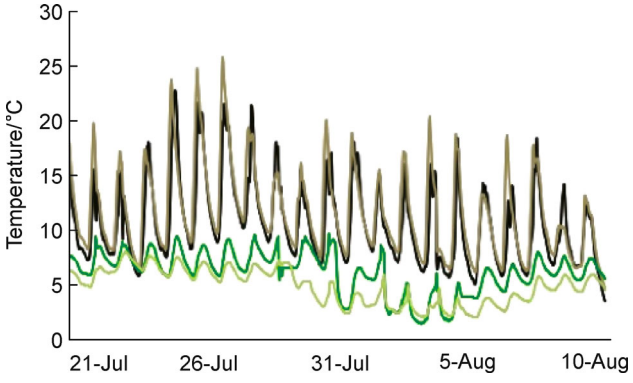

Fig. 2 Soil temperature data for talus (brown lines) and meadow (green lines). Temperatures were recorded at 30-minute intervals by two iButton temperature sensors buried at 5 cm. Temperatures were not collected in outwash soils, which were frozen at the time of sensor installation.

2.4 Net nitrification and net nitrogen mineralization

Net N mineralization rates were calculated by subtracting KCl-extractable NO_3^- -N and NH_4^+ -N present in untreated, homogenized samples from the NO_3^- -N and NH_4^+ -N measured in the treated soils at the completion of the 45-day incubation. We calculated net nitrification as the difference in NO_3^- -N between incubated and initial subsamples.

2.5 DNA extraction and quantification

We determined changes in the abundance of ammonia oxidizers by comparing the quantity of bacterial and archaeal genes encoding ammonia monooxygenase subunit A (amoA) at the start of the incubation (immediately following the seven-day pre-incubation) and at the end of 45 days. At both time points, we isolated total genomic DNA from 0.25 g subsamples of each experimental triplicate using a Powersoil DNA Isolation Kit, following the manufacturer's protocol (MoBio Laboratories, Carlsbad, CA). We quantified these extracts on a multifunction Tecan Infinite M200 plate reader using a Quant-IT dsDNA High-Sensitivity Assay Kit according to the instructions provided (Invitrogen, Carlsbad, CA). This yielded results expressed as ng DNA μL^{-1} extract. We then stored these DNA extracts at -20°C for approximately one month prior to analysis.

2.6 Quantitative PCR assays

We quantified the abundance of bacterial and archaeal amoA genes in our DNA extracts using quantitative real-time PCR (qPCR) performed on a MyIQ Single-Color Real-Time PCR Detection System (Bio-Rad, Redmond, WA). To confirm reproducibility of the method, we loaded reactions into clear 96-well plates in triplicate. All plates contained unknowns, seven-point standard curves, and non-template controls. Our standard was generated from cloned amoA gene fragments (Delgado-Baquerizo et al., 2013). Reaction volumes were 25 µL and included 12.5 µL of ABsolute SYBR Green QPCR mix (Thermo Scientific), 0.25 µL of bovine serum albumin, and 0.3 or 0.5 µM of each primer for archaeal and bacterial amoA, respectively. Standard curves were comprised of serially diluted ($10^1 - 10^7$ copies μL^{-1}) cloned amplicons (30 ng μL^{-1} stock solution) for each gene of interest.

We quantified bacterial amoA using 10 ng of extracted DNA as template and 1.25 µL of the forward and reverse primers amoA-1F (5'-GGGGTTTCTACTGGTGGT-3') and amoA-2R (5'-CCCCTCKGSAAAGCCTTCTTC-3') (Rotthauwe et al., 1997). Archaeal amoA were quantified using 10 ng of DNA extract and 0.75 µL of the primer set Arch-amoAF – Arch-amoAR (5'-STAATGGTCTGGCTTAGACG-3' and 5'-GCGGCCATCCATCTGTATGT-3') (Francis et al., 2005). Cycling conditions for both bacterial and archaeal amoA quantification reactions were 15 min at 95°C, 35 cycles of 94°C for 30 s, 30 s at 55°C, and 30 s at 72°C. We concluded all qPCR runs with a melting curve to assess whether primer dimmer had occurred. Amplification efficiencies ranged from 93% – 99.8% and R^2 values were > 0.9.

2.7 Gross nitrate transformation rates

To determine gross nitrification we performed a 24-hour incubation. Triplicate subsamples were incubated under temperature and moisture treatments identical to the 45-day incubation described above. Also, like the 45-day incubation, we began the experiment with a seven-day pre-incubation and monitored respiration daily using a LI-COR infrared gas analyzer (IRGA) (LI-COR Biosciences, Lincoln, NE).

We quantified gross nitrification and gross NO_3^- -N consumption rates in talus and outwash using a ^{15}N pool dilution technique (Kirkham and Bartholomew, 1954). Gross N transformation rates were not evaluated in meadow soils because we lacked sufficient sample. Immediately following the seven-day pre-incubation, we quantified background NO_3^- -N concentrations for each soil in the manner described above and used these concentrations to calculate the percent and quantity of ^{15}N label required. We adjusted these percentages for outwash further by using microbial biomass data from the 45-day incubation. Our adjustments were based on the prediction that, under the observed conditions of increasing microbial biomass and low initial NO_3^- concentrations, rapid NO_3^- turnover was likely to occur in these samples. Outwash NO_3^- -N concentrations were raised by 130% in samples at 4°C and 100% WHC and 80% in samples at 4°C and 50% WHC, while all other outwash and talus samples were raised by 30%.

Soils were then transferred from Mason jars into doubled gas-permeable polyethylene bags. We added five

atom % $K^{15}NO_3$ dissolved to 100 ppm and 150 ppm dropwise to each bag and manually homogenized the soil and solution until the desired levels of ^{15}N label were reached. This procedure increased soil water content between 0.26% and 0.96%. Within ten minutes of ^{15}N addition, we extracted half of each subsample in 2 M KCl at a ratio of 1:2 and assessed extraction efficiency. We incubated the remaining soil for an additional 24 hours before the final extraction.

We supplemented both sets of KCl extracts with 0.037 atom % KNO_3^- and 2M KCl solution as needed to bring all extractable N levels to between 30 and 80 μg of NO_3^- -N and 53 mL. We then diffused the extracts onto acidified quartz filter disks and analyzed the disks for $^{15}NO_3^-$ -N (Stark and Hart, 1996) using a VG Isochrom continuous flow IRMS (Isoprime Inc., Manchester, UK) connected to a Carlo Erba NA 1500 elemental analyzer at the EcoCore Analytical Service facility at Colorado State University. Using the equations from Kirkham and Bartholomew (1954), we calculated gross NO_3^- transformation rates. Data were removed for any samples containing < 0.45 atom % ^{15}N from the gross nitrification and NO_3^- consumption data sets because such low atom percentages indicate methodological error. Negative gross production and consumption values were replaced with zeros.

2.8 Statistical analysis

We analyzed the effects of temperature and moisture on rates of MBC-specific respiration, as well as changes in ammonia oxidizer abundance and net and gross nitrification with multiple regressions. We treated temperature and moisture as categorical variables. To achieve normality, we power transformed all residuals using the Box-Cox method. One-way ANOVAs were used to assess variability within and among soils for initial AOB abundance, net nitrification, and gross nitrification and NO_3^- immobilization. Differences between soils and treatment conditions were determined using Tukey's HSD post-hoc analysis (Fig. 3). Significance was accepted at a level of probability (P) of < 0.05 for all analyses. All statistical work was performed using SAS JMP 9.0 (SAS Institute Inc., Cary, North Carolina).

3 Results

3.1 Soil parameters

During the month prior to sample collection, temperatures within talus were higher and more variable than meadow soil. Within talus, they ranged from 4.9°C to 25.8°C with a mean of 11.8°C and within meadow soils, they fluctuated from 1.4°C to 8°C and had a mean of 5.5°C (Fig. 2). Outwash soils were frozen at the time of iButton installation and, therefore, not instrumented. However, because they were underwater and located at the terminus of Andrew's glacier, we assumed that temperatures fluctuated little from 1°C (Fig. 1). Outwash soils were submerged and saturated at the time of collection, while talus and meadow were 88% and 85% of WHC respectively.

Clay content was lowest in outwash (12%) and higher in talus (20%) and meadow (25%). The pH of all three soils was slightly acidic (5.0–5.8) (Table 1). Dissolved organic C and N as well as MBC, MBN, and NH_4^+ and NO_3^- values are reported here with standard errors and on a soil dry weight basis. At the time of collection mean organic C and N concentrations were lowest in outwash (0.36±0.08 mg DOC·kg^{-1}; 0.26±0.07 mg DON·kg^{-1}), intermediate in talus (1.3±0.28 mg DOC·kg^{-1}; 0.35±0.07 mg DON ·kg^{-1}), and highest in meadow soils (17±2.6 mg DOC ·kg^{-1}; 3.2±0.59 mg DON·kg^{-1}) (Table 1). In outwash, soil % C was below detection limits. The C:N of talus was 8.6 (±0.01) and that of meadow was 13 (±0.05) (Table 1). Mean DIN (dissolved inorganic nitrogen) concentrations (the sum of NH_4^+ and NO_3^-) in outwash and talus were 18 mg·kg^{-1} and 16 mg·kg^{-1}, respectively. The highest DIN concentration, 24 mg·kg^{-1}, was measured in meadow soil.

Microbial biomass carbon concentrations ranged from 0.05 (±0.0) mg·kg^{-1} in outwash to 8.7 (±2.1) mg·kg^{-1} in meadow (Table 1). During the 45-day incubation, MBC increased in all outwash samples (Table 2). In talus, MBC increased in samples wetted to 50% but not 25% of WHC (Table 2). Meadow soils incubated at 75% WHC and 4°C experienced the greatest MBC growth of all soil types and treatments (140±44 μg·kg^{-1}·d^{-1}). All other meadow samples lost MBC (Table 2).

3.2 Respiration

Microbial biomass carbon-specific respiration rates were highest in outwash (3.2 – 120 mg·kg^{-1}·d^{-1}), followed by talus (0.12 – 15 mg·kg^{-1}·d^{-1}) and finally meadow soil (0.03 – 3.4 mg·kg^{-1}·d^{-1}) (Table 2). Respiration increased significantly with both temperature and moisture. Together these controls explained ~99% of the variability.

3.3 Ammonia oxidizer abundance

All ammonia oxidizer communities were dominated by AOB. At the start of the long-term incubation, AOB copy numbers exceeded AOA by 2 – 4 orders of magnitude in all treated soil samples. By the end of 45 days, AOA abundance dropped to near or below detection limit. Concentrations of AOB varied significantly by site. Abundances increased from talus to outwash to meadow.

Temperature and moisture conditions predicted 63% of

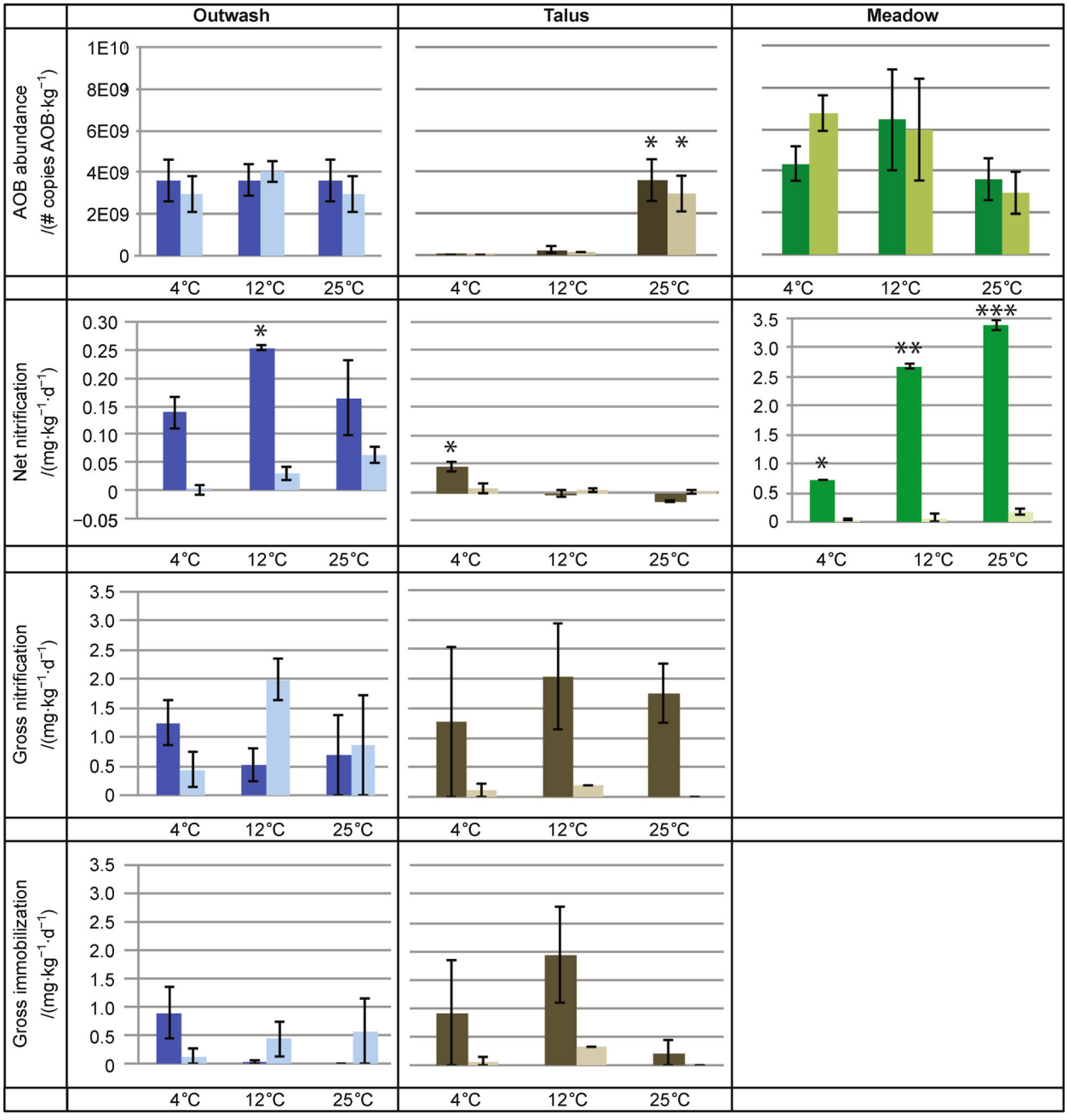

Fig. 3 Concentrations of ammonia-oxidizing bacteria (AOB) as well as rates of net nitrification, gross nitrification, and gross NO_3^- consumption measured during laboratory incubations. Outwash data are represented in blue, talus in brown, and meadow in green. Darker bars indicate higher moisture treatments. Asterisks indicate significant differences within soils at $P < 0.05$.

outwash AOB dynamics during the 45-day incubation as well as 66% in talus and 59% in meadow (Table 3). The highest temperature treatment (25°C) was negatively correlated with AOB abundance in all soils.

3.4 Net nitrification and nitrogen mineralization

Net nitrification was positive in all soils under all treatments with the exception of talus with 50% WHC (high moisture treatment) incubated at 12°C and 25°C (warmer temperature treatments) (Fig. 3). Mean rates (± standard errors) were significantly elevated in meadow (1.18 ± 0.33 mg·kg^{-1}·d^{-1}) compared to outwash (0.11 ± 0.02 mg·kg^{-1}·d^{-1}) and talus (0.01 ± 0.0 mg·kg^{-1}·d^{-1}).

Net NO_3^- production in outwash increased with

Table 1 Physical and chemical parameters of Loch Vale soils

	Outwash	Talus	Meadow
%Clay	12	20	25
pH	5.8	5	5.2
%C	[a]BDL	3.4 (0.02)	14 (0.04)
%N	3.4 (0.00)	0.39 (0.00)	1.07 (0.01)
C:N	BDL	8.6 (0.01)	13 (0.05)
DOC/(mg·kg^{-1})	0.36 (0.08)	1.3 (0.28)	17 (2.6)
DON/(mg·kg^{-1})	0.26 (0.07)	0.35 (0.07)	3.2 (0.59)
MBC/(mg·kg^{-1})	0.05 (0.00)	0.42 (0.09)	8.7 (2.1)
MBN/(mg·kg^{-1})	BDL	0.07 (0.00)	0.56 (0.18)
NO_3^- -N/(mg·kg^{-1})	0.87 (0.17)	2.0 (0.15)	1.7 (0.61)
NH_4^+ -N/(mg·kg^{-1})	17 (0.90)	14 (0.57)	22 (0.67)

Average values (and standard errors) are from the time of collection. Values are expressed on a soil dry weight basis. [a]BDL is below detection limits.

moisture, explaining 73% of the variability observed (Table 2). Talus rates of NO_3^- production decreased at the highest temperature treatment (25°C), however net nitrification in meadow soils increased with both temperature and moisture to explain 91% of variability (Table 2). Ammonium availability at the time of collection was not correlated with net nitrification in any of the soils.

We measured net N immobilization rather than mineralization in outwash and talus (Table 2). In outwash, N was immobilized at a mean rate of 0.1 (±0.02) mg·kg^{-1}·d^{-1}, while talus immobilization rates ranged from 0.08 to 0.22 mg·kg^{-1}·d^{-1}. Meadow soils however had positive N mineralization rates with a mean of 0.13 (±0.03) mg ·kg^{-1}·d^{-1} (Table 2).

3.5 Gross nitrification and nitrate consumption

Temperature and moisture treatment conditions were not significant controls of gross nitrification or NO_3^- consumption, nor was soil site.

4 Discussion

Climate warming in alpine regions is likely to alter nitrification rates, an important feature of high-elevation N cycling. Our investigation suggests that bacterial, not archaeal, ammonia oxidizers are dominant in Loch Vale soils and that soil nutrient status may be an important controller of their relative abundance. The results of our incubations indicate a strong positive relationship between moisture and NO_3^- production. Temperature had variable

Table 2 Average rates of change in microbial biomass carbon, microbial biomass carbon-specific respiration, and net N mineralization in Loch Vale soils at different temperature and percent water holding capacity treatments

% WHC	Temp.	Outwash		Talus		Meadow	
		50%	100%	25%	50%	25%	75%
MBC/(μg·kg^{-1}·d^{-1})	4°C	3.6 (0.7)	2.4 (0.26)	−3.9 (0.68)	0.4 (0.77)	−42 (4.4)	140 (44)
	12°C	3.0 (0.15)	2.4 (0.54)	−3.0 (0.25)	1.8 (1.5)	−69 (8.6)	−19 (15)
	25°C	2.5 (0.4)	3.0 (1.1)	−3.7 (1.8)	3.5 (0.91)	−74 (3.7)	−7.9 (0.62)
[a]Resp/MBC/(mg·kg^{-1}·d^{-1})	4°C	3.2 (2)	23 (1.7)	0.12 (0.02)	2.2 (0.14)	0.03 (0.01)	0.45 (0.02)
	12°C	25 (3.1)	78 (3.3)	0.27 (0.02)	5.8 (0.3)	0.19 (0.06)	2 (0.04)
	25°C	58 (1.7)	120 (4.4)	1.2 (0.4)	15 (0.6)	1.1 (0.25)	3.4 (0.06)
Net N mineralization/(mg·kg^{-1}·d^{-1})	4°C	−0.06 (0.01)	−0.09 (0.02)	−0.08 (0.00)	−0.14 (0.01)	0.00 (0.00)	0.14 (0.08)
	12°C	−0.14 (0.02)	−0.02 (0.01)	−0.12 (0.01)	−0.22 (0.00)	0.14 (0.06)	0.25 (0.06)
	25°C	−0.15 (0.01)	−0.11 (0.07)	−0.08 (0.00)	−0.22 (0.01)	0.25 (0.06)	0.00 (0.07)

Average rates of change (and standard errors) are reported from a 45-day laboratory incubation. Data are expressed on a soil dry weight basis. [a] Resp/MBC is microbial biomass carbon-specific respiration.

effects (and in some cases no effect) on nitrification rates among the soil types, suggesting a complex relationship between *in situ* temperature conditions and ammonia oxidizer community composition and efficiency.

Contrary to our hypothesis, bacteria, not archaea, dominated alpine ammonia oxidizer communities. Ammonia-oxidizing archaea have been found to be ubiquitous and dominant in a wide range of both aquatic and terrestrial ecosystems (Leininger et al., 2006; Prosser and Nicol, 2008) and seem to be more successful than AOB under extreme environmental conditions (Valentine, 2007; Yao et al., 2011; Hatzenpichler, 2012) including arctic and alpine soils (Alves et al., 2013; Tai et al., 2014). It is possible that the primers we selected did not amplify some AOA genes in our soils, contributing to low detection. However, AOB are thought to outcompete AOA under conditions of high N-availability (Martens-Habbena et al., 2009; Di et al., 2010; Delgado-Baquerizo er al., 2013). It is possible that N deposition in extreme environments with limited plant biomass and relatively low soil organic matter could supply sufficient N fertilization to support AOB dominance. Loch Vale is known to receive atmospheric N deposition (Morris et al., 2012). In a comparison of soil parameters from Loch Vale with other arctic and alpine sites (Table 4), we found that MBC concentrations in Loch Vale were among the lowest observed, in some cases by multiple orders of magnitude. In contrast, DIN availability was an average of twelve times higher in Loch Vale than the comparison sites. These high N and low C conditions may favor AOB over AOA. We are not the first to report AOB dominance in alpine or arctic soils receiving N deposition (Boyd et al., 2011; Brankatschk et al., 2011).

Moisture significantly increased nitrification rates, as hypothesized, in all but two talus samples (Fig. 3). This positive relationship is frequently observed because, although nitrification is an aerobic pathway, soil moisture supports substrate diffusion and microbial metabolism (Linn and Doran, 1984). It is important to note that the relationship between volumetric water content and water potential likely differs among the three soil habitats, but we did not quantify those relationships in this study. While our data suggest similar relative responses to increasing moisture among habitats, direct comparison among habitats at similar volumetric contents are not meaningful. Soil water availability in alpine systems is often limited in the summer because annual precipitation is dominated by snow, and water availability decreases after spring snow melt (Rango and van Katwijk, 1990; Kattelmann and Elder, 1991). Climate change is both expected and has already been observed to exacerbate summer water stress by elevating summer air temperatures, increasing evapotranspiration, and advancing peak snowmelt (IPCC, 2014). In glaciated systems, it may also affect the timing and intensity of glacier melt (Hannah et al., 2007; Fountain et al., 2012). Our results suggest that, in a future warmer climate, summer-time nitrification may become increasingly limited by soil moisture availability.

The effect of temperature on nitrification was not linear, nor was it consistent among soil sites. However, our data suggest that Loch Vale ammonia oxidizer communities are adapted to the unique temperature regimes under which they established. For example, talus experiences relatively large diurnal temperature fluctuations (Fig. 2). Highly variable microclimate conditions are thought to support the development of temperature generalists and/or increased microbial diversity (Wallenstein and Hall, 2012). Of the three soil sites, talus was the least sensitive to experimental temperature treatments: the influence of temperature on net nitrification was unclear and it was not significantly correlated with gross nitrification. Stable temperature regimes, such as those in outwash and meadow (Fig. 2), are thought to select for specialist communities that operate most efficiently within narrow temperature ranges (Waldrop and Firestone, 2006; Wallenstein and Hall, 2012). This is consistent with our findings. Outwash and meadow experience relatively small temperature fluctuations (Fig. 2) and nitrification rates in both were responsive to experimental temperature treatments. In outwash, net nitrification was significantly elevated at the intermediate temperature (12°C) (Fig. 3). In meadow, net nitrification was significantly elevated at the highest temperature treatment (25°C) and showed a strong positive correlation with temperature (Table 3). The different temperatures at which maximum nitrification was observed in outwash and meadow may reflect *in situ* conditions: outwash temperatures (assumed ~1°C) were cooler than meadow (1.4°C to

Table 3 Standardized regression coefficients of multiple regression analyses for net nitrification rates and changes in the abundance of ammonia-oxidizing bacteria

	Net nitrification/($mg \cdot kg^{-1} \cdot d^{-1}$)			AOB abundance/(# copies $\cdot kg^{-1} \cdot d^{-1}$)		
	Outwash	Talus	Meadow	Outwash	Talus	Meadow
Temperature	–	[a]T[25°C]: −0.66	T[25°C]: 0.30	T[25°C]: −0.83*	T[25°C]: −0.68*	T[25°C]: −0.88*
Moisture	[b]M[dry]: −0.77*	–	M[dry]: −0.90*	–	M[dry]: 0.50	–
Model R^2	0.73	0.47	0.91	0.63	0.66	0.59

Multiple regression results were significant at $P < 0.05$ and highly significant (*) at $P < 0.001$. [a]Temperature (T) and [b]moisture (M) treatments were analyzed as categorical variables, which are specified in brackets.

Table 4 Comparison of soil and microbial parameters in Loch Vale soils and other alpine and arctic study sites

	System	Location	Month, year	NO_3-N /(mg·kg^{-1})	NH_4^+-N /(mg·kg^{-1})	DIN /(mg·kg^{-1})	MBC /(mg·kg^{-1})	MBN /(mg·kg^{-1})	References
Outwash	Alpine, primary succession	Colorado (40°17′N, 105°39′W)	July, 2010	0.54–1.5	14–19	15–20	0.05–0.05	BDL	Present study
	Alpine, primary succession	Switzerland (46°28′N, 8°28′E)	July, 2008	0.13–0.23	0.03–0.18	0.16–0.41	58–120	6–19	Brankatschk et al., 2011
	Alpine, high-elevation	Chile (24°43′S, 68°32′W)	Feb., 2009	[a]–	–	–	31–58	1.2–2.2	Lynch et al., 2012
	Antarctic Dry Valley	Antarctica (77°37′S, 163°15″E)	Jan., 2002	4.9	0.09	–	26	4.4	Ball et al., 2009
Talus	Alpine, talus	Colorado (40°17′N, 105°39′W)	July, 2010	1.8–2.3	12–15	14–17	0.34–0.51	0.07–0.07	Present study
	Alpine, talus	Colorado (40°03′N, 105°35′W)	July, 1997–1998	–	–	–	0.028–39	–	Ley et al., 2001
	Alpine, talus	Colorado (40°03′N, 105°35′W)	July, 1995	1–1.7	1.5–5.9	2.5 – 6.9	–	3.1 – 12	Williams et al., 1997
	Alpine, talus	Colorado (40°03′N, 105°35′W)	July, 1996	0.42–0.63	1.5–5.9	2–6.6	–	–	Bieber et al., 1998
	Alpine, dry meadow	Colorado (40°03′N, 105°35′W)	June – Oct., 1992	–	~ 8–15	–	–	~ 100–127	Fisk & Schmidt, 1996
	Alpine, dry meadow	California (multiple sites)	Oct., 2003	~ 0.4–0.83	–	~ 0.56–6.8	~ 942–1500	~ 43–65	Miller et al., 2007
	Alpine, lichen heath	Russia (43°27′N, 41°41′E)	Aug., 1999–2001	0.6–1.6	7–19	8.6–20	–	~ 50–70	Makarov et al., 2003
Meadow	Alpine, wet meadow	Colorado (40°17′N, 105°39′W)	July, 2010	0.7–3.2	20–23	20–25	6.6–11	0.38–0.74	Present study
	Alpine, developed soils	Switzerland (46°28′N, 8°28′E)	July, 2008	0.81–1.3	6.7–13	7.5–14	240–900	29–120	Brankatschk et al., 2011
	Low arctic Tundra	Canada (64°52′N, 111°35′W)	June, 2007	BDL–1.2	0.15–13	0.15–14	7,400–12,000	770–960	Chu & Grogan, 2009
	High arctic	Canada (multiple sites)	July, 2006	0.89–4.5	0.74–5.3	1.6–9.8	–	–	Banerjee et al., 2011

[a]The symbol – denotes unavailable data.

8°C). In both habitats NO_3^- production increased with temperatures to optima above ambient conditions. Regardless of the variability in optimum nitrification temperatures among soils, AOB abundance decreased with temperature in all three soils. This suggests variability in ammonia oxidizer community efficiency with temperature. Summer warming in the alpine is likely to increase NO_3^- production overall, but the magnitude of this response may not be generalizable among ammonia oxidizer communities across variable and changing microclimates in the landscape.

Although some consistent responses to experimental treatments were observed, NO_3^- production rates were variable among Loch Vale soils. We cannot draw strong

conclusions based on soil type due to the lack of replicates from individual sites. However, the net nitrification rates we measured in Loch Vale soils were comparable to other alpine regions and followed a broadly similar pattern: lower rates occurred in dry and unvegetated soils, like outwash and talus, and higher rates were observed in more developed soils, like meadow (Table 5). We observed increases in DOC, DON, MBC, MBN, C:N, and clay content from outwash to talus to meadow. However, nitrification was not lowest in outwash. Outwash nitrification not only exceeded talus but also reached rates comparable to those measured in dry meadow samples, despite having concentrations of DOC and MBC over ten times lower than meadow. Outwash also exhibited strong growth responses during the experimental incubation, including the greatest increase in MBC and the highest rates of MBC-specific respiration and net N immobilization. This suggests that *in situ* limitations on microbial growth and activity were relieved in outwash soil under experimental conditions (Ohtonen et al., 1999; Lipson et al., 2009). It is possible that the relatively high nitrification rates in outwash are an artifact of low sample size. However, if this pattern is an indictor of how recently exposed soils (like outwash) may respond to changing climate conditions, it has implications for NO_3^- production in alpine systems experiencing glacier ablation.

This study suggests that increased soil moisture will elevate nitrification rates in a broad range of alpine soils. Increased ambient temperatures will likely elevate nitrification in some soils but have no effect in others, depending on local temperature averages and fluctuations. By comparing Loch Vale soil chemistry with other arctic and alpine sites, we found that high N and low C conditions might favor the dominance of AOB over AOA. It is possible that the relatively high NH_4^+ availability observed in Loch Vale soils also contributed to the surprising lack of a relationship between soil NH_4^+ concentrations and net nitrification by obviating substrate limitation. Our data support the hypothesis that climate warming will increase the biological production of NO_3^- in alpine soils, but suggest that the primary mechanism is the indirect effect of temperature on hydrology and soil moisture. They also suggest that the co-occurrence of climate warming and the direct input of inorganic N into these otherwise nutrient-

Table 5 Comparison of net nitrification and nitrogen mineralization rates in Loch Vale soils and other alpine and arctic study sites

	System	Location	Month, year	Net nitrification /(mg·kg^{-1}·d^{-1})	Net N mineralization /(mg·kg^{-1}·d^{-1})	References
Outwash	Alpine, primary succession	Colorado (40°17′N, 105°39′W)	July, 2010	0.00 – 0.25	– 0.15 – – 0.02	Present study
Talus	Alpine, talus	Colorado (40°17′N, 105°39′W)	July, 2010	– 0.01 – 0.18	– 0.22 – – 0.08	Present study
	Alpine, talus	Colorado (40°03′N, 105°35′W)	July, 1996	0.22 – 1	0.39 – 2.5	Bieber et al., 1998
	Alpine, dry meadow	Colorado (40°03′N, 105°35′W)	June – Oct., 1992	~ 0 – 0.19	~ – 0.02 – 0.23	Fisk & Schmidt, 1996
	Alpine, lichen heath	Russia (43°27′N, 41°41′E)	Aug., 1999 – 2001	0.01 – 0.02	0.1 – 0.14	Makarov et al., 2003
	Alpine, dry meadow	California (multiple sites)	Oct., 2003	[a]BDL	~ 0 – 0.1	Miller et al., 2007
Meadow	Alpine, wet meadow	Colorado (40°17′N, 105°39′W)	July, 2010	0.04 – 3.38	0.00 – 0.25	Present study
	Alpine, dry meadow	California (multiple sites)	Oct., 2003	– 0.13 – 0.18	– 0.12 – 0.18	Miller et al., 2007
	Alpine, humus	Australia (37°S, 146°E)	Dec. – Mar., 2003	~ 0.28 – 0.62	~ 0.9 – 1.7	Huber et al., 2011
	Alpine, grazed rangeland	China (32°53′N, 103°40′E)	Aug., 2006	0.13 – 0.23	0.22 – 0.34	Sun et al., 2009

[a]BDL is below detection limit.

poor soils via atmospheric N deposition is likely to have important effects on alpine nitrification.

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