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The role of physical properties in controlling soil nitrogen cycling across a tundra-forest ecotone of the Colorado Rocky Mountains, U.S.A

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ABSTRACT

There is growing recognition that physical characteristics of landscapes influence nitrogen (N) cycling. The relationships among climate forcing, soil properties, and the fate of N are particularly important in alpine ecosystems vulnerable to climate warming and characterized by shallow, rocky soils. This study evaluated differences in net N mineralization and nitrification rates determined using in-field incubation experiments across patches defined by six plant community types within an alpine catchment of the Colorado Rocky Mountains. We considered not only differences in net N transformation rates across space and time within a growing season, but also whether or not soil properties (i.e., physical and chemical) and conditions (i.e., temperature and moisture) could explain patch-scale variation in rates. Highest net N mineralization and nitrification rates occurred in the dry meadow (3.7 ± 0.5 and 3.4 ± 0.5 μg N cm^{-2} d^{-1}, respectively), while the lowest were in the subalpine forest (−0.3 ± 0.4 and 0.0 ± 0.1 μg N cm^{-2} d^{-1}), which exhibited net N immobilization. The magnitude of differences in net N transformation rates through time differed among patches and was strongly controlled by soil C:N ratios. Dry and moist meadow communities showed the greatest range in net N transformation rates across the growing season and changes were positively correlated with soil moisture. In contrast, inhibition of nitrification at high soil moisture occurred in wet meadow areas. Our data suggest that as the alpine growing season lengthens in a drier, warmer future, changes in soil moisture will likely be a primary factor driving patterns of net N transformation rates.

1. Introduction

The physical properties of terrestrial ecosystems, including topography, soil properties, and hydroclimatic forcing, exert a strong control on the fate and transport of nitrogen (N), a limiting nutrient to primary productivity in many ecosystems (Lovett and Goodale, 2011). In high elevation systems, the role of physical properties is amplified; thin, rocky soils and sparse vegetation lead to rapid movement of atmospherically-derived N from terrestrial to aquatic ecosystems during snowmelt (Brooks et al., 1999; Darrouzet-Nardi et al., 2012; Hood et al., 2003). While many previous studies provide coarse resolution, or a catchment-scale picture of the fate of N in alpine ecosystems, physical properties actually vary over shorter length scales (e.g., meters; Seastedt et al., 2004). This includes variation in soil conditions—temperature and water availability—which are first-order controls on microbially-mediated soil N transformations. Similarly, plant species distributions and rates of primary production, also governed by physical properties, are highly heterogeneous. Thus, parts of an alpine catchment may contribute disproportionately to catchment-scale export of water and N, requiring investigation across scales of interest.

In particular, spatial variation in snow distribution across alpine catchments creates “patch” scale differences in soil temperature and moisture during the growing season (Brauchli et al., 2017; Musselman et al. 2008). This variation maps to differences in plant communities (Bliss, 1963; Niu et al., 2019; Odland and Munkejord, 2008) and suggests similar patch-scale differences may exert controls over soil N cycling processes (Chen et al., 2016; Darrouzet-Nardi and Bowman, 2011). Indeed, field observations and a conceptual model by Brooks et al. (1999) and Brooks and Williams (1999) demonstrate the importance of snowpack development and persistence for belowground heterotrophic N cycling during the winter months.

Abbreviations: DRM, dry meadow; MOM, moist meadow; WEM, wet meadow; SHR, shrub; KRU, krummholz; SUB, subalpine forest

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Patch-scale variability is important for understanding alpine response to climate change. Under a changing climate projected to be characterized by earlier snowmelt and longer growing seasons (e.g., Clow, 2010; Dong et al., 2019), the distribution, size, and persistence of patch-scale water availability will shift. Such changes in the soil environment will likely have direct consequences for the availability and transport of N. Specifically, changes in the rates and timing of net N mineralization and nitrification—both microbially-mediated transformations—will influence inorganic N pools that may be subject to biological uptake, abiotic retention, or gaseous and hydrologic losses. Determining the relationships among variation in physical properties, plant community composition, and soil N cycling is an important next step toward developing a predictive understanding of how hydrologic connectivity and the N budgets of alpine ecosystems will change.

The Colorado Rocky Mountains in the Western U.S.A. have been a focal area for research on N cycling in alpine ecosystems for over four decades (Baron et al., 2000; Williams et al., 1996b). Specific to soil N cycling, past efforts have examined the effects of elevated atmospheric N deposition on alpine meadow plant communities (Bowman et al., 2012, 2015, 2018; Bowman and Steltzer, 1998). Others have focused on examining predictive relationships between soil N cycling and factors such as soil temperature, moisture, C:N, plant species and litter traits (Fisk and Schmidt, 1995; Lu et al., 2012; Osborne et al., 2016). Largely, these efforts have been limited to meadow communities of the alpine tundra (see Fisk et al., 1998; Fisk and Schmidt, 1996; Williams et al., 1996a) and within krummholz (Liptzin and Seastedt, 2009). For example, Steltzer and Bowman (1998) focused on understanding drivers of net N transformation rates in moist meadow communities. Following the period of snowmelt, they found that soil moisture was a significant determinant of net N mineralization rates for the first two months, while it was a significant determinant of net nitrification only during the first month. These studies suggest that N cycling rates vary across plant community types as soil conditions change seasonally. In order to understand the role of physical drivers more broadly, it is critical now to evaluate such relationships across the range of plant community types that co-occur from the tundra downslope to subalpine forests.

In this study, we sought to determine how soil N transformations—specifically, net N mineralization and net nitrification—vary across six dominant plant communities, or patch types, within an alpine catchment of the Colorado Rocky Mountains. This research provides the first field test of recent modeling studies that focused on determining the abiotic factors limiting alpine primary productivity and identified a need for studies that examine N cycling rates and their dominant controls across plant communities (Fan et al., 2016; Wieder et al., 2017). We addressed this knowledge gap by evaluating explicitly the role of soil properties —including changes in soil C:N, soil pH, and bulk density—and conditions—including changes in soil moisture and temperature— in shaping spatial and temporal differences in net N transformations. We designed our study to answer the following questions: (1) Do soil N transformations differ spatially among the six representative plant communities and temporally as the growing season progresses? and (2) What is the relationship between key measures of an alpine ecosystem's physical properties and soil N transformations? With respect to the second question, we were particularly interested in determining whether or not abiotic characteristics of the alpine landscape could be used as predictors of net N mineralization and nitrification rates across plant communities. We hypothesized that plant communities with wetter soils throughout the growing season have higher rates of net N transformations (i.e., soil moisture is a primary control on N cycling in the alpine). We also expected that soil N transformations in different plant communities would show temporal variations that correlate with changes in soil moisture and temperature.

2. Material and methods

2.1. 1 Study area

We conducted this research at the Niwot Ridge Long-term Ecological Research (LTER) site (40°03N, 105°35W) in the Colorado Rocky Mountains, U.S. The climate is characterized by a long, cold winter and short growing season (approximately 90 days, roughly the months of June through August). The mean annual temperature is −3.8 °C, with a mean summer temperature of 5.5 °C and mean winter temperature of −12.7 °C. The annual precipitation is about 1000 mm, most of which falls as snow and is redistributed by wind (Litaor et al., 2008). Winter snowpack primarily determines soil moisture within the growing season and controls plant community composition (Steltzer and Bowman 1998; Walker et al. 1993). Across catchments oriented west-to-east, plant communities shift from dry meadow (DRM, where wind prevents snowbanks from forming and snowmelt occurs earliest) near the Continental Divide (3528 m) to subalpine forest (SUB, where a seasonal snowpack persists; 3425 m). We focused our research on a west-east-oriented headwater catchment within the Niwot LTER that is 0.26 km^2 and drains into the North Boulder Creek Watershed.

In addition to dry meadow and subalpine forest, the catchment is characterized by intervening patches of moist meadow (MOM); wet meadow (WEM), where snowpack either persists longest or snowmelt is consistently transported throughout the growing season; shrub (SHR), where woody plants line the riparian zone of the channel; and krummholz (KRU), located at treeline. These six plant community types are broadly representative of this alpine region (Litaor et al., 2008). For a description of the plant species found in each community, see Table 1. Soil types across the six plant communities include Moran family-Lithic Cryorthents-Rubble land complex where DRM and SHR occur, and Moran family-Lithic Cryorthents-Leighcan family complex in the MOM, WEM, KRU, and SUB areas (SSURGO, 2019).

We established 2 m × 2 m plots (four plots per plant community type, 24 plots total) within the study catchment. The locations of the plots were along study transects created for long-term monitoring of snow depth, soil moisture, and soil temperature within the catchment (Fig. 1). In each plot, we characterized soil properties, changes in soil water content and temperature during the measurement period and conducted repeated measurements of soil N transformations (net N mineralization and net nitrification), described in the following subsections. All data were collected between 1 July and 15 September 2017; this period spans the growing season in the alpine zone, from the onset of snowmelt through the beginning of snowfall.

2.2. Soil water content and temperature

We surveyed soil water content and temperature (0–5 cm depth) within our soil sampling plots weekly or biweekly from 3 July to 9 September in 2017. At each plot, we measured soil moisture (volumetric water content) 5 times using a SM150T soil moisture sensor (Delta-T Devices Limited) and soil temperature three times with a digital thermometer (Digi-thermo, Fisher Scientific), each within a 30 cm × 30 cm area. For each sampling time, we report the mean soil moisture and temperature values of replicate measurements within the plots. Soil moisture was then converted to gravimetric water content with soil bulk density. In order to calculate soil N transformations on a dry soil basis, we also measured gravimetric soil moisture of the soil cores collected for inorganic N analyses.

2.3. Soil sampling

Within our study plots, we collected soil cores for measurement of soil net N transformation rates, as well as soil properties and water content during the 2017 growing season. Soil net N mineralization and nitrification were measured three times during the 2017 growing

Table 1
Soil chemical and physical properties of the plant communities studied (Mean ± SE).

Community type	Soil Temp (°C)[1]	Soil Moisture (%)	SOC (%)[2]	TN (%)[2]	C:N	BD (g cm^{-3})[2]	pH	Dominant species
DRM	9.89 ± 0.87^{a}	20.58 ± 2.64^{c}	8.75 ± 0.16^{bc}	0.73 ± 0.02^{abc}	12.01 ± 0.48^{b}	0.76 ± 0.07^{a}	5.28 ± 0.15^{a}	*Kobresia myosuroides,* *Carex rupestris,* *Selaginella densa,* *Geum rossii*
MOM	7.83 ± 1.31^{ab}	52.45 ± 9.91^{b}	9.19 ± 0.69^{bc}	0.85 ± 0.15^{ab}	11.76 ± 1.91^{b}	0.63 ± 0.10^{ab}	5.20 ± 0.15^{a}	*Geum rossii,* *Deschampsia caespitosa,* *Trifolium parryi,* *Stellaria longipes*
WEM	5.81 ± 1.25^{ab}	95.23 ± 15.46^{a}	10.89 ± 0.85^{ab}	0.86 ± 0.10^{ab}	12.95 ± 0.82^{b}	0.48 ± 0.02^{bc}	5.23 ± 0.20^{a}	*Caltha leptosepala,* *Carex scopulorum,* *Pedicularis groenlandica,* *Rhodiola integrifolia,* *Rhodiola rhodantha*
SHR	4.72 ± 1.34^{b}	91.23 ± 4.77^{a}	12.35 ± 0.94^{a}	0.93 ± 0.14^{a}	13.96 ± 1.66^{ab}	0.31 ± 0.04^{c}	5.10 ± 0.07^{a}	*S. planifolia,* *S. glauca,* *Geum rossii,* *Deschampsia caespitosa,* *Trifolium parryi,* *Polygonum viviparum,* *Rhodiola integrifolia*
KRU	4.89 ± 1.75^{b}	32.43 ± 3.65^{bc}	7.42 ± 0.45^{c}	0.51 ± 0.03^{bc}	14.86 ± 1.49^{ab}	0.78 ± 0.12^{a}	5.10 ± 0.14^{a}	*Picea engelmannii,* *Abies lasiocarpa*
SUB	5.81 ± 1.31^{ab}	22.98 ± 2.72^{c}	7.58 ± 1.57^{c}	0.44 ± 0.12^{c}	18.09 ± 1.35^{a}	0.75 ± 0.07^{a}	4.66 ± 0.07^{b}	*Picea engelmannii,* *Abies lasiocarpa* (tree)

Note: Different superscript letters in same column indicate the values among plant communities are significantly different ($p < 0.05$).

[1] n = 4 for all measurements except soil temperature and soil moisture, for which n = 12.

[2] SOC, soil organic carbon; TN, total nitrogen; BD, bulk density.

season (19 June–13 July, 17 July–16 August, and 23 August–20 September 2017). We used the buried-bag technique (Eno, 1960) for each of these three incubations. Briefly, at each location, paired soil cores from 0 to 15 cm were collected with a 3.5 cm diameter metallic corer. The litter layer was removed from the soil surface before coring. One of the paired soil samples was used to determine initial concentrations of ammonium (NH_4^+) and nitrate (NO_3^-), as well as soil characteristics, including soil organic carbon (SOC), total N and pH. The other paired soil core was placed in a Ziploc bag, and reburied in the original hole. Field incubation lasted approximately one month

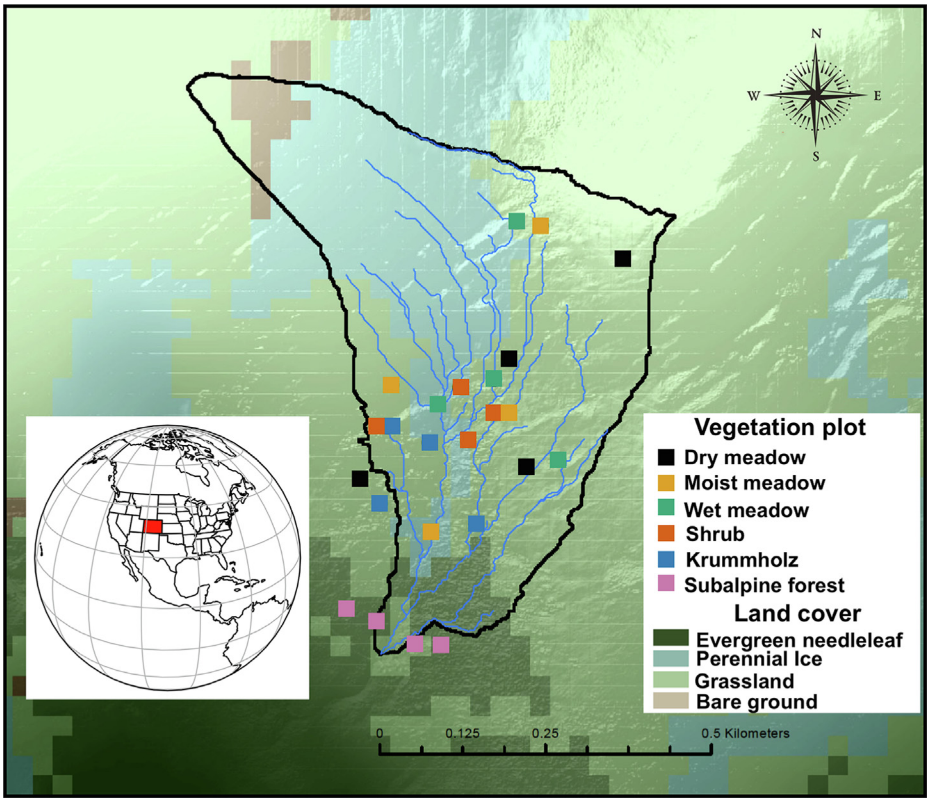

Fig. 1. Plot locations of this study within the Saddle Catchment at Niwot Ridge Long-term Ecological Research site. Land cover classes are also shown on the base map, which was created using a LiDAR 1 m DEM from Niwot Ridge LTER and land cover from the NLCD 2016 dataset (NLCD, 2016).

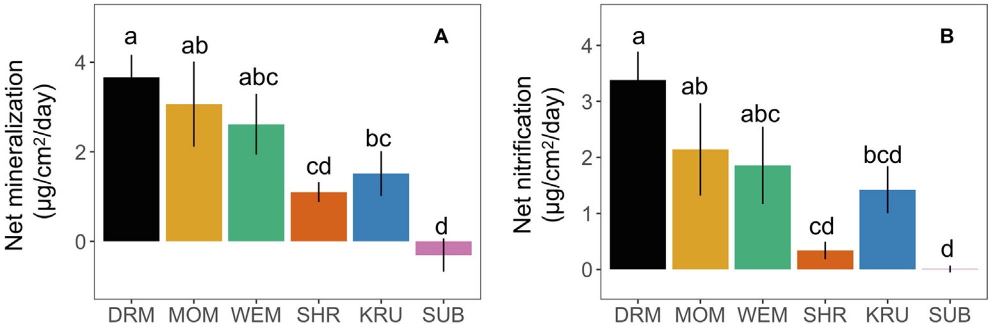

Fig. 2. Mean (± SE) net N transformations in different plant communities over the growing season (n = 12); (A) net N mineralization and (B) net nitrification. DRM, dry meadow; MOM, moist meadow; WEM, wet meadow; SHR, shrub; KRU, krummholz; SUB, subalpine forest. Lowercase letters indicate significant statistical difference among groups.

(24–30 days). Soil bulk density at 0–15 cm depth was determined following Marshall et al. (1996). Soil organic C, total N, pH and bulk density were measured once at all locations during the first soil sampling of the growing season.

2.4. Laboratory processing and analysis

Following field collection, soils were processed for measurements of soil properties and N transformation rates. We transported soil cores to the laboratory, manually removed roots and rocks, and then sieved soils through a 2-mm mesh. To determine soil water content (gravimetric, for determination of inorganic N content), a 5 g subsample of each soil core was oven-dried at 105 °C. Subsamples of each sieved soil sample were also dried at 60 °C for determination of TOC and total N using a Thermo Finnigan FLASH EA 1112 CHN Analyzer and air-dried for determination of pH in 1:5 soil-to-water ratio (analytical precision ± 0.01 for both analyses). Finally, we extracted soils for determination of NH_4^+ and NO_3^- concentrations. Approximately 10 g of sieved, field-moist soil were weighed into a 250 ml flask and mixed with 50 ml of 2 M potassium chloride solution, following Fisk and Schmidt (1995), and shaken continuously for two hours. The supernatants were filtered through Whatman #1 filter paper and frozen until analysis.

All analytical work was performed in the Arikaree Environmental Laboratory at the University of Colorado, Boulder. Ammonium was analyzed on a BioTek Synergy 2 with a detection limit of 0.009 mg N L^{-1} (analytical precision ± 0.001) and NO_3^- was measured on an OI Analytical FS-IV with a detection limit of 0.5603 µg N L^{-1} (analytical precision ± 0.0005). We calculated net N mineralization rate as the difference between final (incubated) and initial (immediately collected after soil coring) inorganic N (NH_4^+ plus NO_3^-) concentrations over time, and net nitrification rate was calculated as the difference between final and initial NO_3^- concentrations over time. We calculated areal estimates using bulk density values determined for each plot.

2.5. Statistical analysis

We used a linear mixed effects model, in which plot is a random effect and community type and time are fixed effects, to test the differences in soil N transformation rates among plant communities and sampling times. Linear and logarithmic regressions were performed to test the relationships between soil N transformation rates and soil physical and chemical properties (i.e., soil temperature, moisture, and C:N). Our data violated the assumptions of normality necessary to apply a parametric test, hence, we used the non-parametric Kruskal-Wallis test with Dunn's multiple comparison test to determine whether or not there was a statistical difference in soil physical and chemical properties among community types. All statistical analyses were done using R software (Version 3.4.3).

3. Results and discussion

We observed that net N transformation rates were not uniform in space or time across the six plant communities, which has important implications for considering how nitrogen cycles within an alpine catchment and how that pattern may shift under a future with longer growing seasons (i.e., warmer and drier conditions). Here, we explore our observations of the differences in net N transformations across the six plant communities present at a plot or patch scale and the role of soil properties and conditions (i.e., temperature, moisture) in determining that variation. We then consider how the arrangement of the plant communities, as well as the physical properties that underly them, may affect patterns of N retention and transport at the catchment scale.

3.1. Differences in net N transformations across plant communities

In our study, net N mineralization and nitrification rates averaged over the growing season were highest in alpine meadow communities (i.e., DRM, MOM, and WEM; Fig. 2). Of the meadow communities, we observed the highest mean rates of net N mineralization and nitrification in DRM (3.7 ± 0.5 and 3.4 ± 0.5 µg N cm^{-2} d^{-1}, respectively; mean ± SE; all values for 0–15 cm depth) and MOM (3.1 ± 1.0 and 2.1 ± 0.8 µg N cm^{-2} d^{-1}), followed by WEM (2.6 ± 0.7 and 1.9 ± 0.7 µg N cm^{-2} d^{-1}, see Fig. 2). These positive rates indicate that soils of the meadow communities produce inorganic N that is then available for plant uptake, gaseous losses, or export to the stream. Our results are comparable to those measured by Steltzer and Bowman (1998) and Fisk and Schmidt (1995, 1996), who also quantified soil net N transformation rates in a nearby area at Niwot Ridge LTER (Table 2).

In contrast to the meadow communities, we observed significantly lower average net N mineralization and nitrification rates in treeline (i.e., KRU and SUB) and near-stream communities characterized by woody species (i.e., SHR). In KRU, net N mineralization and net nitrification rates were 1.5 ± 0.5 and 1.4 ± 0.4 µg N cm^{-2} d^{-1}, respectively, followed by SHR (1.1 ± 0.2 and 0.3 ± 0.2 µg N cm^{-2} d^{-1}). The mean net N mineralization and nitrification rates in SUB were the lowest at −0.3 ± 0.4 and 0.0 ± 0.1 µg N cm^{-2} d^{-1} for net N mineralization and nitrification, respectively (Fig. 2), suggesting microbial immobilization of inorganic N in alpine forest soils during the growing season.

The patterns in net N transformations across plant communities were supported by soil C:N data and consistent with previous research demonstrating its influence on soil N cycling. We found that communities with woody vegetation (i.e. SHR, KRU, SUB) tended to have higher soil C:N ratios than meadows (i.e., DRM, MOM, and WEM); with highest mean C:N in SUB (18.1 ± 1.4, followed by KRU (14.9 ± 1.5), SHR (13.9 ± 1.7) and WEM (12.9 ± 0.8), and lowest in DRM (12.0 ± 0.5) and MOM (11.8 ± 1.9) (Table 1). Of the soil properties measured, soil C:N emerged as the only predictive variable of net N transformation rates across all plant communities (Table 1, Fig. 3; $p < 0.05$), aligned with findings from previous studies (see Darrouzet-Nardi and Bowman, 2011; Finzi et al., 1998; Vervaet et al., 2002; Zhu

Table 2
Comparison of net N transformations with previous studies at Niwot Ridge Long-term Ecological Research (LTER).

Location	Net N mineralization[1] (μg N cm^{-2} d^{-1})	Net N nitrification[1] (μg N cm^{-2} d^{-1})	Species	Reference
Moist meadow	0.78–9.22	1.56–6.33	*Acomastylis rossii*; *Deschampsia caespitosa*	Steltzer and Bowman (1998)
Talus field	2.06	0.87	*Kobresia myosuroides*; *Deschampsia caespitosa*; *Acomastylis rossii*; *Bistorta bistortoides*	Bieber et al. (1998)
Dry meadow	1.09	1.01	*Kobresia myosuroides*,	Fisk and Schmidt (1996)
Dry meadow	2.6 ± 0.81	2.2 ± 0.63	*Kobresia myosuroides*	Fisk and Schmidt (1995)
Moist meadow	4.01 ± 0.21	1.2 ± 0.3	*Acomastylis rossii*	Fisk and Schmidt (1995)
Wet meadow	5.21 ± 1.35	0.12 ± 0.06	*Carex scopulorum*	Fisk and Schmidt (1995)

[1] We report means from the literature, and when possible, ± SE.

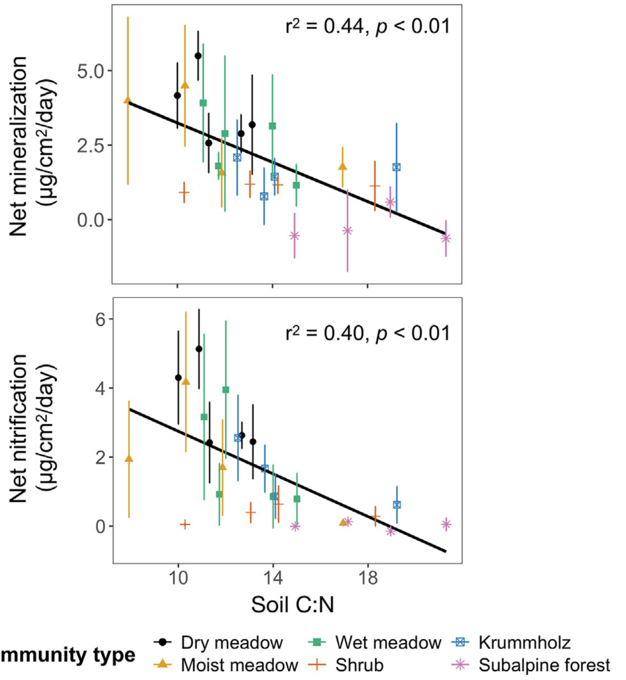

Fig. 3. Relationship between soil C:N and the mean soil N transformation rates (A) net N mineralization and (B) net nitrification. We show means ± SE, averaged by plot over all sampling times during the growing season (n = 3 sampling times).

and Carreiro, 2004). Thus, in the forested parts of the catchment, we would expect limited loss of inorganic N from the terrestrial ecosystem relative to meadow communities.

3.2. Soil moisture and temperature controls on patch scale net N transformations

Considering the role of physical properties—particularly soil temperature and moisture—in determining spatial and temporal patterns of soil N cycling, we found that three primary typologies emerged across the six alpine plant communities. Dry meadow and MOM maintained consistently warm, relatively drier conditions, WEM and SHR had persistent cool, wet conditions, and KRU and SUB had cool, dry conditions (Table 1, Fig. 4). These three temperature and moisture regimes created different temporal trajectories in net N transformation rates over the period of measurement; results of a linear mixed-effects model demonstrate that, indeed, the interaction between plant community type and sampling time for both net N mineralization and nitrification are statistically significant ($p < 0.01$, Fig. 5, Table 3).

We found that at the start of the growing season, the highest net N transformation rates were in the DRM and MOM communities, the relatively warmer, drier patches of this landscape, suggesting that they experience optimum soil temperature and moisture conditions to support microbially-mediated transformations early in the season (Figs. 4 and 5). In contrast, the WEM and SHR areas, which had standing water and were comparatively cooler at the start of the growing season, may experience episodic anoxia during this time that inhibits aerobic processes, as reported in Brooks et al. (1996). This trajectory was particularly evident in WEM, where net nitrification increased significantly from −0.1 ± 0.0 μg N cm^{-2} d^{-1} to 2.1 ± 0.2 μg N cm^{-2} d^{-1} ($p < 0.05$) over the growing season (Fig. 5B). Mid-season (July) emerged as the closest to a transition point: when net N transformations in DRM, MOM, and KRU had decreased and net N transformation rates in WEM had increased. Of all the communities within the catchment, SUB had the least temporal variation in rates: both net N mineralization and nitrification were stable and low, hovering at or below 0 μg N cm^{-2} d^{-1} across the sampling period (Fig. 5), again, suggesting that the lower part of the catchment may play an important role in retaining N.

Given the significant differences in net N transformation rates over time within many of the plant communities, we parsed out the degree to which temporal changes in soil moisture and temperature determined these patterns (Fig. 6 and Table A1). We found that the relationships between net N transformation rates and soil moisture and temperature differed by plant community type. Interestingly, the seasonal net N transformation rates for DRM and MOM—relatively warmer patches in the landscape—were negatively correlated with soil temperature (Fig. 6A and C). It is possible that since warmer temperatures were also associated with periods of lower soil moisture (Fig. 4), soil microbial activity was reduced. But the negative temperature–N transformation relationship contradicts many previous studies that reported increasing N transformation rates with higher soil temperature (e.g., Yin et al., 2012; Zaman and Chang, 2004). Another possible explanation is that in this cold tundra-forest ecotone, higher temperatures may stimulate gross N mineralization and/or nitrification, but N immobilization by soil microbes could also be higher. Previous studies support this interpretation. For example, Brooks et al. (1996) found that net N mineralization occurred in soil under the snowpack during the spring, but net N immobilization by microbial uptake was observed after snowmelt. Thus, greater N uptake by soil microbes under higher soil temperature conditions might cause lower net N transformation rates for these two plant communities. Unraveling the proximal drivers of this response likely has important implications for projecting changes in soil N transformations under environmental change.

In contrast to temperature, soil moisture tended to create a positive response in net N mineralization in the DRM, MOM, and SHR plant communities (Fig. 6B, Table A1). Soil moisture stimulated net nitrification rates in KRU and SUB (Fig. 6D). In WEM, we observed a negative logarithmic relationship between soil moisture and net nitrification (Fig. 6D). Again, we believe that super-saturation of soils in the WEM inhibited aerobic N processes (Fig. 4). Overall, the significant

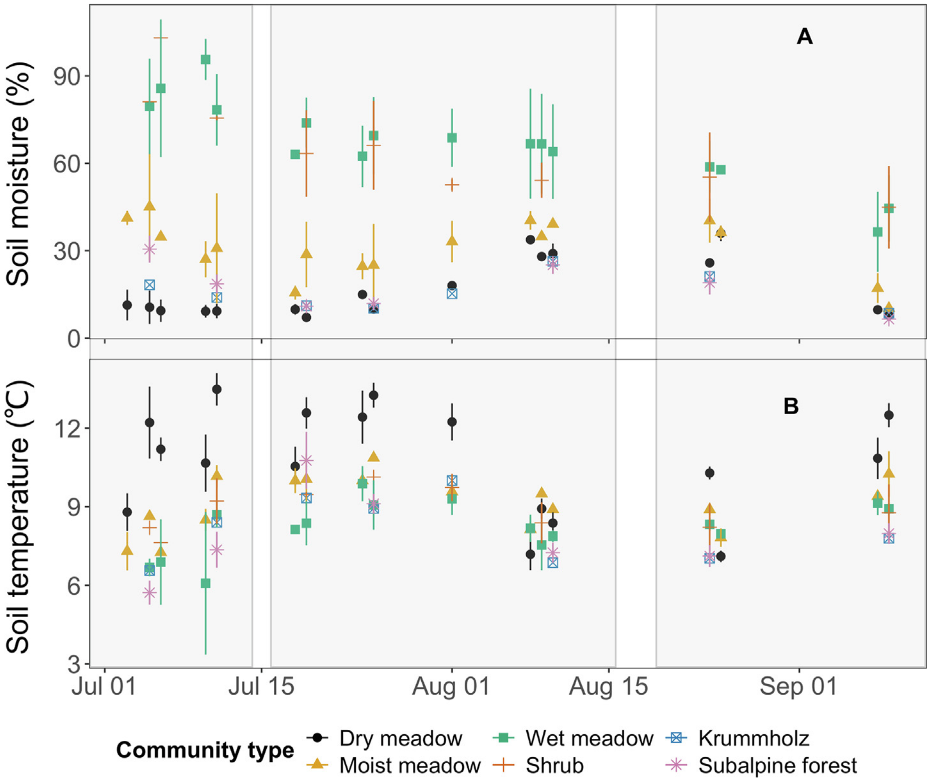

Fig. 4. Changes in (A) soil moisture and (B) soil temperature in different plant community types over the course of the growing season. Values are shown as means ± SE (n = 4 for each plant community type). Grey bars are used to delineate the period of soil incubation when moisture/temperature investigation occurred.

role of soil moisture in controlling N cycling in this ecosystem is consistent with findings from recent modeling studies (Fan et al., 2016; Wieder et al., 2017) showing that water is a primary limiting factor to microbial activity at patch scales within the alpine ecosystem.

3.3. Extending patch-scale N rates to the catchment-scale

In translating our observations across plant communities at the plot- or patch-scale into a catchment-scale picture, we can begin to explore the implications for N cycling under a warmer, drier climate. Our study suggests that DRM and MOM—the relatively warmer, drier plant

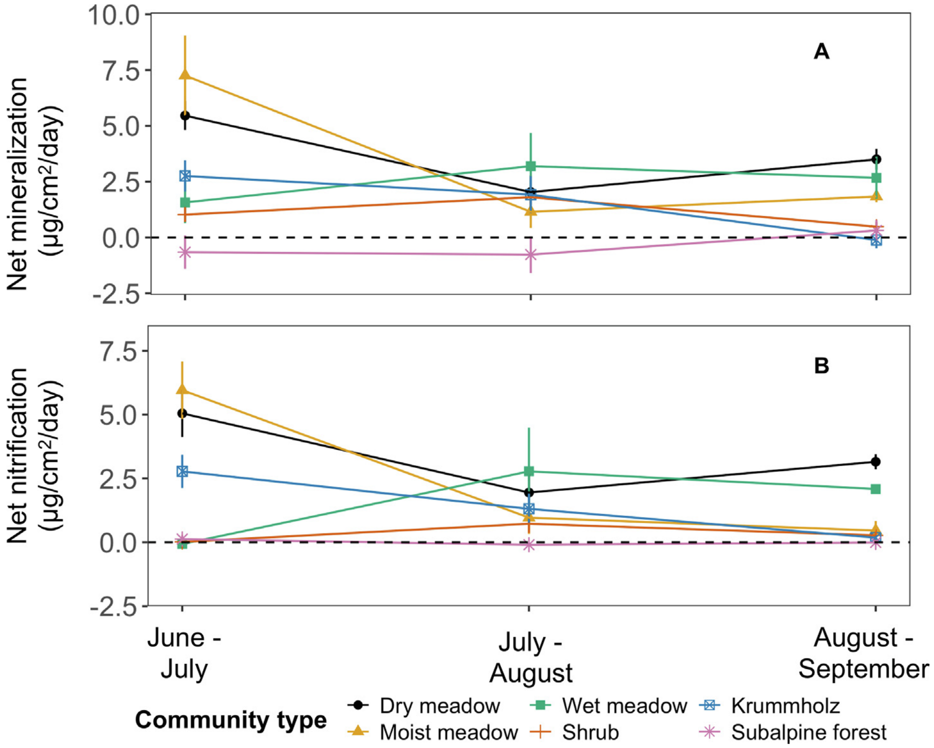

Fig. 5. Temporal variation of mean net soil N transformations (± SE) in different plant community types across the three incubation periods. (A) Net N mineralization and (B) net nitrification (n = 4 for each plant community type).

Table 3
Linear mixed models for examining the effects of plant community type and sampling time on soil N transformations.

		df	F-ratio	*p*-Value
Net N mineralization	Sampling time	2	6.16	< 0.01
	Community type	5	8.10	< 0.01
	Sampling time * Community type	10	3.78	< 0.01
Net nitrification	Sampling time	2	6.10	< 0.01
	Community type	5	6.22	< 0.01
	Sampling time * Community type	10	5.62	< 0.01

communities—have the greatest likelihood of producing inorganic N in excess of microbial demand early in the growing season. The fate of inorganic N produced early in the growing season likely depends on hydrologic conditions. Given that DRM occurs mostly in locally elevated areas of the catchment with limited snowpack development, has lower plant community biomass than MOM or WEM (Seastedt, in press), and may be largely hydrologically disconnected from the stream, it is possible that inorganic N released early in the season may persist in soils until a significant rainfall event increases soil moisture and causes subsurface N transport. Overall, we can expect that earlier snowmelt (Clow, 2010) and warmer soil temperatures will lead to warmer, drier conditions throughout the growing season, further limiting N cycling and transport. The occurrence of rain on snow and extreme precipitation events, which are also projected to increase during the spring to summer transition (Brönnimann et al., 2018; Musselman et al., 2018), will likely become increasingly important for stimulating N cycling and transport in plant communities that persist within relatively drier patches of the landscape.

The other groupings that we identify within the catchment—WEM and SHR, which remained cool and wet throughout the growing season and KRU and SUB, which were cool and dry—play different roles in the catchment-scale picture of N cycling. Unlike all other plant communities, both WEM and SHR have the potential for experiencing the problem of "too much"; that is, super-saturated soil moisture conditions that inhibit aerobic N cycling processes (Figs. 4 and 6). In KRU and SUB, dry conditions—the problem of "too little" moisture—limit N cycling processes, resulting in net N retention (microbial immobilization) in the lower parts of the catchment at and below treeline. An open question remains as to how surface water distributions across alpine catchments will change under a warmer, drier climate. Consistently wet areas (i.e., WEM and SHR) may decrease in their footprint if they dry out earlier in the growing season. If the patterns in our results hold, net N transformation rates—in particular, nitrification—may increase earlier in the season in WEM and SHR, assuming the plant communities themselves persist under altered forcings and low temperatures do not limit microbial N cycling. Given their closer physical proximity to the stream channel (Fig. 1), increases in net nitrification rates in these communities may have greater impact on hydrologic N losses from the watershed. In contrast, the cool, dry communities (i.e., KRU and SUB) may be more subjected to drought. As such, they would likely continue to be areas of net N immobilization and/or have limited terrestrial N losses.

The tight coupling of the alpine N cycle to the hydrologic regime suggests that changes in the delivery, storage, and transport of water in the future will affect plant communities in multiple ways, both directly (e.g., plant-water relations) and indirectly (e.g., via changes in nutrient cycling). Important, future research includes developing a complete, catchment scale picture of how abiotic characteristics of the landscape change spatially and temporally, as well as investigating N cycling and transport at hillslope-to-catchment scales. This could be accomplished with tracer studies that illuminate the roles and connectivity of different "patches" across the landscape. These efforts will aid in creating a robust hydrological modeling framework to test alternative climate forcing and determine how plant communities and biogeochemical cycling may shift over time.

3.4. Limitations of the research

Our study yielded new, important results of the differences in net N transformation rates within soils underlying alpine plant communities. Importantly, we examined how soil properties and conditions may explain differences in space and time. However, it is important to note that this study was conducted over the course of one growing season; in alpine ecosystems, we can expect that interannual variation in snowpack and snowmelt dynamics, in particular, will affect microbially-

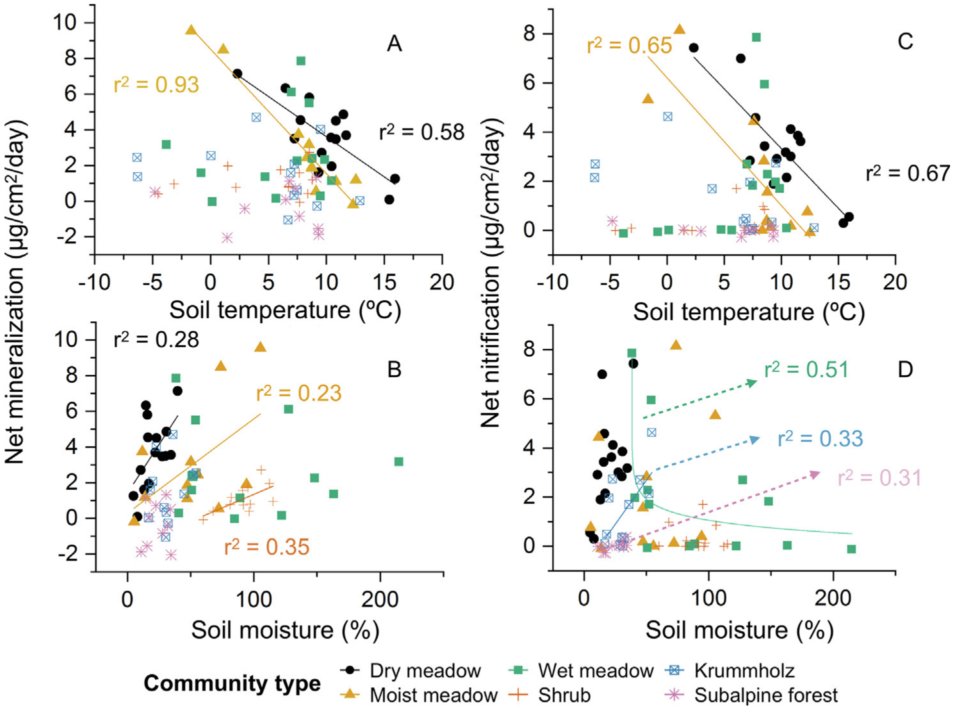

Fig. 6. Relationship between physical drivers (soil temperature and moisture) and seasonal N transformations in different plant community types. (A) Net mineralization and soil temperature, (B) net N mineralization and soil moisture, (C) net nitrification and soil temperature and (D) net nitrification and soil moisture. Equations for the lines are in Table A1 (Appendix A).

Table A1
Relationship between physical drivers (soil temperature and moisture) and seasonal N transformations in different plant community types.

	Net N mineralization		Net nitrification	
Plant community	Temperature	Moisture	Temperature	Moisture
DRM	$y = 8.13–0.78 * x$; $r^2 = 0.58, p < 0.05$	$y = 1.41 + 0.11 * x$; $r^2 = 0.28, p < 0.05$	$y = 8.19–0.48 * x$; $r^2 = 0.67, p < 0.05$	
MOM	$y = 8.53–0.69 * x$; $r^2 = 0.93, p < 0.05$	$y = 0.28 + 0.05 * x$; $r^2 = 0.23, p = 0.08$	$y = 6.21–0.52 * x$; $r^2 = 0.65, p < 0.05$	
WEM				$y = 3.24–0.53 * \ln(x-38.43)$; $r^2 = 0.51, p < 0.05$
SHR		$y = -1.66 + 0.03 * x$; $r^2 = 0.35, p < 0.05$		
KRU				$y = -0.90 + 0.07 * x$; $r^2 = 0.33, p < 0.05$
SUB				$y = -0.32 + 0.01 * x$; $r^2 = 0.31, p = 0.05$

mediated N transformations, as well as the phenological trajectories of plant communities adapted to these systems. Indeed, our study highlighted that soil N cycling rates are sensitive to differences in soil moisture and temperature, the patterns of which may vary across years. In addition, this research identified that wetter communities (e.g., SHR and WEM) might experience periods during which aerobic N transformations are inhibited (e.g., nitrification), yet we did not measure dissolved oxygen concentrations or the activities of microbial communities involved in N cycling, for example, which would act as another constraint on interpretation of our data. Given the bounds around our study, it is important to treat it as a first step toward developing greater understanding of the interactions and feedbacks among hydroclimatic dynamics, soil N cycling, and ecological communities in alpine regions. Ultimately, longer-term observations, ideally across a broader network of sites and including more environmental and biological variables, will be needed to excite coupled hydrologic-biogeochemical models that can be used to explore how alpine ecosystems will shift in response to environmental change.

4. Conclusions

This study demonstrated that across six plant communities in an alpine tundra-forest ecotone, rates of net N mineralization and nitrification not only differed, driven by soil moisture, temperature, and C:N ratios, but also experienced different trajectories through time. During the brief alpine growing season, the relatively warmer, drier meadow communities (dry and moist meadow communities) had the highest net N transformation rates at the beginning of the season, which declined with decreases in soil moisture. In contrast, treeline communities, krummholz and subalpine forest, exhibited net immobilization of inorganic N, with a low probability of significant gaseous losses or transport to the stream. Finally, the wet meadow and shrub communities had cooler, wetter conditions that may have inhibited aerobic microbial processes, especially early in the growing season. This study suggests that while multiple physical properties and conditions of landscape patches may affect plant community distributions and soil N cycling, in alpine systems, soil moisture, temperature, and C:N are key first-order controls. In working toward robust prediction of how alpine N cycling will respond to environmental change, future research should include targeted field-based tracer studies and development of modeling frameworks that explore the interactions among hydroclimatic forcing, soil properties, and N cycling.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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Appendix A

See Table A1.

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