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REVEALING THE DIRECT AND INDIRECT EFFECTS OF CLIMATE
CHANGE ON SOIL NUTRIENT DYNAMICS AND FORAGE RESOURCES IN
MOUNTAIN ECOSYSTEMS

A Dissertation Presented

by

Kenna E. Rewcastle

to

The Faculty of the Graduate College

of

The University of Vermont

In Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
Specializing in Natural Resources

January, 2022

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ABSTRACT

Modern climate change is already altering the structure and function of ecosystems around the world in nontrivial ways. Mountain ecosystems in particular will continue to experience a greater magnitude and rate of climatic warming than the global average, threatening the stability of key ecosystem processes like nutrient cycling as well as the supply of benefits from ecosystem services provided by mountains. While significant advancements have been made to address the direct effects of rising temperatures on nutrient cycling dynamics, our understanding of the synergies between the direct effects of warming and the indirect effects of climate change, mediated by the response of plant soil properties, lags behind.

This dissertation leverages a global network of climate change experiments in mountains to understand the direct and indirect effects of warming on nutrient cycling and forage resource production in alpine ecosystems around the world. First, I use a series of plant removal experiments distributed across an elevational gradient in the Colorado Rocky Mountains to explore how the effects of biodiversity loss on nitrogen cycling vary across a natural temperature gradient. Second, I identify globally consistent climate change effects on nitrogen and phosphorus cycling across seven sites in the warming and (species) removal (WaRM) network of climate change experiments in mountains. Finally, I focus on a single WaRM network site in the Colorado Rocky Mountains to analyze the effects of climate change on the quality and quantity of forage resource production in a federal rangeland. Taken as a whole, this body of research lends insight to the future of alpine nutrient dynamics in a warmer world and describes opportunities to link empirical evidence from global change experiments to management decisions in order to sustain essential ecosystem services in the face of climate change.

CITATIONS

Material from this dissertation has been accepted for publication in *Ecology* on May 27, 2021, in the following form:

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DEDICATION

To Mom and Dad,
for the road trips and camping adventures that first prompted me
to appreciate and question the vast differences among ecosystems.

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Special thanks are due to my collaborators in the WaRM Network, without whom my research would not be possible. For your sore fingers and raw cuticles after shoving thousands of resin strips into the ground around the world, and for jumping through countless international shipping hoops to return my samples to me: thank you! To the many undergraduates who helped me make an estimated 6,616 resin strips and spent hot days in the field with me collecting data, I can't thank you all enough. Without your enthusiasm and willingness to help me with my science arts and crafts, I would still be in the lab cutting resin strips and listening to podcasts.

To my fellow plague doctors and graduate students, the camaraderie and solidarity of working with you to complete my dissertation during a global pandemic has had an immeasurable impact on me and my ability to keep trudging

towards the finish line. For those masked smizes when passing each other in the Spear Street Lab and virtual catch-ups: thank you all so much! Big thanks to my Mom, Dad, and sister for always humoring my complaints and celebrating all of my accomplishments, big and small, and for your many life-hacks and your sage advice. Last but not least, a lifetime of gratitude goes to my partner, Gabby Freeman, for her love, support, and patience throughout the creation of this dissertation, for luring me away from my desk and into the mountains to ski, climb, and mountain bike, and for not letting me lose sight of my love for the outdoors in spite of the painstaking hours spent studying nature in a window-less lab. Here's to many more adventures with you.

TABLE OF CONTENTS

CITATIONS	ii
DEDICATION	iii
ACKNOWLEDGEMENTS	iv
INTRODUCTION	1
References	6
Figures	11
CHAPTER ONE: PLANT REMOVAL ACROSS AN ELEVATIONAL GRADIENT MARGINALLY REDUCES RATES, SUBSTANTIALY REDUCES VARIATION IN MINERALIZATION	12
Abstract	12
Introduction	13
Materials and Methods	17
Results	25
Discussion	29
Acknowledgements	34
References	36
Tables	41
Figures	42
Appendix	44
TEMPERATURE DIRECTLY AFFECTS NITROGEN AVAILABILITY BUT INDIRECTLY AFFECTS PHOSPHORUS AVAILABILITY IN ALPINE ECOSYSTEMS GLOBALLY	48
Abstract	48
Introduction	48
Results	52
Discussion	57
Materials and Methods	61
Acknowledgments	68
References	68
Figures and Tables	74
Appendix	81

WARMING REDUCES THE QUANTITY AND QUALITY OF LIVESTOCK FORAGE RESOURCES IN A COLORADO RANGELAND	86
Abstract	86
Introduction	87
Methods.....	91
Results.....	97
Discussion	98
Acknowledgements.....	101
References.....	101
Figures and Tables	107
Appendix.....	111
CONCLUSION	113
COMPREHENSIVE BIBLIOGRAPHY	117

INTRODUCTION

Nitrogen (N) and phosphorus (P) are essential nutrients for plant growth and are the two nutrients that most broadly limit primary productivity in terrestrial ecosystems globally (Chapin *et al.*, 1986; Elser *et al.*, 2007; Harpole *et al.*, 2011). Nitrogen is a key constituent of amino acids, the building blocks of proteins, nucleic acids, the most basic structural units of DNA, and is an essential element in chlorophyll, a crucial pigment involved in photosynthesis. Phosphorus is also important for the construction of nucleic acids and is found in cell membranes that are primarily comprised of phospholipids; P is also an essential component of ATP, the basic energy currency used to power biochemical reactions in cells. Both N and P are often co-limiting to plant growth and primary productivity (Harpole *et al.*, 2011), but the relative importance of N vs. P limitation is often determined by climate and ecosystem age (Vitousek, 2004; Menge *et al.*, 2012; Delgado-Baquerizo *et al.*, 2020). Because nutrient limitation of plant productivity is widespread, changes to the plant-available pool of soil nutrients in the face of climate change can determine the tipping point between positive or negative productivity responses to climate change (Menge and Field, 2007; Wieder *et al.*, 2015; Zaehle *et al.*, 2015). If nutrients become more abundant and alleviate nutrient limitations on productivity, we may see an increase in above- and belowground biomass that could mitigate future climate change (Aerts *et al.*, 2006; Natali *et al.*, 2011). However, if climate change were to decrease the availability of N or P, heightened nutrient limitation would exacerbate climate change by reducing plant productivity and carbon (C) sequestration in plant biomass (Peñuelas, 2017; Querejeta, 2021). Furthermore, climate-

driven changes to nutrient availability and plant productivity could limit the quality and quantity of forage resources available to the livestock and wildlife that graze in mountain rangelands around the world (Sala *et al.*, 2017). Understanding global patterns of the consequences of climate change for nutrient availability is an important component in predicting the future of ecosystem functions and services in mountain ecosystems and identifying potential climate feedbacks.

Climate change can have direct effects on N- and P- availability as warming accelerates the rate of the chemical reactions and the microbial processes that control nitrogen transformations. In temperature-limited ecosystems with sufficient moisture, warming can have a positive impact on nutrient availability (Melillo *et al.*, 2011; Bai *et al.*, 2013; Yue *et al.*, 2018; Shaw and Cleveland, 2020). However, in arid ecosystems, microbial moisture limitation can prevent the positive effects of warmer temperatures on soil nutrient availability (Delgado-Baquerizo *et al.*, 2013a; Delgado-Baquerizo *et al.*, 2013b; Querejeta, 2021). Climate change can also have indirect effects on N- and P- availability as plant community and edaphic properties shift in response to changing climate (Moreau *et al.*, 2019; Liu *et al.*, 2021; Wang *et al.*, 2021). Changes to plant community diversity can impact the efficiency of plant nutrient uptake (Hooper and Vitousek, 1998; Wei *et al.*, 2017), and shifts in plant physiology in response to climate change can affect the quality of litter inputs to the soil system, with lower quality litter (higher C:N ratios) resulting in microbial immobilization of soil nutrients that ultimately reduces the plant-available soil nutrient pool (Wang *et al.*, 2021). In addition to the effect of climate change on soil C:N, rising temperatures can affect other edaphic properties like

soil pH (Wang *et al.*, 2014) and soil chemical stoichiometry (Dijkstra *et al.*, 2012; Jiao *et al.*, 2016), which in turn will mediate the impact of climatic changes on soil nutrient pools. Disentangling the relative importance of the direct and indirect impacts of climate change on soil nutrient dynamics will be an important step in determining the ecosystem characteristics that make nutrient cycling in certain regions especially susceptible to the effects of climate change.

Mountains are an ideal system in which to study the effects of climate change on nutrient dynamics and the ecosystem services that they support. Because of the fairly reliable relationship between elevation and temperature, elevational gradients serve as natural experiments in which scientists can isolate the influence of temperature on ecosystem dynamics (Sundqvist *et al.*, 2013). Mountain ecosystems globally are expected to experience a greater rate and magnitude of climate change than will low-elevation ecosystems (IPCC, 2007) and are also threatened by land use change and the growth and expansion of human population centers into these ecologically sensitive ecosystems (Grêt-Regamey *et al.*, 2012; Elsen *et al.* 2018). The 1.2 billion people that live in proximity to mountains benefit from the material (Viviroli *et al.*, 2007; Sala *et al.*, 2017) and non-material (Grêt-Regamey *et al.*, 2012; Knez and Eliasson, 2017) ecosystem services that mountains provide. Mountains therefore present not only an ideal ecological setting in which to study the impacts of climate change (Payne *et al.*, 2017), but also provide opportunities to directly apply research on the ecological implications of climate change to the sociological impacts by reframing these results in the context of mountain ecosystem services.

Ecological experiments produce data that can be used to predict the effects of climate change on the biophysical processes that underly the ecosystem services through which humans derive benefits from nature (Millennium Assessment, 2005; Haines-Young and Potschin, 2010; Wong *et al.*, 2015; Ricketts *et al.*, 2016). Therefore, studying both the sociological and ecological consequences of climate change together will produce a more holistic understanding of how climate change will impact mountain ecosystems. To understand the relative representation of biophysical ecosystem function research and ecosystem services research in mountains within the applied ecological literature, I conducted a literature search to identify peer-reviewed studies published in the journal *Ecological Applications* that investigate coarse categories of key ecosystem functions and ecosystem services in mountains ranges of the contiguous United States. While this search was inevitably blind to the vast amount of grey literature documenting ecosystem functions and especially ecosystem services on public lands, I chose *Ecological Applications* as a focal journal in this search because of the journal's overarching theme of publishing research that applies ecological science to environmental problems. Ecosystem functions included in this search were as follows: carbon cycling (primary productivity, respiration, decomposition), nutrient cycling (N- and P-mineralization, N-fixation), soil formation (pedogenesis), erosion rates, pollination, and herbivory. Ecosystem services included in this search were as follows: supporting services (nutrient cycling, soil formation, primary productivity, pollination, pest control), provisioning services (food, fresh water, timber production, forage resource production), regulating services (carbon sequestration, climate regulation, flood

regulation, water purification, air filtration, pollution remediation), and cultural services (aesthetic, spiritual, educational, recreational).

The overwhelming majority of search results investigated ecosystem functions (Figure 1), but many of these studies of ecosystem function document biophysical processes that also constitute measurements of supporting ecosystem services like nutrient cycling (Figure 1). The ratio of ecosystem function to ecosystem service research among the thirty-eight articles retained in the final search results was 2.1. Only four studies explicitly researched ecosystem services alone, and the most common ecosystem service research investigated supporting ecosystem services that were explicitly measured as ecosystem functions in the literature, mostly regarding nutrient cycling (Figure 2). A large portion of all mountain ecosystem literature was conducted on public lands managed by the US Forest Service, highlighting the opportunity to link ecosystem function and service research together in federal public lands to gain a more comprehensive understanding of the innerworkings of these ecosystems in order to develop management plans that balance numerous ecological and sociological priorities.

This dissertation investigates the direct and indirect impacts of climate change on nutrient cycling in mountain ecosystems and extends these ecological results to gain insight into the future of an important ecosystem service in a mountain rangeland. First, I measure the impact of removing a dominant plant species across an elevational gradient on N-mineralization rates, a process that recycles organic N inputs into forms that can be taken up by plants. Second, I use a globally-distributed network of climate change experiments in mountains to understand the impact of climate change on soil nutrient

availability. In this second chapter, I optimize a technique using resin strips to measure N- and P-availability in the warming and (species) removal network (WaRM) to compare the relative effects of the direct and indirect impact of climate change on pools of essential plant nutrients around the world. In my third chapter, I measure changes in the quality and quantity of livestock forage resource production in response to warming and the removal of the dominant plant species in a sub-alpine rangeland in Colorado, USA. Together, these results reveal global patterns of climate change impacts on nutrient dynamics and identify climatic, edaphic, and vegetative characteristics that mediate the effects of warming on soil nutrients. This research also demonstrates the potential of reframing ecological data from climate change experiments to answer questions about the future of ecosystem services to better inform land management decisions in the face of global change.

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Figures

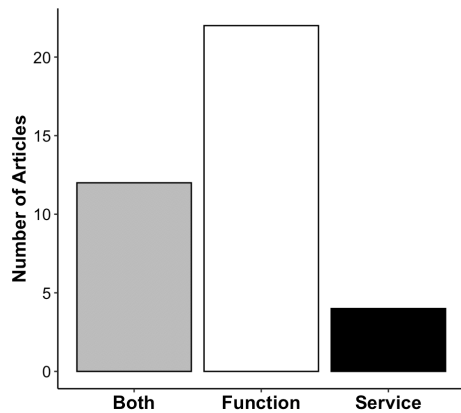


Figure 1. Literature search results showing the number of articles published in *Ecological Applications* that document ecosystem services, ecosystem functions, or both, in mountain ecosystems of the contiguous US.

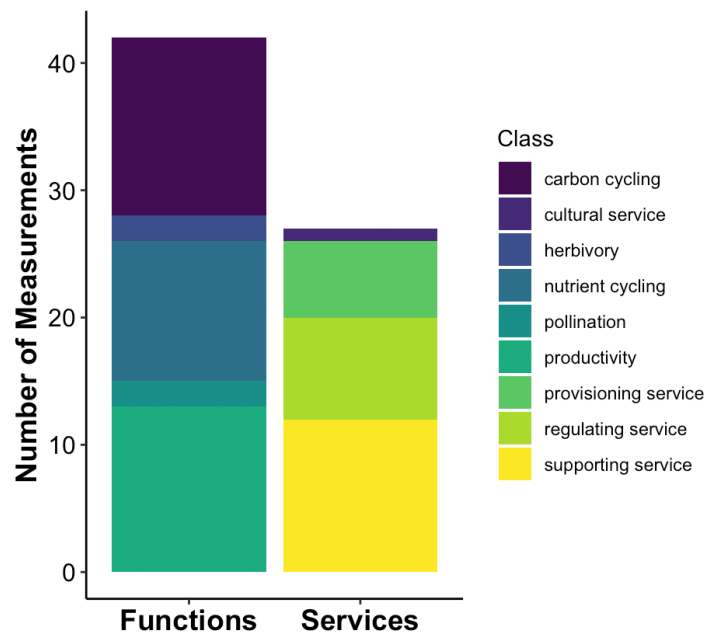


Figure 2. Literature search results showing the number of measurements of unique ecosystem functions and services binned according to broad classes of functions and services.

CHAPTER ONE: PLANT REMOVAL ACROSS AN ELEVATIONAL GRADIENT MARGINALLY REDUCES RATES, SUBSTANTIALLY REDUCES VARIATION IN MINERALIZATION

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Abstract

The loss of aboveground plant diversity alters belowground ecosystem function; yet, the mechanisms underpinning this relationship and the degree to which plant community structure and climate mediate the effects of plant species loss remain unclear. Here, we explored how plant species loss through experimental removal shaped belowground function in ecosystems characterized by different climatic regimes and edaphic properties. We measured plant community composition as well as potential carbon (C) and nitrogen (N) mineralization and microbial extracellular enzyme activity in soils collected from four unique plant removal experiments located along an elevational gradient in Colorado, USA. We found that regardless of the identity of the removed species or the climate at each site plant removal decreased the absolute variation in potential N-mineralization rates and marginally reduced the magnitude of N-mineralization rates. While plant species removal also marginally reduced C-

mineralization rates, C-mineralization, unlike N-mineralization, displayed sensitivity to the climatic and edaphic differences among sites, where C-mineralization was greatest at the high elevation site that receives the most precipitation annually and contains the largest soil total C pools. Plant removal had little impact on soil enzyme activity. Removal effects were not contingent on the amount of biomass removed annually, and shifts in mineralization rates occurred despite only marginal shifts in plant community structure following plant species removal. Our results present a surprisingly simple and consistent pattern of belowground response to the loss of dominant plant species across an elevational gradient with different climatic and edaphic properties, suggesting a common response of belowground ecosystem function to plant species loss regardless of which plant species are lost or the broader climatic context.

Introduction

Loss of plant species from communities will impact the structure and function of ecosystems as interactions among plant species, evolutionary dynamics such as competition and facilitation that shape plant communities, and plant-soil linkages shift in response to diminished biodiversity (Pugnaire *et al.*, 2019). Ecologists often explore the impact of plant species loss on ecosystem function by building correlations between ecosystem functions and aspects of plant community structure such as dominant plant functional type, functional traits, species relative abundances, and the diversity of the remaining plant community (Symstad *et al.*, 1998; Lyons and Schwartz, 2001; Gilman *et al.*, 2010; Ockendon *et al.*, 2014). However, the properties of communities or ecosystems

that determine ecosystem sensitivity to changes in plant communities or to abiotic changes remain unclear (Klanderud, 2005; Gilman *et al.*, 2010; Wardle *et al.*, 2011; Adler, 2012). Furthermore, we know little about the sensitivity of belowground soil processes to changes in species interactions relative to aboveground ecosystem functions (Zak *et al.*, 2003). Despite ample research defining the relationship between species richness and ecosystem function in experimental and observational frameworks (Tilman *et al.*, 1996; Grace *et al.*, 2016), we also know that the loss of individual species from a plant community can have a different impact on the biodiversity–ecosystem function relationship than is captured by studies that assess this relationship in the direction of increasing diversity across a biodiversity gradient (Naeem *et al.*, 1995; Fox and Kerr, 2011; Kardol *et al.*, 2018). Plant removal experiments, especially when conducted across an environmental gradient, can be used as a tool to address many of these problems that arise when attempting to quantify the impact of losing a plant species on ecosystem function (Sundqvist *et al.*, 2013).

Some plant species have a disproportionately large impact on soil processes due to their dominance (Smith and Knapp, 2003; Avolio *et al.*, 2019), the uniqueness of their traits in a community, or their longevity on the landscape, i.e. long-lived perennial species. The loss of these influential plant species from a community should have a greater impact on ecosystem processes than the loss of a plant species with a less pronounced presence in the community (Tilman *et al.*, 1997; Chapin *et al.*, 1998; McLaren and Turkington, 2010). In short, the identity of the plant species that is lost

from an ecosystem should matter when predicting the impact of species loss on belowground processes (Wardle *et al.*, 1999; Johnson *et al.*, 2008). In a 2003 review, Díaz *et al.* proposed three mechanisms as pathways by which plant species removal impacts ecosystem function as the loss of a single plant species shifts species interactions: 1) Ecosystems could respond to the loss of the specific functional role filled by the removed species, 2) changes to ecosystem function could be a response to the re-assembly of the remaining community members following the loss of a species, and 3) changes to ecosystem function could be a response to the disturbance of the removal treatment itself through loss of aboveground biomass. By incorporating treatments that account for each of these mechanisms of plant species removal impact, removal experiments are uniquely positioned as an experimental framework to discern the pathways by which removing a single plant species can impact belowground ecosystem function.

Environmental conditions such as growing season temperature and precipitation modulate the relationship between above- and below-ground ecosystem components, meaning that the loss of the same plant species could have a starkly different impact on belowground processes in ecosystems characterized by different climates (Klanderud and Totland, 2005; Brooker, 2006; Bardgett *et al.*, 2013). Changes in climate as well as the associated environmental stress alter both the direction and magnitude of plant-soil feedbacks (van der Putten *et al.*, 2016; Baert *et al.*, 2018). The nature of this feedback effect is highly variable and depends on the context of both present environmental

conditions and the legacy of historical climate (Kaisermann *et al.*, 2017). The soil microbial communities involved in carbon (C) and nitrogen (N) mineralization, the nutrient recycling processes in terrestrial ecosystems, may also be limited by different abiotic factors than is the aboveground community. Thus, global change drivers may decouple above- and below-ground linkages as plant and microbial communities respond differently to environmental change (Wardle *et al.*, 2013; Classen *et al.*, 2015).

Taken together, the effect of losing a plant species from a community on belowground ecosystem processes likely depends on both the functional identity of the plant species removed, climatic context, and the degree to which plant community structure shifts following the species loss (Díaz *et al.*, 2003; McLaren and Turkington, 2010; Wardle *et al.*, 2011; Pugnaire *et al.*, 2019). However, the influence of the combination of factors described above on the relationship between plant species removal and belowground ecosystem processes has yet to be empirically tested using field experiments. Therefore, to understand the biotic and abiotic variables that shape the impact of species loss on potential C- and N-mineralization, we sampled a series of plant removal experiments established at different sites across an elevational gradient. We predicted that the effect of removing a dominant plant species would vary across the environmental gradient, with the greatest decrease in belowground mineralization rates following plant removal occurring at the lowest elevational site where moisture limitation, i.e. environmental stress, is the highest (García-Palacios *et al.*, 2018; Pugnaire *et al.*, 2019). We also hypothesized that the impact of plant species removal on

belowground processes would scale with the amount of biomass removed from each plot (Díaz *et al.*, 2003; McLaren and Turkington, 2015). Our results lend insight to how the loss of species from communities might alter important nutrient cycles in climatically different ecosystems through the restructuring of plant communities and ecosystem function.

Materials and Methods

To investigate the impact of removing a plant species on C- and N-mineralization, we sampled four existing, independent plant removal experiments located at four locations along an elevational gradient near the Rocky Mountain Biological Laboratory, Gothic, Colorado, USA. Each of the four experiments removed different focal plant species, and the experiments have been running from five to seventeen years. A dominant plant species was removed at each site along the elevational gradient, but because there is nearly complete turnover of the plant community across the elevational gradient, the identity of the removed species was different at each elevation, confounding the functional type of the removed species as well as environmental conditions across the elevational gradient.

At the low elevation site, located at 2740 m asl (38.71 N, -106.82 W), we removed the dominant plant species *Wyethia x magna* (Asteraceae), a perennial forb that is a stable hybrid of *Wyethia amplexicaulis* and *W. arizonica* (Weaver, 1915), by clipping aboveground biomass to the soil surface annually for five years prior to sampling. Plots at

this site were 2.0 m $\times$ 2.0 m in area (n = 8). Soils at the low elevation site were classified as Mayoworth loam. At the mid-low elevation site, located at 2890 m asl (38.95 N, -106.98 W), we maintained a seventeen-year removal of *Linaria vulgaris* (Plantaginaceae), a perennial, invasive forb with an extensive horizontal root system, in 2.0 m $\times$ 2.0 m (n = 6) (Wilke and Irwin, 2010). Plants were removed from the mid-low elevation site by gently pulling on the base of the plant to remove the plant and a small portion of the *L. vulgaris* root mat. Soils at the mid-low elevation site were classified as Tine sandy loam and Bassel sandy loam, depending on the slope of each plot. At the mid-high elevation site, we removed *Festuca thurberi* (Poaceae), a perennial grass that forms shallow but dense root systems, by clipping to the soil surface annually for seven years prior to sampling. Removal treatments at the mid-high elevation site (2904 m asl, 38.94 N, -106.99 W) were applied in 1.5 m $\times$ 1.5 m (n = 4) (Read *et al.*, 2018, Henning *et al.*, 2019), with soils at this site classified as Leaps silty clay loam. In the *W. magna* and *F. thurberi* removals at the mid-high and low elevation sites, a small amount of glyphosate herbicide was applied to the remaining base of the stems after the aboveground biomass was removed to attempt to kill belowground biomass. Herbicide was only applied to stem bases at these sites for the first two years of the removal treatments, and because of the meticulous way in which it was applied to the base of the remaining stems following removal using a paintbrush, we are confident that herbicide application had negligible effects on the fitness of the other plant species. At the high elevation site (3460 m asl, 38.99 N, -107.06 W), we removed the dominant species *Juncus drummondii* (Juncaceae), a perennial rush that grows in thick bunches, by clipping aboveground biomass to the soil

surface annually for five years before sampling. Plots at this site covered an area of 2.0 m × 2.0 m (n = 8). Soils at the high elevation site were classified as Moran-Rubble land complex, characterized by extremely gravelly loam/sandy loam. Roots of the removed plants species were left intact at all sites that used clipping to removed aboveground biomass in removal treatments (low, mid-high, and high elevation sites) in order to minimize disturbance caused by the removal treatment for the remaining plant species and the soil community. While *L. vulgaris* individuals were removed by tugging gently on the base of the stem, removing some root biomass in the process, the majority of the root runners that extend horizontally just beneath the soil surface remained behind in the soil.

In addition to the control (i.e. no plant biomass removed from plots with the focal species naturally present) and individual species removal treatments present at all sites, the mid-low and mid-high elevation sites had an additional random biomass removal treatment where biomass from random plant species was removed to reflect the amount of biomass that was removed annually from the treatments in which a specific plant species was removed. This treatment was intended to isolate the disturbance effect that plant removal has on the remaining plant community through loss of aboveground biomass. Finally, a natural control treatment, i.e. plots where the focal plant species was naturally absent, existed at the mid-low elevation site. Table 1 summarizes site-level experimental design, climate data for the 2018 growing season, relative abundance of the

focal species at each site, and the average amount of biomass removed annually from removal treatment plots at each site.

During the peak of the 2018 growing season, when aboveground biomass was greatest at each site, we conducted plant community surveys by visually assessing the percentage of the plot area covered by each plant species. Rare species were recorded as covering < 1 %. At the low, mid-high, and high elevation sites, data were collected annually on the amount of plant biomass removed from each plot that received a removal treatment by collecting removed biomass in paper bags and drying the plant biomass for 48 h at 60 °C. We calculated the average amount of biomass removed annually from each plot by pooling the total amount of biomass removed over the entire length of the experiment at each site, and dividing this cumulative number by the length of each experiment in years (Table 1). On July 23rd-25th, 2018, we took two separate soil cores (< 15 cm deep), one for the potential mineralization incubation and one for extracellular enzyme assays, from random locations within each plot. Soil samples were refrigerated and transported to the University of Vermont, Burlington, VT USA for processing. We sieved each sample to remove rocks and large plant material (> 2 mm) and measured gravimetric water content (g H₂O g⁻¹ dry soil) by drying 10 g of field-moist soil in an oven at 105 °C for 48 hours (Robertson *et al.*, 1999). We measured soil organic matter content using the loss on ignition method (SOM-LOI) by combusting oven-dried soil samples (105 °C) at 550 °C for six hours, and then measuring SOM-LOI (g C kg⁻¹ dry

soil) by quantifying the mass difference between oven-dried and combusted soil samples (Hoogsteen *et al.*, 2015).

To measure the effect of plant removal on potential C- and N- mineralization in soils under standardized environmental conditions, we conducted a 30-day laboratory incubation of soils exposed to ideal moisture and temperature conditions (30% volumetric water content, 20 °C) (Robertson *et al.*, 1999). 30% volumetric water content was the maximum soil moisture content recorded during the growing season at these four sites in the two years preceding this study, so this moisture threshold was chosen to represent ‘ideal’ but realistic conditions under which we could investigate the full capacity of the microbial community in sampled soils to mineralize C and N. We divided field-moist soil samples from each plot into paired 10 g subsamples. One subsample was extracted immediately using a 2.0 M KCl solution to measure extractable NH_4^+ and NO_3^- . We incubated the second subsample in the dark for 30 days in 1 L clear, glass jars fitted with rubber septa in the metal lid. We measured the CO_2 evolved in the headspace of the jars via direct injection by using a syringe to sample the air in each sealed jar and injecting 7 mL of air into a LI-COR 7810 trace gas analyzer (LI-COR Instruments, USA) at six time points (days 1, 2, 4, 8, 16, and 30 of the incubation) to track potential C-mineralization ($\mu\text{g C g}^{-1} \text{ dry soil day}^{-1}$). At the completion of the incubation, we extracted the incubated soil subsample with 2 M KCl to again measure extractable NO_3^- and NH_4^+ concentration. We measured the concentration of NO_3^- and NH_4^+ in the extractions colorimetrically (Doane and Horwath, 2003) using a Synergy HT microplate

fluorimeter/spectrophotometer (Synergy HT, Biotek Inc., Winooski, VT, USA). We then calculated total N-mineralization rates by subtracting the sum of NO_3^- and NH_4^+ (i.e. inorganic N) in the initial subsample from the sum of extractable inorganic N in the final subsample and dividing the amount of inorganic N produced during the reaction by the length of the incubation in days (mg N kg^{-1} dry soil day^{-1}).

In addition to a laboratory incubation of soils to measure N- and C-mineralization rates, we measured the activities of six different soil extracellular enzymes to understand how plant removal impacts potential microbial activity. Using the protocol established by Saiya-Cork *et al.* (2002), we assayed the carbon degrading enzymes α -glucosidase (AG), β -glucosidase (BG), Cellobiohydrolase (CBH), and β -Xylosidase (XYL), nitrogen acquiring enzyme β -N-acetylglucosaminidase (NAG), and phosphorus acquiring enzyme Acid phosphatase (PHOS). All assays were performed by incubating enzymes in a soil slurry prepared with a buffered solution (pH 5.0 sodium acetate buffer) at an ideal temperature (20.0 °C) with non-limiting amounts of substrate. Following incubation, potential enzyme activities were quantified using a Synergy HT microplate spectrophotometer (Biotek Inc., USA).

To analyze shifts in plant community structure in response to the plant removal treatments across the elevational gradient, we performed non-metric multidimensional scaling (NMDS) on the plant community survey data in each plot using the ‘metaMDS’ function in the vegan: Community Ecology Package in R (Oksanen *et al.*, 2019) with

distance between plant communities in plots within the same treatment calculated according to the modified Gower ('altGower') method (Anderson *et al.*, 2006). We performed a permutational multivariate analysis of variance using the 'adonis' function in the vegan package with two thousand permutations to quantify the extent to which the removal treatment explains dissimilarity between communities. To calculate dissimilarity among plant communities at each site and with the removal treatments, we chose to use the modified Gower method (Anderson *et al.*, 2006) ('altGower' in the 'vegdist' function in the vegan package). The modified Gower method for calculating dissimilarity between communities is most appropriate for our study because it explicitly weights an order-of-magnitude change in abundance equivalent to a change in species composition. This feature is important because this analysis relies on our ability to detect changes in abundance driven by our removal treatments despite high turnover in species composition across the elevational gradient that would overwhelm changes in abundance in most other dissimilarity indices that consider abundance (Anderson *et al.*, 2006). Finally, we used the 'betadisper' function to evaluate the homogeneity of variances in community structure across treatment groups to understand how the removal treatments, and separately, site, affect the variation in plant community structure. This test calculates the average linear distance between individual plots within a treatment group and the within-group centroid which represents the median community structure for that group.

To measure the impact of plant removal on potential C- and N-mineralization, potential soil enzyme activity, and SOM-LOI content, we performed ANOVAs using the

‘Anova’ function in the car package to measure the extent to which elevation, removal treatment (dominant species removal vs. non-removal), and the interaction between these two variables explained variation in C- or N-mineralization (Fox and Weisberg, 2019). To account for heteroscedasticity in potential N-mineralization rates among removal treatment and site groups, we used a White-adjustment for corrected standard errors within the ‘Anova’ function (White, 1980). Additionally, to understand if the effect of species removal on mineralization rates was mediated by simply the removal of aboveground biomass, we again conducted ANOVAs to analyze variation in potential mineralization rates across removal treatments using only the mid-low and mid-high elevations where random biomass removal treatments were applied. To further understand whether potential mineralization rates are influenced by the amount of biomass removed from each plot, we analyzed linear relationships between average biomass removed annually from each plot and the residual variation in C- and N-mineralization after accounting for the effects of removal treatments and site. Finally, we conducted an ANOVA using only the mid-low elevation plots which included a treatment where the focal species, *L. vulgaris*, was naturally absent to analyze the similarity between mineralization rates in focal species removal plots and mineralization rates in plots where the focal species was absent. A high degree of similarity between potential mineralization rates in removal treatment plots and focal species absent plots would lend support to one of the hypotheses proposed by Díaz *et al.* (2003), that the impact of removing a species from a system is mediated by the loss of functions or influence uniquely attributed to that plant species. To understand how site and removal treatment

impact variation among potential C- and N-mineralization rates, we also performed modified Levene's tests (applying an ANOVA test to the absolute deviation of each observation from the group median) using the 'levene.test' function in the lawstat package (Brown and Forsythe, 1974; Gastwirth *et al.*, 2019). All statistical analyses were performed in RStudio (R version 3.6.3 "Holding the Windsock") (Rstudio Team, 2016).

Results

Plant species removal marginally decreased the magnitude of potential N-mineralization rates by 27% ($F_{1,43} = 3.32$, $p = 0.075$) and significantly decreased the variation in potential N-mineralization ($p = 0.016$), regardless of plant species removed or climate at each elevation (Fig. 1a). Neither site ($F_{3,43} = 0.84$, $p = 0.481$) nor the interaction between site and removal treatment ($F_{3,43} = 0.35$, $p = 0.791$) significantly affected N-mineralization. Variation in potential N-mineralization rates within a single site was relatively homogenous across the elevational gradient ($p = 0.462$). Conversely, potential C-mineralization rates varied significantly across the elevational gradient ($F_{3,42} = 5.31$, $p = 0.003$), with notably higher C-mineralization rates at the high elevation site confirmed by a Tukey HSD test (Fig. 1b). Plant species removal tended to decrease potential C-mineralization rates by 9% ($F_{1,42} = 3.22$, $p = 0.08$), whereas the interaction of site and plant removal treatment had no discernible impact on potential C-mineralization rates ($F_{3,42} = 0.57$, $p = 0.637$). Rates of C-mineralization over the course of the incubation showed consistent patterns across all treatments and sites, with CO₂ efflux peaking during the first days of the incubation and stabilizing at a lower mineralization rate after

the first week of the incubation (Appendix S1: Fig. S1). SOM content, measured via LOI, reflected the same pattern as potential C-mineralization rates, where SOM-LOI was greatest at the high elevation site ($F_{3,42} = 3.93$, $p = 0.015$) with no detectable response to removal treatments ($F_{1,42} = 1.00$, $p = 0.322$) nor an interaction between removal treatments and site ($F_{3,42} = 0.52$, $p = 0.669$) (Appendix S1: Fig. S2). We did not find an effect of site or removal treatment on the variation in potential C-mineralization rates within a treatment group at each site (site $p = 0.349$, removal treatment: $p = 0.112$).

While the activity of all soil extracellular enzymes differed significantly across the elevational gradient (AG: $p = 0.002$, BG: $p < 0.001$, CBH: $p = 0.007$, XYL: $p = 0.010$, NAG: $p < 0.001$, PHOS: $p < 0.001$), we did not detect a response of potential soil enzyme activity to the plant removal treatments (AG: $p = 0.232$, BG: $p = 0.113$, CBH: $p = 0.241$, NAG: $p = 0.533$, PHOS: $p = 0.220$), with the exception of XYL activity that decreased marginally with plant removal ($F_{1,36} = 3.65$ $p = 0.064$) (Appendix S1: Fig. S3). Activity of NAG, a nitrogen degrading enzyme, and XYL, a carbon degrading enzyme involved in the breakdown of hemicellulose, both showed significant differences in response to the interaction between site and removal treatment (NAG: $F_{3,41} = 3.55$, $p = 0.023$; XYL: $F_{3,36} = 4.33$ $p = 0.010$).

Plant species removal at all sites had only a marginal impact on plant community structure ($F_{1,43} = 1.81$, $p = 0.060$), but community structure shifted significantly across the elevational gradient, largely driven by species turnover ($F_{3,43} = 7.76$, $p < 0.001$; Fig.

2). We did not detect a significant interactive effect between plant removal treatment and site on plant community structure ($F_{3,43} = 0.054, p = 0.125$). Overall, site, removal treatment, and the interaction of these two parameters explained 40% of the variation in plant community structure across all plots. Furthermore, neither site nor removal treatment altered the dispersion or within-group variation in plant community structure (site: $F_{3,47} = 1.23, p = 0.310$; removal treatment: $F_{1,49} = 0.10, p = 0.750$; Appendix S1: Fig. S4).

Our comparison of plant community structure and potential soil mineralization rates in random biomass removal plots vs. focal plant species removal plots verified that the effect of removal treatments does not stem from biomass removal alone. However, we could not detect a distinct effect of plant removal on plant community structure or potential mineralization rates in data from this subset of field sites. When analyzing the plant community structure at the two sites that included random biomass removal treatments (mid-high and mid-low elevation sites), we found only a marginally significant difference in plant community dissimilarity across removal treatments ($F_{2,23} = 1.45, p = 0.083$) and did not find a significant change in the distribution of variation in plant community structure in response to either of the removal treatments ($F_{2,26} = 0.135, p = 0.875$). Likewise, potential C-mineralization ($F_{2,22} = 0.68, p = 0.519$) and potential N-mineralization ($F_{2,23} = 0.98, p = 0.389$) were seemingly unaffected by removal treatments, and mineralization rates in random biomass removal plots were indistinguishable from the rates in control plots (C-mineralization: $p = 0.750$, N-

mineralization: $p = 0.667$) and species removal plots (C-mineralization: $p = 0.928$, N-mineralization: $p = 0.912$). Linear regressions correlating the amount of biomass removed annually with the residual variation in N- and C-mineralization rates after accounting for the effects of site and removal treatment further supported our finding that the amount of aboveground biomass removed was not significantly correlated with belowground mineralization rates in these meadow ecosystems (C-mineralization: $p = 0.588$, N-mineralization: $p = 0.455$). These results indicate that the mechanism driving changes in belowground ecosystem function in response to plant removal treatments stems beyond loss of aboveground biomass.

By isolating the mid-low elevation site “natural removal control” plots where the focal species, *L. vulgaris*, was naturally absent from plots, our results showed that none of our removal treatments had a discernible effect on any plant community properties or ecosystem function rates as measured above (community dissimilarity: $F_{3,18} = 0.86$, $p = 0.735$; community dispersion: $F_{3,18} = 0.48$, $p = 0.703$; potential C-mineralization: $F_{3,17} = 1.41$, $p = 0.275$; potential N-mineralization: $F_{3,18} = 0.83$, $p = 0.494$). Furthermore, potential C-mineralization and N-mineralization in the plots where *L. vulgaris* was naturally absent were indistinguishable from potential mineralization rates in control plots (C-mineralization: $p = 0.906$, N-mineralization: $p = 0.993$) and *L. vulgaris* removal plots (C-mineralization: $p = 0.9997$, N-mineralization: $p = 0.905$), indicating that the effect of removing the dominant species cannot be attributed to the loss of the specific influence of this species on belowground processes.

Discussion

By incubating soils sampled from plant species removal experiments spread across an elevational gradient, our results show that species removal consistently decreases the variation in potential N-mineralization rates, with the magnitude of N-mineralization rates in plant removal plots being marginally lower. These results were consistent across the entire elevational gradient, with no differences in potential N-mineralization rates among sites, a finding that stands in contrast to our hypothesis that the effect of dominant plant species removal would be mediated by variation in climate and environmental stress across the elevational gradient. While potential C-mineralization rates also decreased subtly with removal treatments, we found significantly higher mineralization rates at the high elevation site where soil moisture across the growing season is relatively higher. This result likely reflects SOM content across the elevational gradient, where potential C-mineralization rates are highest at the high elevation site where SOM content was significantly greater than at all other sites (Appendix S1: Fig. S2). We also found that variation in soil potential N-mineralization rates was significantly lower in the plant species removal treatment, indicating convergence in potential N-mineralization with the loss of a plant species regardless of its identity. Interestingly, we observed these changes in belowground processes in response to plant species removal despite little to no change in overall plant species composition and potential extracellular enzyme activity with the removal of a focal species in each ecosystem.

Why might there be an interactive effect of elevation and removal on XYL and NAG enzyme activities? We suspect that shifts in NAG activity in response to removal might be sensitive to the changes in edaphic properties like soil total C and soil moisture that vary across the elevational gradient. The NAG activity patterns revealed here likely mirror our N-mineralization results because this enzyme is a key agent in the nitrogen mineralization process. Additionally, the interactive effects of site and removal treatment might be linked to the functional identity of the plant species removed at each site. XYL enzymes hydrolyze specific linkages in β -(1,4)-xylose compounds found in the cell walls of plant species. As the cell walls of monocot species substitute a different xylan compound as the structural backbones of cell walls, the biomass of dicot species contains more of the β -(1,4)-xylose XYL substrate (Hatfield *et al.*, 2017). Therefore, removal of a monocot (as at the high and mid-high elevational sites) vs. the removal of a dicot (mid-low and low elevational sites) could have contrasting effects on the synthesis and activity of extracellular enzymes like XYL that aid in the decomposition of lignocellulosic biomass.

Previous work in these meadow ecosystems revealed fairly strong resistance to change in both above- and belowground communities to *F. thurberi* removal, where plant community composition, community-weighted plant functional traits, and fungal colonization of plant roots showed no clear response to removal of the dominant species or nitrogen fertilization (Read *et al.*, 2018; Henning *et al.*, 2019). Alpine ecosystems

experience frequent disturbances at a variety of scales, from burrowing mammals to avalanches and landslides, possibly conditioning these ecosystems and the plant and soil communities that inhabit montane meadows to a relatively large degree of disturbance, resulting in resilience to more minor disturbances plant species removal. These results suggest that plant species loss impacts belowground processes by some other mechanism beyond the loss of the specific influence of the removed plant species on belowground nutrient cycling.

By comparing the response of potential N-mineralization to removal of four distinct species along an elevational gradient, we can discern between the mechanisms by which plant removal might impact ecosystem function proposed by Díaz *et al.* (2003). Because removal decreased potential N-mineralization at all field sites, regardless of the functional identity of the plant species removed, our results suggest that this ecosystem response is not due to the loss of the influence of a particular species, eliminating the first mechanism as a plausible explanation. When considering the “natural removal control” plots at the mid-low elevation, we find that any response of N-mineralization rates to the removal of this species was not due to the loss of a specific function performed by the removed species, *L. vulgaris*, because N-mineralization rates did not differ between plots where *L. vulgaris* was present and plots where *L. vulgaris* was naturally absent. The results from our analysis of shifts in the structure of the plant communities in each experiment in response to removals (Fig. 1a) showed that the removal had only a marginal effect on plant community structure, making it unlikely that community re-

assembly following removal could be driving the shift in ecosystem function found here. Finally, potential N-mineralization rates did not differ significantly between control plots and random biomass removal plots, indicating that disturbance is also unlikely to be the dominant driver of shifts in potential N-mineralization rates in response to removal. Our experimental design therefore allows us to speculatively rule out all three of the mechanisms that drive removal effects as proposed by Díaz *et al.* (2003), so we turn to other more indirect mechanisms that might drive variation in mineralization rates following species removal.

Plant removal may have several indirect impacts on belowground microbial processes that could explain our results. Removals across all experiments were conducted by either clipping aboveground biomass of the removed species to ground level, or by gently pulling on aboveground biomass to break shoots from the extensive network of belowground roots, as in the *L. vulgaris* removal. This method of removal leaves much of the belowground biomass of the removed plant behind, potentially constituting a significant pool of N that is immobilized in plant root litter. Several studies estimate that root mean residence time is approximately four years for fine roots in ecosystems characterized by a -1.8 to 2.7 °C range in mean annual temperature (Gill and Jackson, 2000; Leifeld *et al.*, 2015), and root turnover in grasslands globally is limited by precipitation (Wang *et al.*, 2019). Estimates of fine root decomposition in arid grasslands with precipitation regimes similar to the climate of this study system indicate that as much as 60% of root biomass remains after 4-10 years of decomposition, immobilizing 60% of the

N content of root litter at the onset of decomposition (Parton *et al.* 2007). Delay in root decomposition following the onset of plant removal could lead to a short-term decrease in the size of the soil N pool that is available to microbes and plants until the roots of removed plants are decomposed. Our data lend some support to this explanation when N-mineralization rates are analyzed within the context of each individual experiment across the elevational gradient. Results from the mid-low elevation site, where *L. vulgaris* has been actively removed for seventeen years, show no effect of removal—or any of other treatments—on potential N-mineralization rates, possibly indicating that the legacy of the removal treatment has faded as roots have decomposed following removal to release N immobilized in belowground *L. vulgaris* root litter. In contrast, the effect of species removal on soil N-mineralization rates remains across all three younger experiments. Immobilization of N in belowground root litter might therefore be a mechanism by which loss of species locally could reduce ecosystem N cycling in the short-term.

Species removal likely affects ecosystem function more generally by reducing ecosystem resilience to climatic extremes (Tilman and Downing, 1994). This response to species removals may be a belowground manifestation of an effect that Kardol *et al.* (2018) found in a long-term plant removal experiment where plant species loss led to greater temporal variability in aboveground plant biomass. Perhaps plant species loss leads to similar variability belowground where properties such as soil microbial community composition, microbial biomass, or microbial activity and carbon use efficiency in communities that have lost plant species are especially vulnerable to

climatic extremes, driving marked shifts in belowground processes that are not seen in more diverse and resilient communities. Heightened temporal variability of above- and/or below-ground ecosystem components in response to species loss may also negatively impact ecosystem resilience (Oliver *et al.*, 2015). As 2018 was an especially dry summer in our study area, loss of the ability of plant and microbial communities to function in spite of climatic events like a severe drought may explain lower mineralization rates in plant removal plots.

In conclusion, we found that removing the dominant plant species consistently reduces the variation in soil N- mineralization rates, while marginally decreasing the magnitude of C- and N-mineralization rates, in alpine meadows. We find these changes to belowground function in response despite only subtle shifts in aboveground plant community structure and no clear changes in extracellular enzyme activity in response to plant removal. While our results are limited in their ability to pinpoint a clear mechanism by which species loss affects potential soil mineralization rates, the results do offer an unexpectedly simple pattern describing the overall effect of species loss on soil N and C cycling that holds across an elevational gradient. Moreover, our study offers insight into how loss of aboveground plant species might indirectly impact belowground processes with implications for ecosystem function in a future world characterized by global change.

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Tables

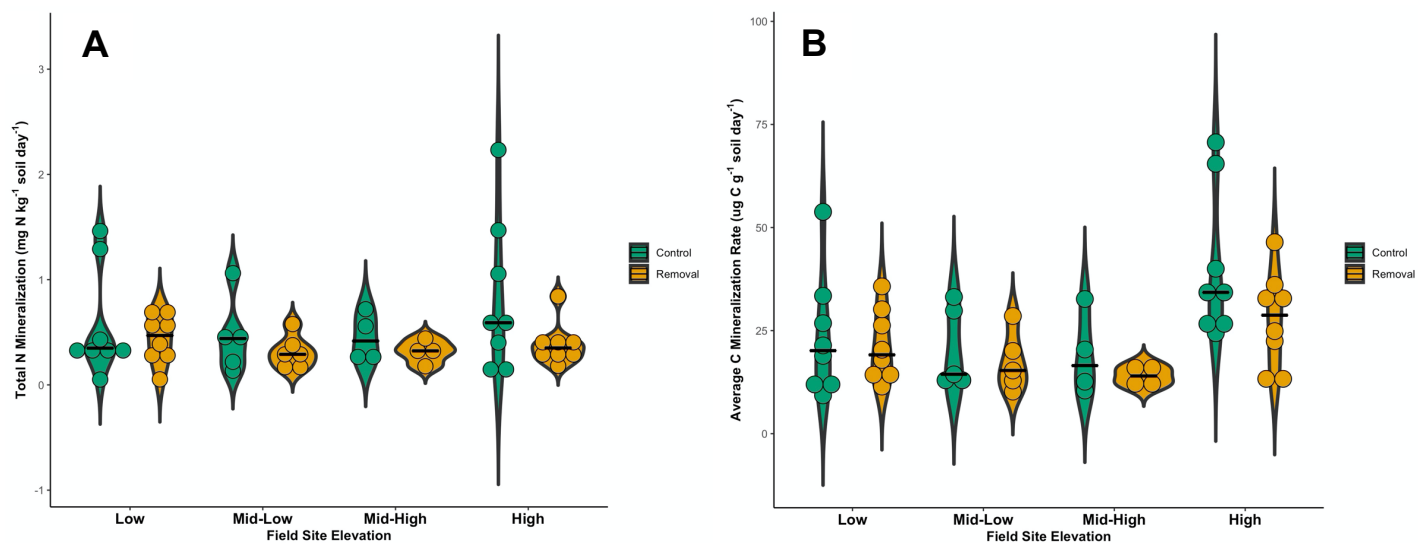
Table 1. Summary of experimental design and climatic conditions across the elevational gradient.

Site	Length of Experiment (yr)	Plant Species Removed	Replication (n)	Elevation (m asl)	Mean Growing Season Temp. (C)	Growing Season Precipitation (mm)	Mean Growing Season Soil Moisture (VWC)	Relative Abundance of Focal Species	Average Biomass Removal Rate (dry g y ⁻¹)	Average Soil Total C (g kg ⁻¹ dry soil)
Low Elevation	5	<i>Wyethia x magna</i>	8	2740	15.6	61.4	3.61%	19.9%	173.02	111.6
Mid-Low Elevation	17	<i>Linaria vulgaris</i>	6	2890	12.1	98.3	9.67%	19.8%	—	109.4
Mid-High Elevation	7	<i>Festuca thurberi</i>	4	2904	—	—	—	29.5%	29.51	104.2
High Elevation	5	<i>Juncus drummondii</i>	8	3460	12.2	127.6	7.71%	19.1%	52.49	153.5

Focal species removed, experimental design, and climate variables for each of the four field experiments included in this study. Both mid-elevation sites are located in close proximity to one another and therefore share climate data. Collection of growing season climate data for all sites began on June 1st, 2018, and ended on August 31st, 2018, with the exception of the high-elevation field site where the weather station was installed on June 27th at the beginning of the growing season. The relative abundance of the focal species targeted in removal treatments at each site was calculated by dividing the percent of the plot area covered by the focal species in control plots by the total area covered by all plant species in each control plot. Data quantifying the amount of biomass removed annually from removal treatments at the mid-low elevation site were not collected. Climate data for the mid-elevation sites are made available through the Rocky Mountain Biological Laboratory (RMBL, see Acknowledgements).

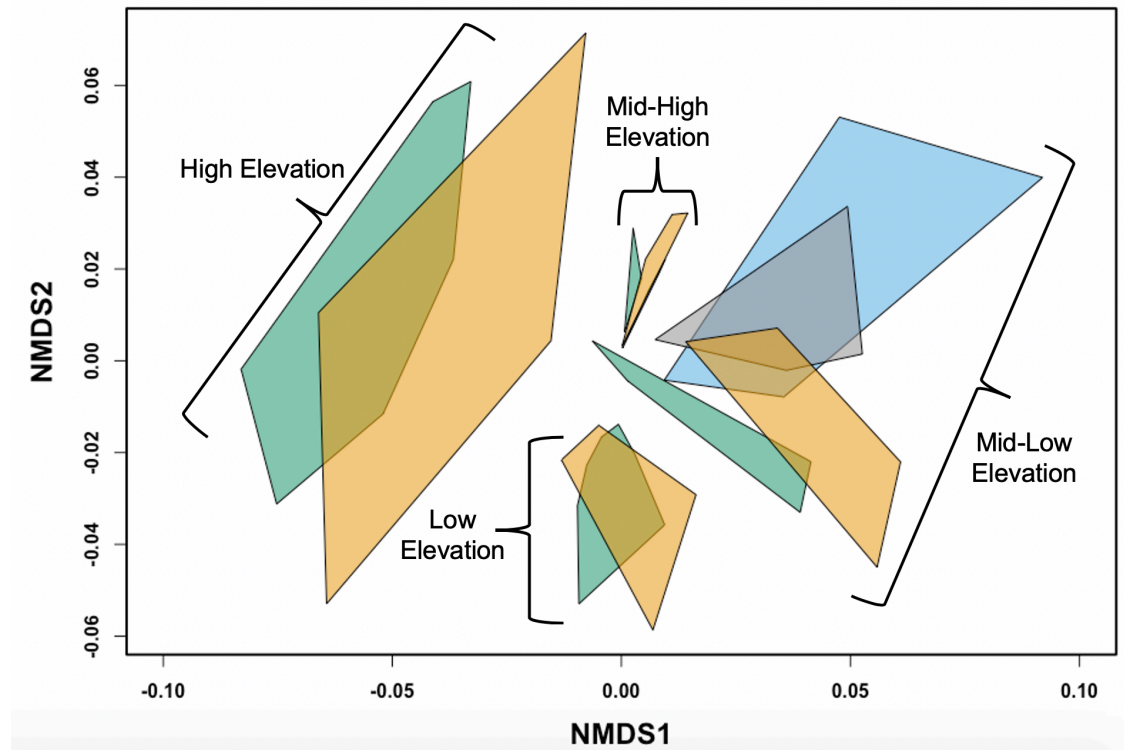
Figures

Figure 1.



A) Plant removal decreased the variation in and, marginally, the magnitude of N-mineralization rates. Site and the interaction between elevation and removal treatment had no discernible effect. B) C-mineralization rates varied significantly among sites and were marginally impacted by plant species removal while the interaction between site and species removal treatment did not significantly impact C-mineralization rates. Crossbars indicate group medians.

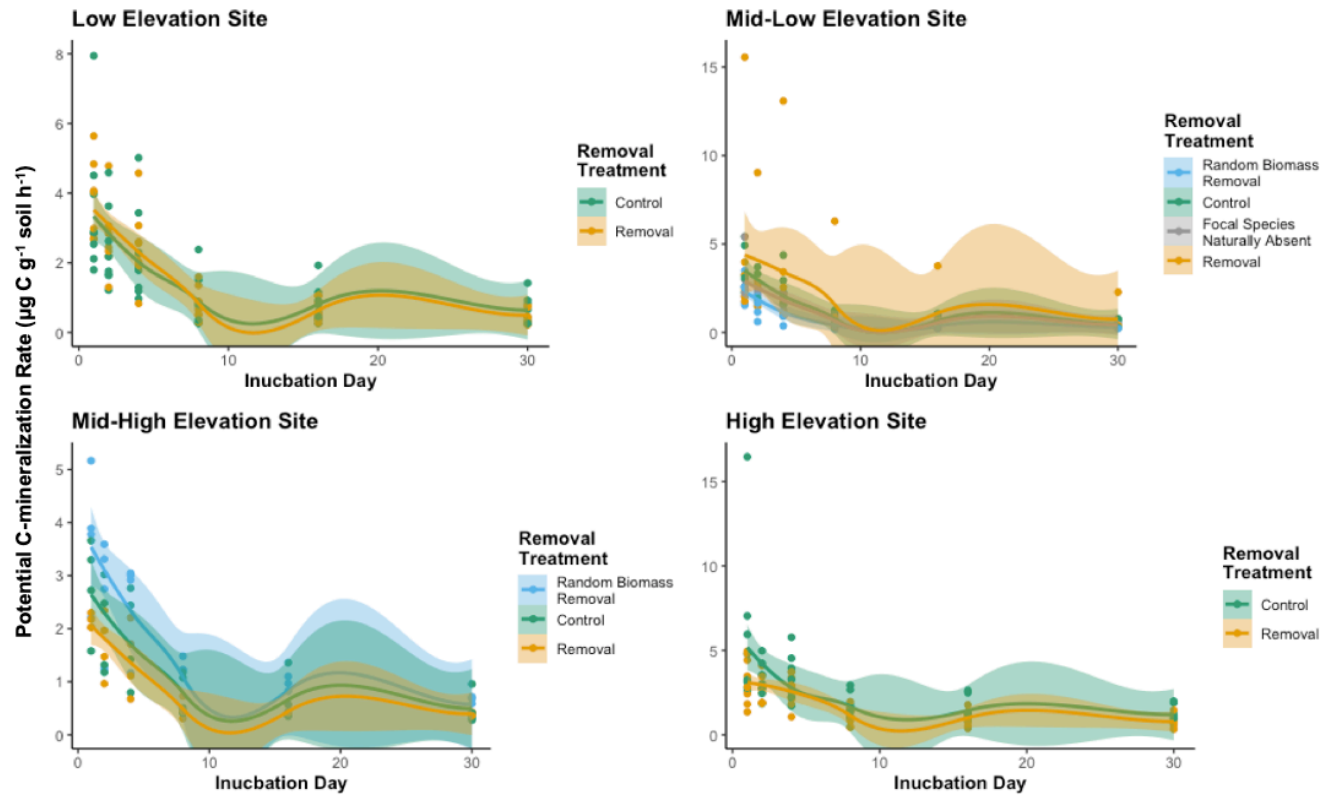
Figure 2.



An NMDS ordination of plant community structure in response to plant removal treatments at four different sites along an elevational gradient. Polygons encompass communities in all plots within a specific removal treatment at each site. Teal polygons indicate control treatments, gold polygons encompass communities that received the plant removal treatment, blue polygons indicate the random biomass removal treatment, and the gray polygon at the mid-low elevation site indicates a natural removal control treatment where the focal plant species, *Linaria vulgaris*, naturally did not occur. Community structure varied by site but only varied marginally with removal treatments and was not significantly impacted by an interaction between removal treatment and site.

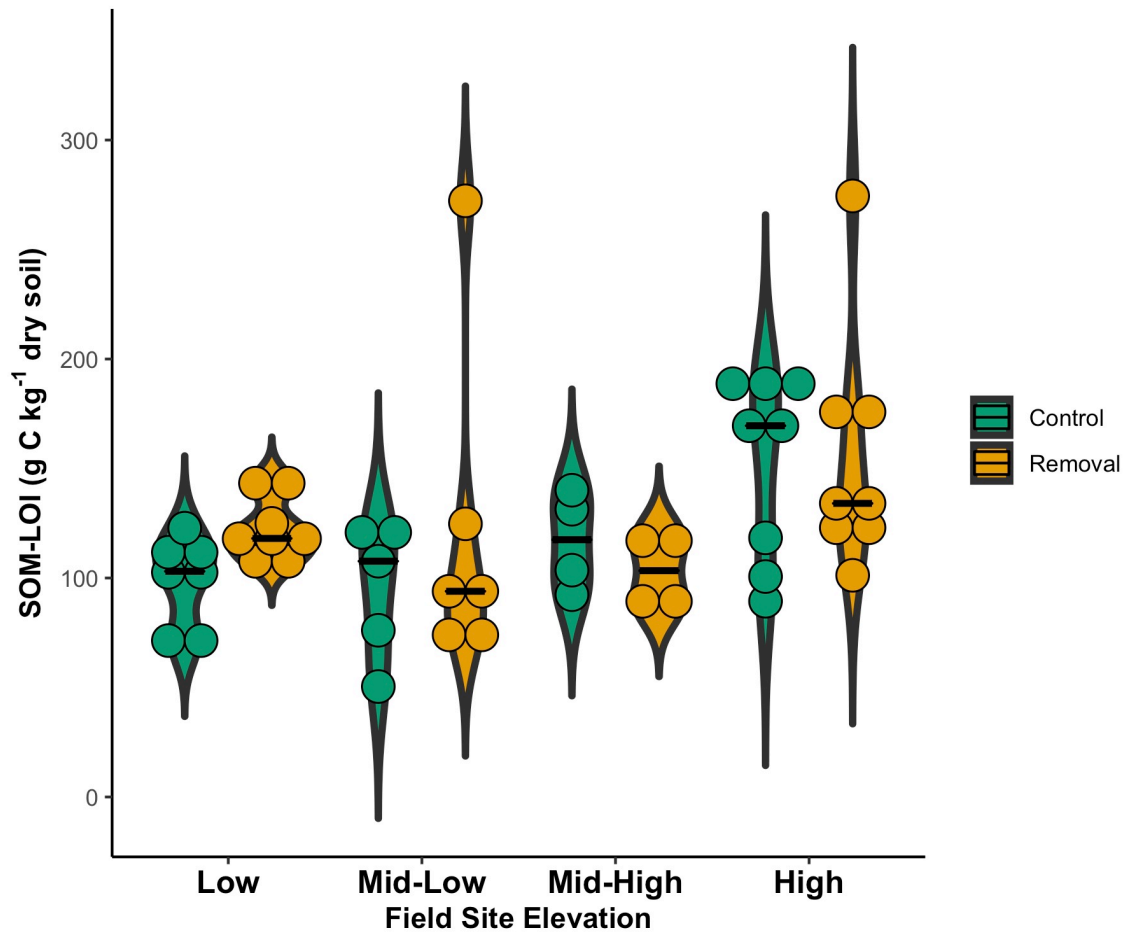
Appendix

Figure S1.



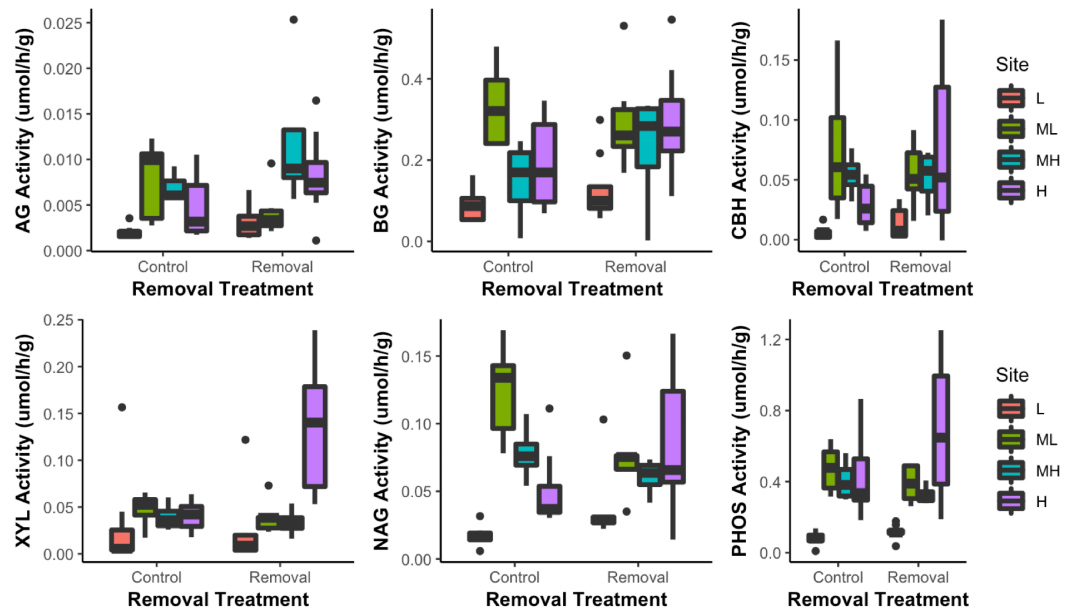
The pattern of C-mineralization rates over the course of the thirty-day incubation period did not vary across removal treatments or across the elevational gradient. However, the magnitude of C-mineralization rates was greatest at the high elevation site, consistent with the result that total C-mineralization was greatest at the high elevation site (Fig. 1b) and that SOM content was also highest at the high elevation site (Fig. S3).

Figure S2.



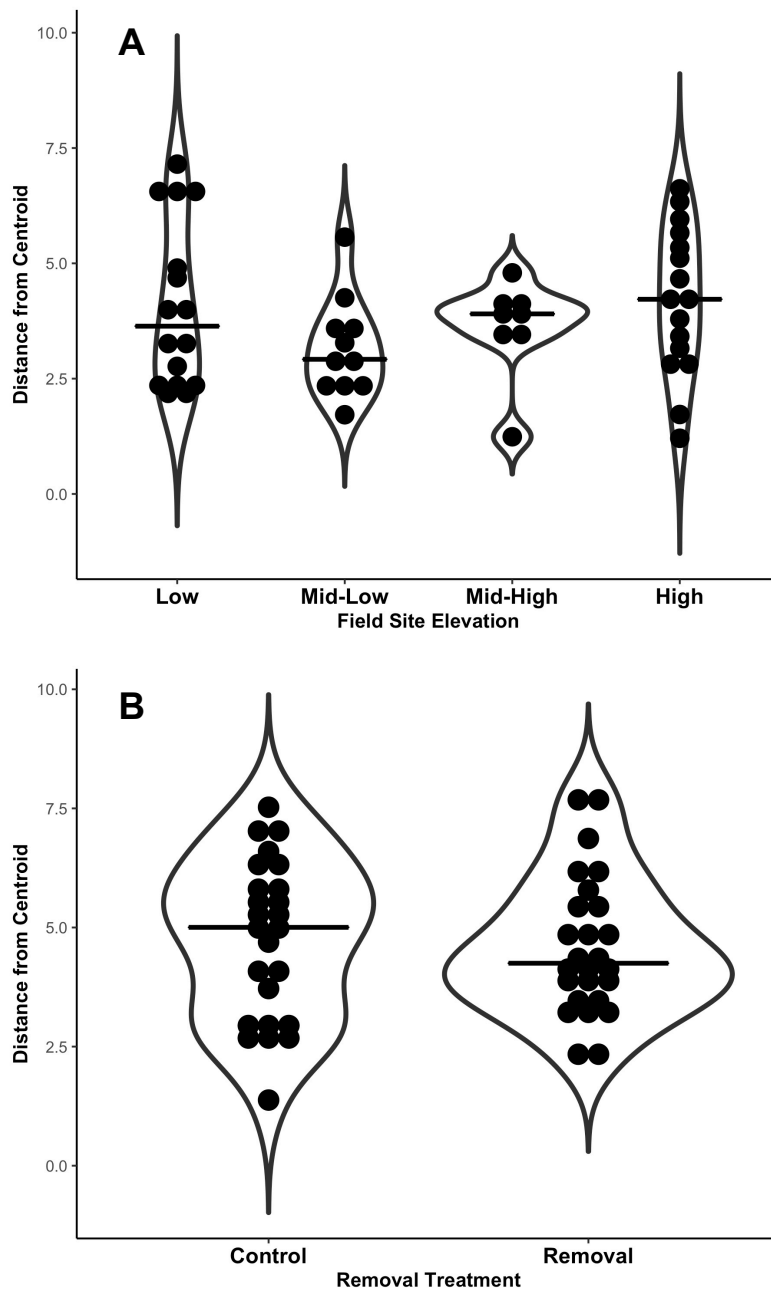
Removal treatments had no discernible impact on SOM content, measured via LOI, across the elevational gradient. SOM content at the high-elevation site is notably greater than SOM content at all other sites.

Figure S3.



Potential extracellular enzyme activities of six different enzymes in soils sampled from plant removal experiments at four different sites across an elevational gradient (L = Low, ML = Mid-Low, MH = Mid-High, H = High elevation sites). Activity of all enzymes varied significantly by site but not by removal treatment. However, enzymes NAG and XYL showed a significant response to the interaction between removal treatment and site.

Figure S4.



Neither site (A) nor the plant removal treatment (B) affected the distribution of variation in plant community structure within treatment/site groups. Crossbars indicate group medians.

TEMPERATURE DIRECTLY AFFECTS NITROGEN AVAILABILITY BUT INDIRECTLY AFFECTS PHOSPHORUS AVAILABILITY IN ALPINE ECOSYSTEMS GLOBALLY

Abstract

Nitrogen (N) and phosphorus (P) are essential plant nutrients that are co-limiting to primary productivity in ecosystems around the world. Climate change can both directly impact the size of soil nutrient pools as warmer temperatures impact rates of nutrient transformations and can also indirectly impact soil nutrient pools as vegetative and edaphic responses to warmer temperatures mediate the impact of climate change. We used resin probes to measure the plant-available pool of nutrients in the warming and (species) removal (WaRM) network of globally distributed climate change experiments in mountains to understand the pathways by which climate change will affect pools of available nutrients. Using structural equation modelling, we found that temperature directly affects soil N-availability, but indirectly affects soil P-availability in a relationship that's mediated by the impact of temperature on edaphic properties. Together, these results indicate divergent mechanisms through which climate change might impact the availability of two essential nutrients in mountain ecosystems, with consequences for the plausibility of a climate mitigation pathway that relies on increased plant productivity in a warmer world.

Introduction

Nitrogen (N) and phosphorus (P) are key nutrients that are essential to plant growth. The availability of these resources is often limiting to primary productivity (Chapin *et al.*, 1986; Vitousek 2004; Elser *et al.*, 2007; LeBauer and Treseder, 2008;

Harpole *et al.*, 2011), with the relative importance of N and P limitation varying across gradients of ecosystem age (Walker and Seyers 1976; Vitousek 2004; Menge *et al.*, 2012; Izquierdo *et al.*, 2013), climate (Reich and Oleksyn, 2004; Delgado-Baquerizo *et al.*, 2020; Du *et al.*, 2020), and plant community characteristics (Niklaus *et al.*, 2001; Delgado-Baquerizo *et al.*, 2020; Liu *et al.*, 2021). The impacts of climate change on pools of plant-available N and P will, in part, determine the capacity of plant productivity globally to respond to climate change (Dukes *et al.*, 2005; Menge and Field, 2007; Wieder *et al.*, 2015), with important consequences for climate feedbacks (Hobbie *et al.*, 2002; Goll *et al.*, 2012). If climate change exacerbates nutrient limitation, a preeminent threat in arid ecosystems (Lou *et al.*, 2018; Peñuelas *et al.*, 2017; Querejeta *et al.*, 2021), productivity will decline, muting negative feedbacks to climate change as less carbon is stored in plant biomass. However, if climate change increases the availability of N and P (Aerts *et al.*, 2006; Natali *et al.*, 2011), perhaps through the acceleration of the microbial processes that release plant-available forms of N and P (Gao and Yan, 2019; Shaw and Cleveland, 2020), larger nutrient pools could support greater plant productivity which would mitigate the effects of rising greenhouse gas emissions.

The size of the plant-available N and P pools is determined by a balance of the biological and physiochemical processes that regulate inputs and losses of N and P in soil systems. Biological N-fixation, carried out by both symbiotic and free-living N-fixing bacteria, is the dominant pathway by which N enters terrestrial ecosystems (Vitousek *et al.*, 2013), with atmospheric N-deposition (Fowler *et al.*, 2013) and weathering of parent material (Houlton *et al.*, 2018) also contributing relatively small amounts of N to the soil system. P primarily enters terrestrial ecosystems through the weathering of mineral rocks

(Walker and Seyers, 1976; Vitousek, 2004). Once present in soil systems, mineralization of organic matter which releases inorganic forms of N and P, is the dominant pathway by which nutrients are recycled in terrestrial ecosystems. Rates of mineralization depend on the quality of litter inputs (Booth *et al.*, 2005; Parton *et al.*, 2007; Manzoni 2008), with lower quality inputs (higher C:N ratios) resulting in microbial immobilization of N and P, constituting a loss of N and P from the plant-available pool, instead of mineralization which releases labile forms of N and P to the soil system. Mineralization rates are also highly temperature-sensitive, where warmer temperatures kinetically accelerate the chemical and microbial reactions that mineralize dissolved organic nutrients (Sierra, 1997; Sardans *et al.*, 2006). Soil pH is also an important characteristic in regulating N and P inputs and losses. pH structures the soil bacterial community, which can affect the presence of N-fixing bacterial communities (Delgado-Baquerizo *et al.*, 2018), and P becomes biologically unavailable in highly acidic soils as base cations form precipitates with labile P compounds and tightly bind P to soil particles (Walker and Seyers, 1976; Vitousek, 2004). Finally, soil moisture and precipitation patterns regulate additional losses of N and P from terrestrial ecosystems. Negatively charged N and P compounds are repelled by negatively charged soil particles and are especially susceptible to leaching given ample amounts of precipitation (Perakis and Hedin, 2002), and moisture-saturated soils with low oxygen concentrations experience increased gaseous losses of N as N₂O through denitrification (Grosso *et al.*, 2000).

Warming can both directly and indirectly impact N- and P-availability by altering the controls on and rates of individual processes involved in terrestrial nutrient cycling. While increasing ambient temperatures will have direct consequences for the kinetic rates

of microbial and chemical processes (Melillo *et al.*, 2011; Bai *et al.*, 2013; Yue *et al.*, 2018; Shaw and Cleveland, 2020), indirect pathways by which warming will impact ecosystem function involve the response of plant communities and shifts in edaphic properties in response to changing climate. To this point, climate-driven changes to plant community diversity, especially if these changes involve shifts in the relative abundance of legumes associated with N-fixing bacteria, could certainly impact the available nutrient pool (Di Palo and Fornara, 2015; Moreau *et al.*, 2019; Liu *et al.*, 2021). Higher plant functional diversity has been shown to reduce soil N content due to increased plant uptake of N (Hooper and Vitousek, 1998; Niu *et al.*, 2010; Wei *et al.*, 2017).

Physiological changes to plant litter quality could also affect soil C:N and shift the dominant microbial nutrient transformation from mineralization to immobilization with higher soil C:N (Sardans *et al.*, 2008; Wang *et al.*, 2021), a net loss of N and P from the plant-available pool. Even absent changes to plant community diversity or physiology, warming could impact soil nutrient availability indirectly by altering soil pH (Wang *et al.*, 2014) and soil chemical stoichiometry (Billings and Ballantyne, 2013; Dijkstra *et al.*, 2012; Jiao *et al.*, 2016). Ultimately, the effects of climate change on plant-available nutrient pools will likely be shaped by background variation in local climatic, edaphic, and plant community characteristics and the response of above- and below-ground communities to climate change.

Here, we use a globally distributed network of climate change experiments in mountain ecosystems to reveal the direct and indirect effects of climate change on N- and P-availability. The warming and (species) removal in mountains (WaRM) network uses open-top warming chambers (OTCs) to implement a warming treatment, simulating the

direct effects of climate change, and removes the dominant plant species, altering plant community interactions to simulate the indirect effects of climate change, at a high and low elevation in mountain ranges around the world. Seven global locations are included in this study (Table 1). Alpine ecosystems are ideal for studying the effects of rising temperatures on nutrient availability as ecosystem function in mountains is often temperature limited, and alpine regions globally face a greater rate and magnitude of climate change than do other terrestrial ecosystems (IPCC, 2013; Sundvist *et al.*, 2013). Sites included in the WaRM network encapsulate a large amount of variation in climate as well as background edaphic and plant community characteristics (Table 1), allowing us to not only explore the effects of warming and shifts in species interactions on nutrient availability, but to also explore the context dependency of these effects. We hypothesize that warming will most strongly, directly impact N-availability due to the tight linkages between temperature and mineralization rates, while P-availability will be shaped indirectly by warming through warming-driven changes to soil edaphic properties. We also expect to find a large amount of variation in nutrient availability writ-large and in nutrient responses to warming and species removal treatments across the network given widespread variability in the biotic and abiotic characteristics that shape each site. This work will lend insight to the consequences of climate change for nutrient availability and will help reveal which ecosystem characteristics mediate the response of plant-available nutrients to the direct and indirect effects of climate change.

Results

Nitrogen-Availability

Linear regressions between N-availability and individual predictor variables revealed that the most important factor shaping N-availability, based on adjusted R^2 values, was mean summer temperature (Fig. 1, see SI Appendix Table S1 for full results from linear regressions/t-tests); N-availability was negatively correlated with mean summer temperature ($p < 0.001$), and temperature explained 7.2% of the variation in N-availability in experimental plots across the WaRM network. Despite a clear relationship with temperature, t-tests revealed that warming treatments had no discernible impact on N-availability ($p = 0.138$), nor did dominant species removal ($p = 0.212$). N-availability was significantly higher at low elevation locations across the seven global sites ($p = 0.023$). Total plant cover was positively correlated with N-availability ($p = 0.001$, $R^2 = 0.033$), while soil pH ($p = 0.008$, $R^2 = 0.019$) and soil C:N ($p < 0.001$, $R^2 = 0.059$) were negatively correlated with N-availability.

We evaluated three different structural equation models (SEMs) representing our hypotheses concerning the pathways by which climate shapes inorganic N-availability and P-availability globally: 1) warming and subsequent shifts in air temperature directly impact nutrient availability (Fig. 2A), 2) increases in air temperature directly impact nutrient availability and indirectly impact nutrient availability via shifts in total plant cover (Fig. 2B), and 3) increases in air temperature driven by warming directly impact nutrient availability and indirectly effect nutrient availability through shifts in plant cover and edaphic characteristics (Fig. 2C).

Our data on N-availability in response to climate change treatments in the WaRM network best supported our third hypothesis illustrated using SEMs, that warming both directly and indirectly influences nutrient availability predominantly via shifts in

edaphic properties (a composite variable comprised of the effects of pH and soil C:N) in response to increasing mean growing season temperatures (Fig. 3A; see SI Appendix Fig. S1 for SEM model fit for models representing hypotheses 1 and 2). Specifically, the best-fit SEM indicated that the strongest pathway by which warming and the subsequent increase in mean growing season temperatures impacts N-availability is through a direct, negative relationship between air temperature and N-availability (Fig. 3B). This direct effect of temperature on N-availability accounts for 92% of the total effect of temperature on N-availability, while the indirect effect of temperature on N-availability filtered by the negative relationship between temperature and edaphic properties and the much weaker, positive relationship between edaphic properties and N-availability accounts for the remaining 8% of the effect of temperature on N-availability. Total vegetative cover and removal, as a consequence, did not significantly shape N-availability despite a marginal, positive relationship between mean air temperature and total vegetative cover. The fixed effects in the SEM representing our third hypothesis explained 7% of the total variation in N-availability (marginal R^2), and the fixed and random effects in this model together explained 53% of variation in N-availability (conditional R^2), indicating that a large amount of variability in controls on N-availability exists across the seven WaRM network sites.

Potential evapotranspiration (PET), a site-level proxy for aridity across global locations in the WaRM network, explained 38% of residual variation in N-availability not accounted for by the best-fit SEM (Fig. 4A). A linear regression between PET, a variable calculated for each site that was derived from a database of geographically explicit climatic measurements (Harris *et al.*, 2020), and residuals in N-

variability from the best-SEM average for each field site revealed a positive, marginally significant relationship between aridity and N-availability ($p = 0.082$, Adjst. $R^2 = 0.38$, $F_{1,5} = 4.70$). In contrast, we did not find a relationship between the relative abundance of herbaceous plant species at the plot-level and residual variability in N-availability from the best-fit SEM (Fig. 4B; $p = 0.191$, Adjst. $R^2 = 0.00$, $F_{1,320} = 1.72$). Findings from these regressions further support the key result from our models of N-availability, that N-availability is most strongly shaped directly by climatic conditions, including mean growing season air temperatures that are explicitly impacted by warming and site-level aridity.

Phosphorus-Availability

Similar to N-availability analyses where we used t-tests and linear regressions to isolate the influence of individual predictor variables on nutrient availability, we found that warming ($p = 0.814$) and removal treatments ($p = 0.805$) had no discernible impacts on P-availability (Fig. 5). P-availability, like N-availability, was highest at low elevation locations across the WaRM network ($p < 0.001$), despite a significant negative relationship between mean summer growing season temperature and P-availability ($p = 0.006$, $R^2 = 0.024$). Total vegetative cover in experimental plots explained the most variation in P-availability, with results again showing a positive relationship between P-availability and vegetative cover ($p < 0.001$, $R^2 = 0.140$). Soil pH ($p = 0.004$, $R^2 = 0.026$) and C:N ($p < 0.001$, $R^2 = 0.065$) were again negatively correlated with P-availability. Full P-availability linear model results from regressions and t-tests are available in SI Appendix Table S2.

Our P-availability data once again best-supported the SEM representing our third hypothesis, that warming both directly and indirectly impacts P-availability (Fig. 3C; see SI Appendix Fig. S2 for SEM fit for hypotheses 1 and 2). In this model, the composite edaphic variable, comprised of the effects of soil pH and C:N on P-availability, most strongly influenced P-availability (Fig. 3D). In contrast to the SEM describing pathways by which warming impacts N-availability, the best-fit SEM for P-availability revealed that warming and the subsequent increase in growing season temperatures predominantly influences P-availability indirectly through the negative relationship between temperature and edaphic properties and the positive relationship between edaphic properties and P-availability. The positive, direct effect of warming on P-availability, while only marginally significant, partially counteracted the negative, indirect effect of warming on P-availability. The competing direct and stronger indirect effects of warming resulted in a weak but positive total effect of temperature (direct + indirect effects) on P-availability. The removal treatment and total vegetative cover had no discernible impact on P-availability, as was the case in the best-fit N-availability SEM. Fixed effects in the best-fit P-availability SEM explained 6% of the variation in P-availability, while the fixed and random effects together explained 42% of the total variation in P-availability, again indicating high variability in controls on P-availability across field sites in the WaRM network.

The relationship between residual variation in P-availability from the best-fit SEM and PET was negligible, in contrast to results from N-availability models (Fig. 4C; $p = 0.964$, Adjst. $R^2 = -0.25$, $F_{1,4} = 0.00$). However, we found a significant positive relationship between P-availability SEM residuals and the relative abundance of

herbaceous plants within each experimental plot (Fig. 4D; $p = 0.002$, Adjst. $R^2 = 0.03$, $F_{1,273} = 9.56$). The results from these linear regressions again support our SEM findings, where the direct relationship between climate and P-availability is weak to negligible, but a strong indirect relationship exists between warming and P-availability via shifts in above- and below-ground characteristics. The dominance of the indirect pathway of warming effects on P-availability stands in contrast to the strong direct effects of warming on N-availability, possibly signaling differences in the relative importance of abiotic vs. biotic controls on N and P cycling individually.

Discussion

Our results from both SEM models and linear regressions indicate that temperature directly impacts N-availability, but the relationship between temperature and N-availability is surprisingly negative, in contrast to our hypothesis. P-availability was indirectly impacted by temperature, and SEM analyses revealed that the effect of temperature on P-availability is mediated by the relationship between temperature and soil edaphic properties. While temperature was the single most important variable in explaining network-wide variation in N-availability, total vegetative cover explained the most variation in P-availability, again highlighting the direct climatic linkages that shape N-availability vs. the indirect pathways by which climate impacts P-availability. We found clear relationships between mean summer air temperature, total vegetative cover, soil pH, and soil C:N and N- and P-availability despite a large amount of variation in the climatic, edaphic, and vegetative characteristics that shape each site in this global network of climate change experiments.

Both N- and P-availability were highest in acidic soils. While this result runs counter to prevailing theory surrounding P-dynamics, where phosphate ions are often occluded by iron and aluminum ions that are mobilized in acidic soils (Walker and Seyers, 1976; Vitousek, 2004), this relationship could be a result of the underlying geology in these alpine ecosystems. In alkaline soils, phosphate ions can become occluded in calcium precipitates, and many micronutrients such as magnesium and zinc also become sorbed to mineral surfaces (Neina, 2019). Acid-phosphatase, an important enzyme that degrades organic molecules containing P to release inorganic P into the soil solution, is optimally efficient in acidic soils (Sinsabaugh *et al.*, 2008); increased P-availability in acidic soils might therefore indicate that the activity of enzymes like acid-phosphatase mediate the size of the available-P pool. Nitrification, an important N-transformation that produces nitrate ions, also releases H^+ to the soil solution, contributing to soil acidification as this species of inorganic N becomes more abundant.

We also found that N- and P-availability increase with greater plant cover, with plant cover explaining the largest amount of variation in P-availability of any single predictor variable explored in this study. In mountain environments often characterized by high-disturbance and high-stress, this relationship between nutrient availability and plant cover could stem from plant facilitative dynamics, where greater plant cover creates microclimatic refugia, fostering conditions that are optimal for the microbial activity that supplies available-nutrients to the soil system (Wright *et al.*, 2017). Furthermore, the positive effects of plant cover on nutrient availability might stem from rhizosphere priming, where the contribution of simple sugars from root exudates and the production of extracellular enzymes by mycorrhizal associates stimulates microbial decomposition

of organic substrates and the release of inorganic nutrients (Dijkstra *et al.*, 2013). Both N- and P-availability declined with larger soil C:N ratios, a result that is in line with current ecological theory that suggests that lower quality soil substrates lead to microbial immobilization of nutrients instead of the release of available soil nutrients through microbial mineralization (Sardans and Estiarte, 2008; Wang *et al.*, 2021).

While N-availability across the WaRM network exhibited a strong relationship with temperature, as hypothesized, the negative direction of this relationship is rather counterintuitive given evidence of accelerated rates of nutrient transformations in warmer temperatures (Bai *et al.*, 2013). We speculate that this negative relationship between N-availability and temperature and the positive relationship between N-availability and PET could be a result of decreased plant uptake of soil N in cooler, drier climates. Plant-uptake of N is essentially a loss of N from the soil available-N pool, so a reduction in plant-uptake in climatic conditions that are traditionally seen as unfavorable for plant growth could result in more N in the soil solution that could be bound to the resin nutrient strips. Drier conditions could also limit leaching, an additional loss of soil nutrients from the soil available nutrient pool that predominantly affects negatively charged nutrients like nitrate and phosphate. A meta-analysis of warming effects on N pools and fluxes (Bai *et al.*, 2013) found highly variable effects of warming on inorganic N pools, despite consistent positive effects of warming on N fluxes like N-mineralization. The results of this metanalysis together with our results may indicate that rates of microbial immobilization of N or plant N uptake determine whether higher N-mineralization rates in a warmer world translate to greater soil inorganic N-availability,

i.e. rates of N losses determine the final pools in which added N contributed from greater rates of N-mineralization ultimately accumulate.

While temperature has a direct negative relationship with N-availability, as evidenced by the linear regressions presented in Fig. 2, the dominant pathway by which warming impacts P-availability is indirect, mediated by the relationship between temperature and soil pH and C:N. By analyzing the relationships between temperature and the parameters that most strongly shape P-availability (total vegetative cover, soil pH, and soil C:N), we find that rising temperatures negatively impact P-availability by exacerbating conditions that result in lower P-availability such as higher soil pH, lower plant cover, and higher soil C:N ratios (SI Appendix Fig. S3).

Because of the nuanced ways in which warming affects N- vs. P-availability, climate change could decouple N and P cycles in mountain ecosystems hinging on the effect of climate change on the edaphic and vegetative characteristics that mediate the relationship between climate and P-availability (Dijkstra *et al.*, 2012). Because N and P are co-limiting to primary productivity (Harpole *et al.*, 2011), the divergent mechanisms that determine the effect of climate change on soil nutrients could limit the capacity of primary productivity in alpine grasslands to serve as a negative feedback to climate change. Some ecosystems will experience synergies where climate impacts availability of both nutrients in the same way, but if warming were to constrain availability of one or both nutrients, any positive effects of warming on the availability of a single nutrient will be diminished (Vitousek *et al.*, 2010). Our results highlight the importance of considering multiple pathways of climate change impacts and indicate that ecosystems that differ in background climate, vegetation, and edaphic properties will

likely experience contrasting and highly localized effects of and responses to climate change in mountain ecosystems around the world.

Materials and Methods

Experimental Design

In order to understand how climate change impacts the structure and function of alpine ecosystems globally, we established the warming and (species) removal in mountains (WaRM) network of climate change experiments in ten different mountain ranges around the world (Sundqvist *et al.*, 2020). Seven of these sites, located in Argentina, Canada, Greenland, New Zealand, Sweden, Switzerland, and the United States of America are included in this study (Table 1). At a high and low elevation at each site, we established a series of climate change treatments that impose the direct (shifts in ecosystem function caused by abiotic warming) and indirect effects of climate change (shifts in ecosystem structure and function caused by changes to the plant community in response to climate change) in 2 m x 2 m plots. We established a warming treatment, reflecting the direct impact of a warmer climate on plant and soil communities, by erecting hexagonal open-top warming chambers (OTCs) comprised of six trapezoid-shaped plexiglass panels; erected chambers had a ground-level diameter of 170 cm. To experimentally implement the indirect effect of climate changes via shifts in plant community structure, we imposed a removal treatment where the dominant plant species at each elevation was removed by clipping all aboveground biomass of the dominant species to the soil surface. Dominance was defined as the plant species that covered the greatest amount of surface area in the control plots across each elevation within a global site. A warming x removal treatment was also established, where plots received both the

warming and species removal treatments to understand the interactive effects of simultaneous warming and plant community shifts. Control plots, which received neither treatment, were also established and monitored. All four treatments were replicated eight times in a full-factorial design except for at the Swedish site, where treatments were replicated five times at both elevations. For this study, only five replicates of each treatment are included for the USA high elevation site due to a deep snow-bed deposited by an avalanche that covered the remaining plots for the entirety of the sampling period.

Measuring Soil Nutrient Availability Using Resin Strips

In order to measure the impact of warming and shifts in plant species interactions on soil nutrient availability, we installed ion-exchange resin membrane strips in WaRM network plots during the summer of 2019 (summer 2018-2019 for Southern Hemisphere sites) (Kivlin *et al.*, 2018; Hovenden *et al.*, 2008). As opposed to bulk soil extractions which tend to overestimate the size of soil inorganic N and P pools and don't account for physiochemical constraints that might limit the fraction of soil nutrients that are effectively bioavailable, the use of resin strips provides a better estimate of bioavailable nutrients by simulating passive root uptake of nutrients from the surrounding soil (Cain *et al.*, 1999; Lajtha *et al.*, 1999). Nutrient concentrations extracted from resin strips therefore reflect the pool of nutrients that were available for plant uptake during the period in which resin strips were incubated *in situ* in experimental plots. Resin strips, measuring 6 cm x 1 cm, were cut from sheets of cation and anion ion-exchange membrane (Membranes International Inc., Ringwood, NJ, USA) and a plastic cable-tie was attached to each membrane through a circular hole punctured into the top of the membrane strips with a standard paper hole punch (hole diameter: 6.35 mm).

After cutting, anion resin strips were soaked in a 0.5 M NaHCO_3 solution to activate the membranes, and cation resin strips were soaked in a 0.5 M NaCl solution for 24 hours. All membranes were prepared at the University of Vermont, and anion and cation membranes were shipped to field sites in separate plastic bags containing a small amount of deionized water to prevent the strips from drying out before field deployment. Three cation resin strips were deployed per plot to measure ammonium (NH_4^+) availability, three anion strips were deployed per plot to measure nitrate availability (NO_3^-), and three additional anion strips per plot were deployed to measure P-availability. Resin strips deployed in New Zealand were constructed from a different variety of ion exchange membrane (anion and cation exchange membranes, VWR International LLC, Radnor, PA, USA), and phosphorus availability was not measured at this site. A laboratory incubation where resin strips of the variety used in New Zealand and resin strips of the variety used in the rest of the network were incubated in 10 ppm solutions of NH_4^+ and NO_3^- to determine a conversion factor that could be used to convert nutrient concentrations derived from membranes deployed in New Zealand to comparable concentrations found using the membrane deployed at all other sites. All resin strips were inserted into the soil so that the membrane was completely submerged in soil at the beginning of the growing season when warming chambers were erected, and resins were harvested from plots at the peak of the growing season, when plant biomass was greatest, usually amounting to a 4-6 week incubation period.

To measure NH_4^+ availability, all cations from a single plot were extracted together in 40 mL of 2.0 M KCl to capture nutrient availability across the entire expanse of the plot. Likewise, three anion resin strips from a single plot were extracted together in

40 mL of 2.0 M KCl to measure NO_3^- availability, and the remaining three anion resin strips deployed in each plot were extracted together in 40 mL of 1.0 M HCl to measure P-availability. Concentrations of NH_4^+ in the corresponding cation resin extracts were determined colorimetrically using the sodium salicylate reagent method (Forster, 1995), concentrations of NO_3^- in the corresponding anion resin extracts were determined colorimetrically using the vanadium chloride reagent method (Doane and Horwath, 2003), and concentrations of available P were measured in the corresponding HCl resin extracts using an inductively coupled plasma spectrophotometer (ICP-Optical Emission Spectrophotometer Avio 200, Perkin Elmer, Waltham, MA, USA). We report both the availability of inorganic N- (NH_4^+ and NO_3^-) availability and P-availability in units of micrograms of nutrients per cm^2 of resin stick surface area per week of incubation (μg nutrient $\text{week}^{-1} \text{ cm}^{-2}$).

Climate, Soil, and Plant Community Measurements

In order to understand the factors that control nutrient availability in alpine ecosystems globally, we collected several datasets that characterize the climatic, edaphic, and vegetative characteristics of each site. To measure air temperatures in each plot, we installed iButton temperature loggers (Thermochron DS1921G iButton, Maxim Integrated Products, Inc., San Jose, CA, USA) 10 cm above the soil surface attached to pin flags and covered with reflective material to shade the iButtons from UV radiation in each plot (Sundqvist *et al.*, 2020). Temperature loggers recorded the air temperature every ninety minutes, and air temperatures for each plot were averaged across the entire growing season to yield mean growing season temperature. If plot-level temperature data was not available for the 2019 growing season, temperature data was used from a

previous year during which the summer climate at that location most closely resembled the climate of 2019 (estimated using the Climatic Research Unit (CRU) database, Harris *et al.*, 2020) in order to capture network-wide variation in growing season temperatures and the magnitude of warming effects at each site. CRU data were also used to calculate potential evapotranspiration (PET) at each site, used as a proxy for aridity that was used to contextualize trends in climate impacts on nutrient availability revealed at each site.

To measure soil C:N content and soil pH, four 2.5 cm diameter x 5 cm deep soil cores were collected from each plot, pooled together, and sieved using a 4 mm sieve. Soils were air-dried at each site before shipping soils to the University of Vermont, where samples were ground to fine a powder using a ball-mill grinder (Mini-Beadbeater-96, BioSpec Products, Inc., Bartlesville OK, USA) and soil C:N content was measured using a LECO CHN628 analyzer (LECO Corporation, Saint Joseph, MI, USA). Soil pH was also measured on air-dried soil by combining 10 g of air-dried soil with 30 mL of 0.01 M CaCl₂ to create a soil slurry (Little, 1992). Plant community cover, where the proportion of the plot surface area covered by each individual plant species as well as the cumulative area covered by bryophytes and lichen is recorded, was measured at the peak of the growing season in a 70 cm diameter circle in the center of each plot to eliminate any edge-effects impacting plant community dynamics. The relative abundance of herbaceous plant species was calculated by adding the percent of each plot occupied by legumes, forbs, and graminoids and dividing this sum by the total cover of plant species from all growth forms.

Structural Equation Modeling

We used a series of structural equation models (SEMs) to explore the pathways by which warming directly and indirectly, via shifts in plant community and edaphic properties, affects nutrient availability in alpine ecosystems globally (Fig. 2A-2C). First, in order to detect and remove outliers from samples that were likely contaminated during the extraction process and therefore exhibit extremely high nutrient availability, we employed a generalized ESD test to determine the likelihood that suspected outliers are drawn from the same distribution as the rest of the nutrient availability data (calculated for NH_4^+ , NO_3^- , and P separately) within a single site (Denton *et al.*, 2017; Rosner, 1983). Confirmed nutrient availability outliers at the higher end of each site-level data were assumed to be contaminated and were removed from all analyses. Each of the three hypothetical models described in Fig. 2A-2C were fit separately to the datasets for inorganic N- and P-availability. All pathways in each of the three SEMs were incorporated into the SEM as linear mixed effect models which include a random intercept for site, allowing us to control for site-level differences in nutrient availability that are not explicitly included in the model. Our most complex model which incorporates the influence of soil characteristics includes a composite variable for edaphic properties. This composite variable is comprised of both soil pH and soil C:N content and was constructed by first verifying that soil pH and soil C:N are both negatively related to availability of both inorganic N and P-availability. The edaphic properties composite variable was then calculated by weighting the raw value for soil pH and soil C:N measured within each plot by the magnitude of the relationship between each individual variable and inorganic N- and P-availability. Weights were derived from multiple linear regressions describing the effect of pH and soil C:N on inorganic N, and

separately, P-availability, where the slope estimates for soil C:N and soil pH were used as the weighting terms in composite variable construction. Edaphic property composite variables were calculated separately for inorganic N- and P-availability. The natural log transformation was used for inorganic N- and P-availability throughout SEM analyses, including in the construction of the edaphic composite variable, to satisfy assumptions of normality. Among the three hypothetical models, we identified the model and corresponding hypothesis that was best supported by our data for inorganic N- and P-availability based on the model that resulted in the highest marginal R^2 (describes variation explained only by the fixed effects in the model) and the conditional R^2 (describes variation explained by both the fixed and random effects in each model).

We analyzed linear relationships between SEM residuals from the best-fit models explaining variation in inorganic N- and P-availability and site-level PET estimates for the 2019 growing season to understand how aridity might mediate the response of nutrient availability to warming and plant removal treatments. In conjunction with this analysis of the influence of climate, we also analyzed the relationship between SEM residuals and the proportion of total plant cover constituted by herbaceous plant species in each plot to understand how vegetative characteristics mediate the impact of our climate change treatments on nutrient availability.

Isolated Linear Relationships Explaining Nutrient Availability

To understand the isolated impact of warming, dominant species removal, soil pH and C:N, and total plant cover on N- and P-availability, we conducted separate linear

regressions between each nutrient and single predictor variables, separately. N- and P-availability were transformed to normality using a natural log transformation.

All statistical analyses were conducted in R version 4.0.5 “Shake and Throw” (R Core Team) with use of the *piecewiseSEM* (Lefcheck, 2016) and *nlme* (Pinheiro *et al.*, 2021) packages.

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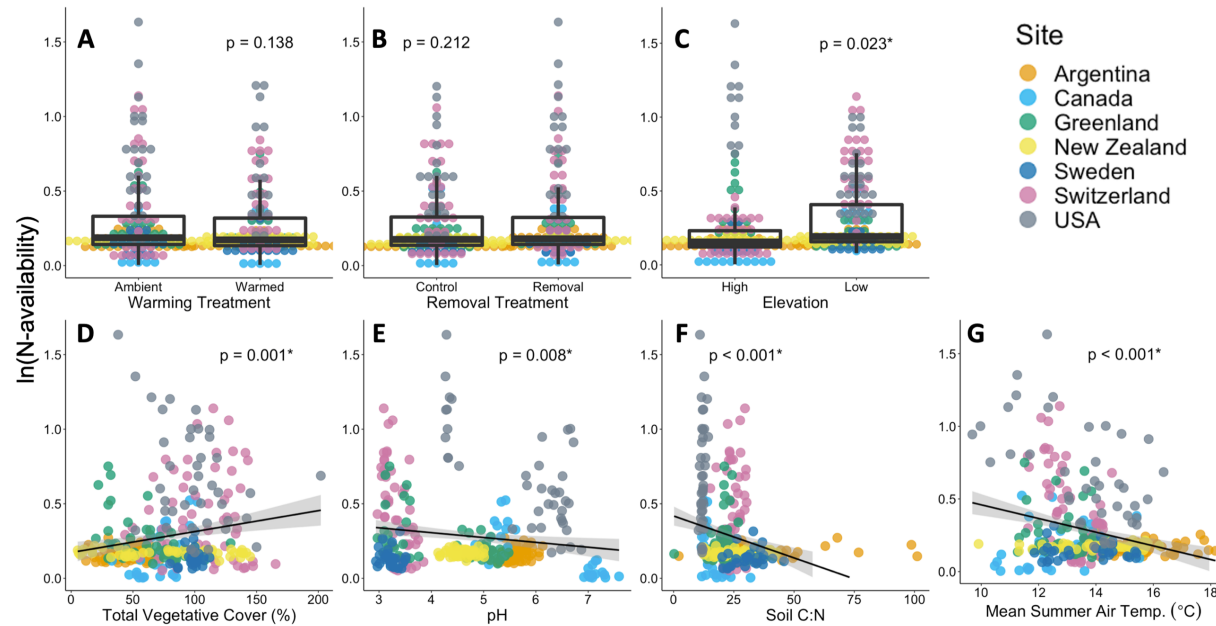
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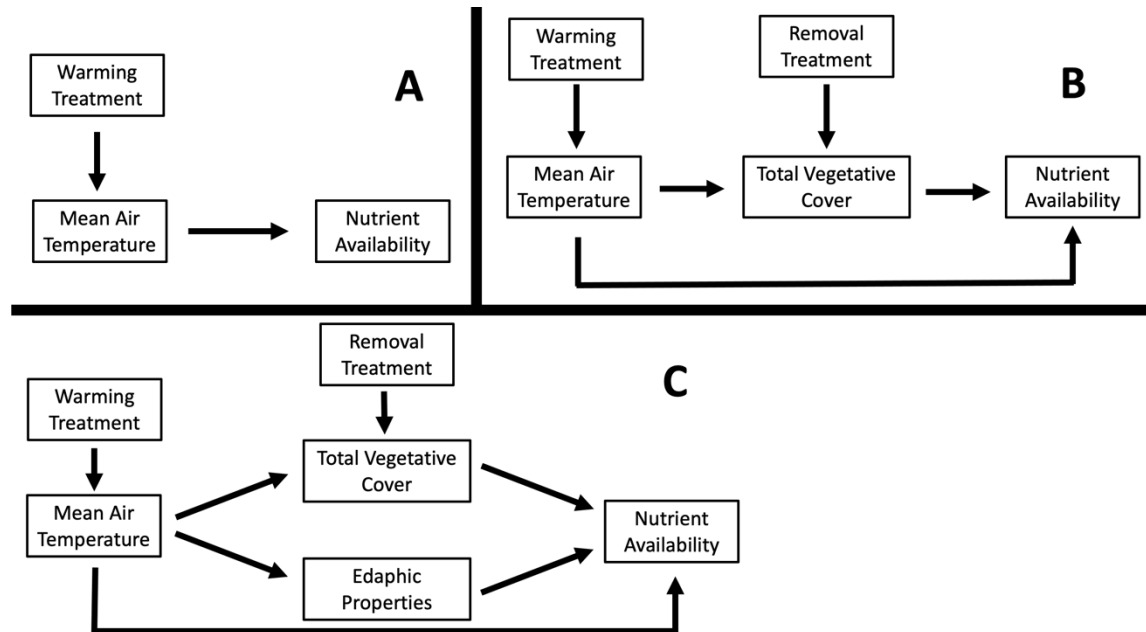
Figures and Tables

Figure 1.



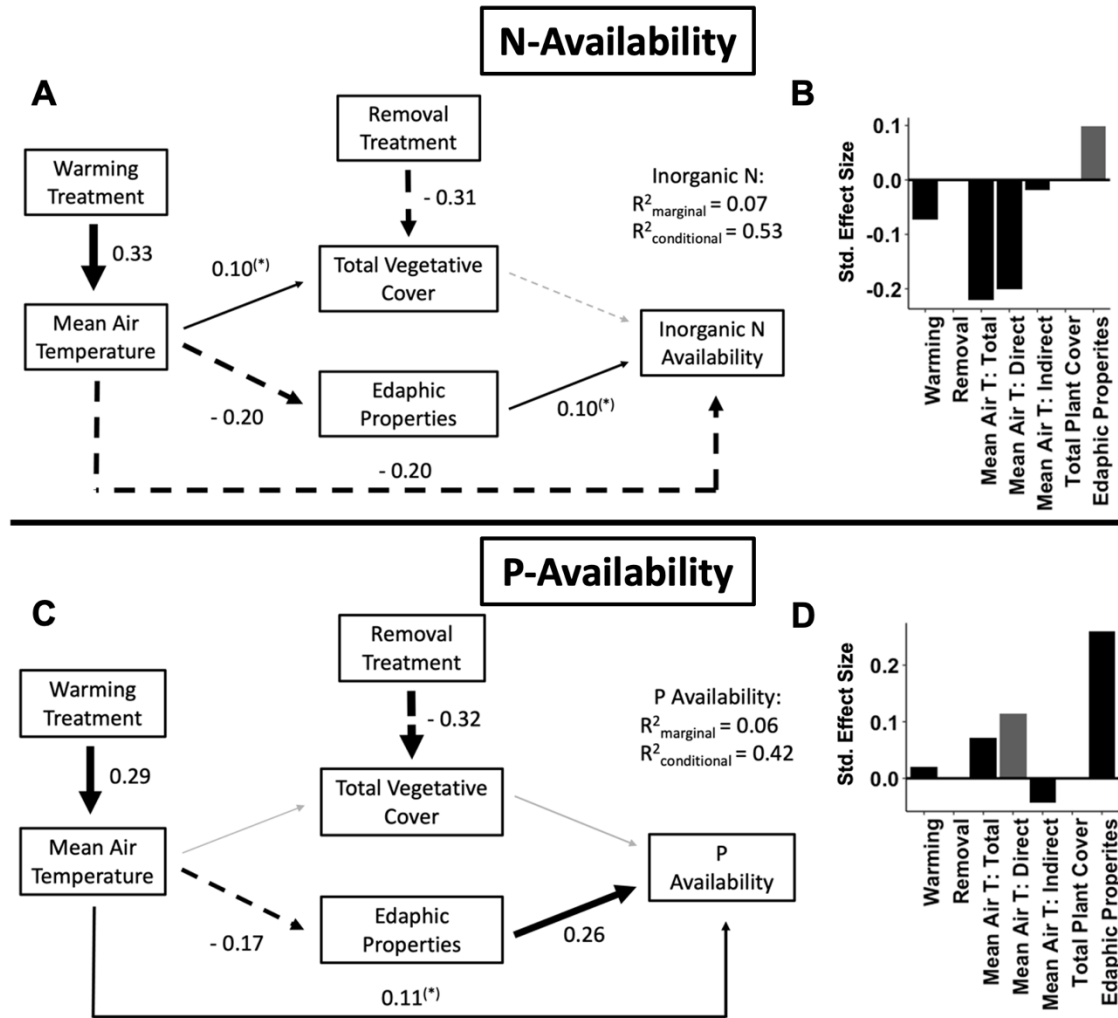
T-tests revealed that A) warming and B) removal had no significant effect on N-availability, while C) N-availability was greatest at low elevations. Linear regressions revealed D) a positive relationship between total vegetation cover and N-availability and negative relationships between E) pH, F) soil C:N, and G) mean summer air temperature and N-availability.

Figure 2.



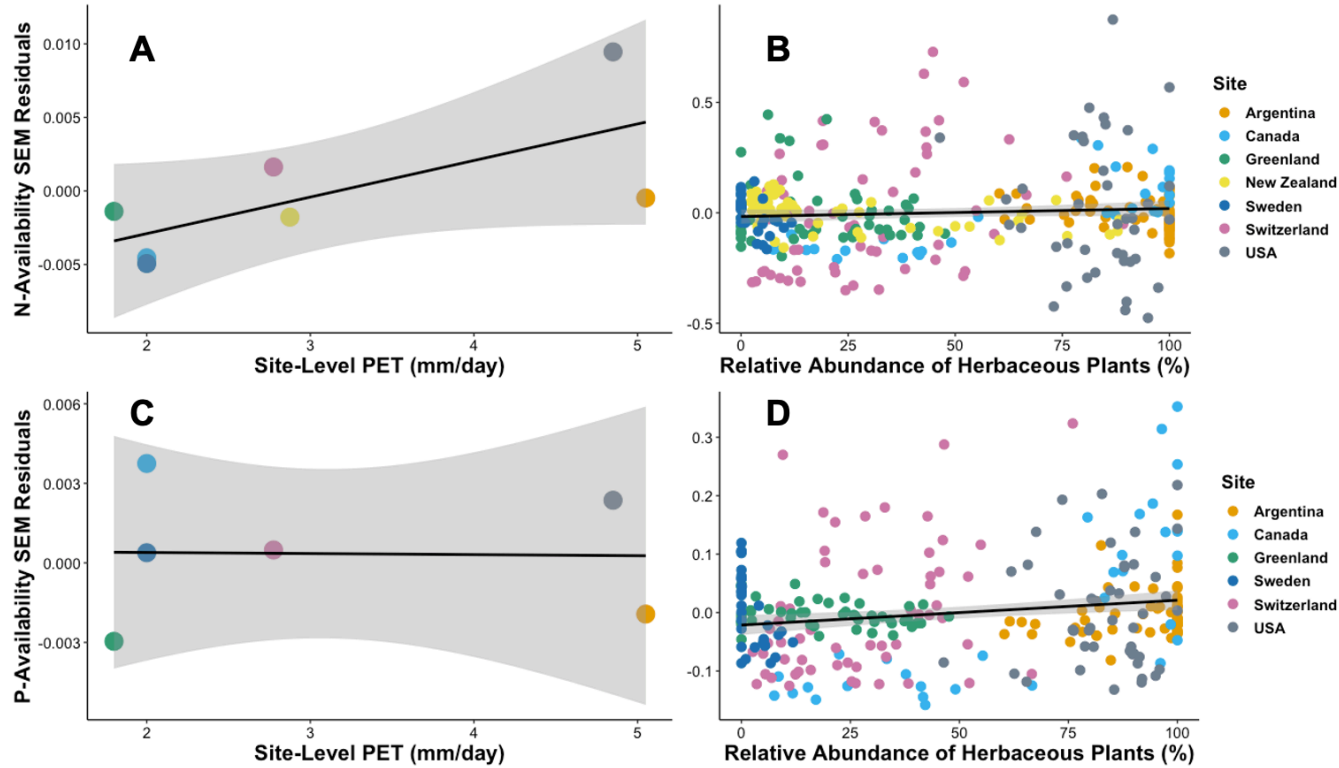
Hypothetical SEMs that represent three separate hypotheses regarding the pathways by which warming and subsequent changes in temperature might directly (A) or indirectly via shifts in plant community dynamics (B) or indirectly via shifts in edaphic properties (C) impact nutrient availability.

Figure 3.



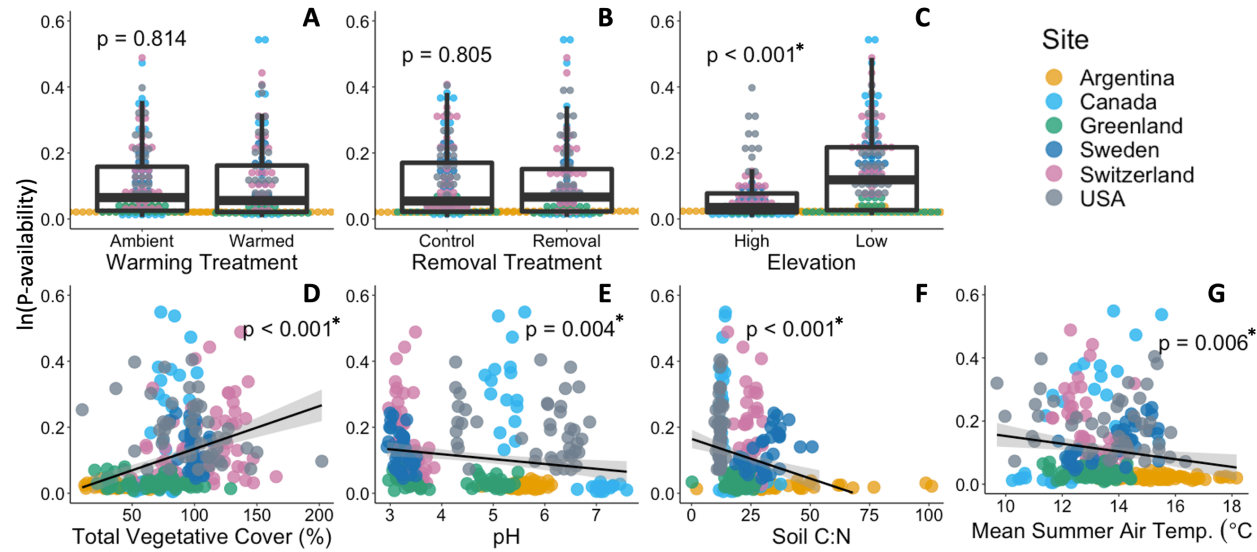
Best-fit SEMs describing the impact of warming and shifts in plant species interactions on A) inorganic N-availability and C) P-availability. Solid black lines indicate significant positive relationships, while dashed black lines indicate that the connected variables are significantly, negatively linked. Gray lines indicate insignificant relationships. Coefficients listed above each pathway indicate the standardized effect size of the relationship between the connected variables. Coefficients followed by (*) indicate marginally significant pathways ($0.10 > p > 0.05$). Standardized effect sizes are shown for each parameter in the B) N-availability model and C) P-availability model. Black bars indicate significant pathways ($p < 0.05$) and gray bars indicate marginally significant pathways ($0.10 > p > 0.05$).

Figure 4.



Linear relationships between residual variation in N-availability from the best-fit SEM and site-level PET (A) and the relative abundance of herbaceous plants (B), and linear relationships between residual variation in P-Availability from the best-fit SEM and site-level PET (C) and the relative abundance of herbaceous plants (D). For PET regressions, N- and P-availability residuals were averaged by site in order to match the scale of PET measurements, which were derived from a global climate dataset (Harris *et al.*, 2020) for each field site location.

Figure 5.



T-tests revealed that A) warming and B) removal had no significant effect on P-availability, while C) P-availability was greatest at low elevations. Linear regressions revealed D) a positive relationship between total vegetation cover and P-availability and negative relationships between E) pH, F) soil C:N, and G) mean summer air temperature and P-availability.

Table 1. Geographic locations, climatic characteristics, and information on experimental treatments for the seven WaRM network sites included in this study

Country	Year of establishment	Elevation (m a.s.l.)	Latitude	Longitude	MST (°C)	MSP (mm)	Dominant vascular plant species (removed)	Growth form
Sweden	2014	894	68.294	19.099	9.7	300	<i>Empetrum hermaphroditum</i>	Woody evergreen
		498	68.314	19.163	12.9	300	<i>Empetrum hermaphroditum</i>	Woody evergreen
Greenland	2015	450	61.155	-45.379	11.8	244	<i>Betula glandulosa</i>	Woody deciduous
		50	61.183	-45.370	12.8	264	<i>Betula glandulosa</i>	Woody deciduous
Canada	2015	1900	60.954	-138.423	11.0	186	<i>Carex consimilis</i>	Sedge
		1431	60.979	-138.408	12.5	186	<i>Salix reticulata</i>	Woody deciduous
Switzerland	2014	2353	46.774	9.857	7.95	453	<i>Vaccinium uliginosum</i>	Woody deciduous
		2101	46.775	9.863	7.22	453	<i>Vaccinium uliginosum</i>	Woody deciduous
USA	2013	3460	38.992	-107.067	10.9	151	<i>Juncus drummondii</i>	Sedge
		2740	38.715	-106.823	14.9	143	<i>Wyethia x magna</i>	Forb
Argentina	2016	1321	-41.654	-71.073	14.2	62	<i>Acaena splendens</i>	Woody
		772	-40.998	-71.088	15.5	71	<i>Papostipa speciosa</i>	Grass
New Zealand	2015	1611	-39.278	175.626	12.4	150	<i>Gaultheria collensoi</i>	Woody
		1071	-39.294	175.726	14.5	150	<i>Calluna vulgaris</i>	Woody

MST = Mean Summer Temperature

MSP = Mean Summer precipitation

Appendix

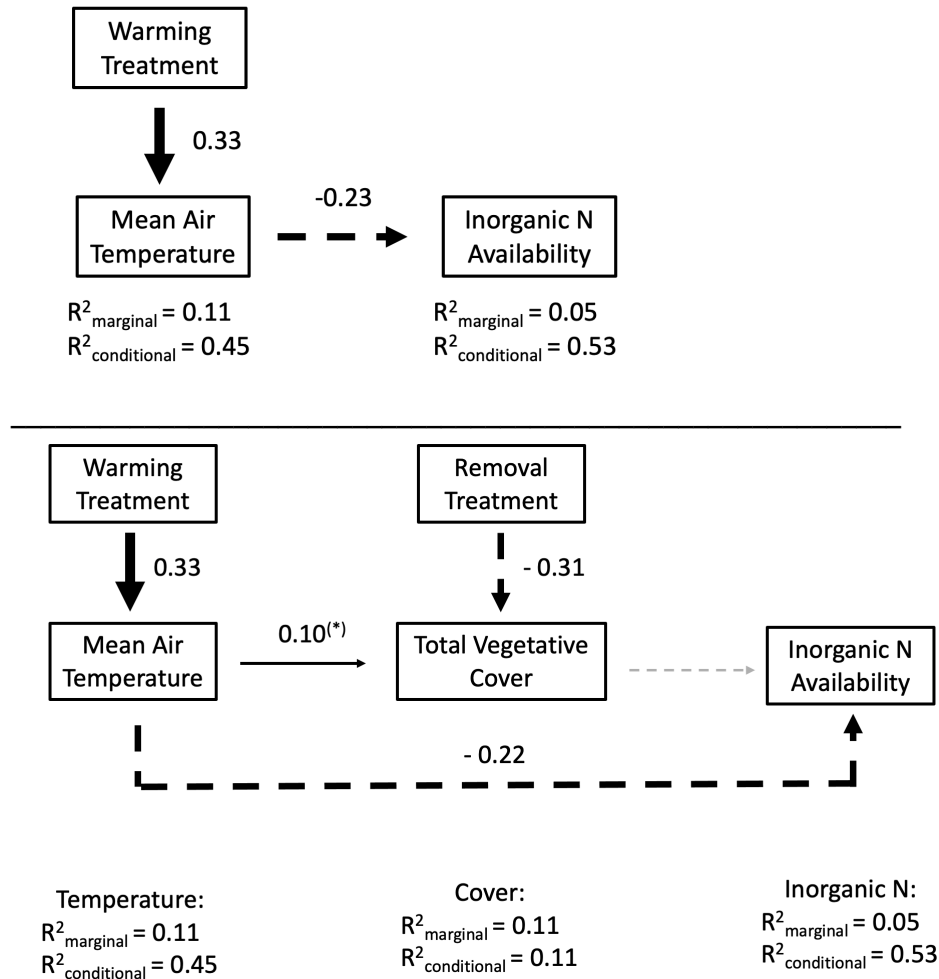


Figure S1. Inorganic N-availability data fit to SEMs representing A) the hypothesis that warming only directly influences inorganic nitrogen availability and B) that warming both directly and indirectly impacts inorganic N availability via shifts in total vegetative cover. Solid black lines indicate significant positive relationships, while dashed black lines indicate that the connected variables are significantly, negatively linked. Gray lines indicate insignificant relationships. Coefficients listed above each pathway indicate the standardized effect size of the relationship between the connected variables. Coefficients followed by (*) indicate marginally significant pathways ($0.10 > p > 0.05$).

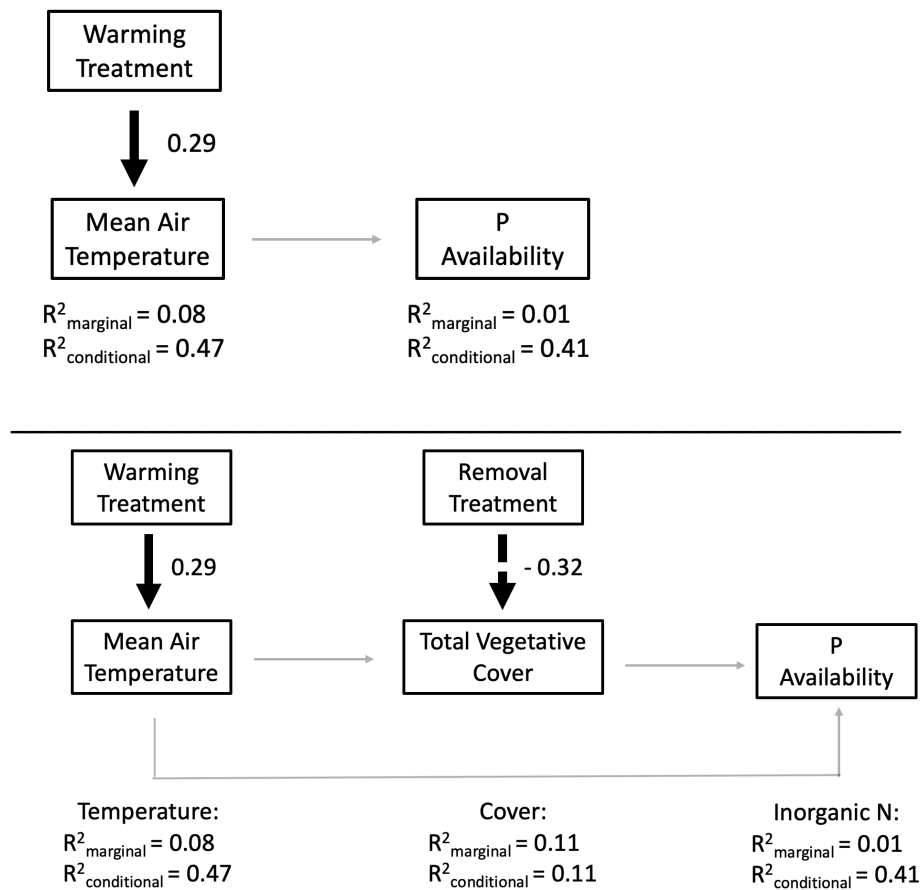


Figure S2. P-availability data fit to SEMs representing A) the hypothesis that warming only directly influences inorganic nitrogen availability and B) that warming both directly and indirectly impacts P availability via shifts in total vegetative cover. Solid black lines indicate significant positive relationships, while dashed black lines indicate that the connected variables are significantly, negatively linked. Gray lines indicate insignificant relationships. Coefficients listed above each pathway indicate the standardized effect size of the relationship between the connected variables. Coefficients followed by (*) indicate marginally significant pathways ($0.10 > p > 0.05$).

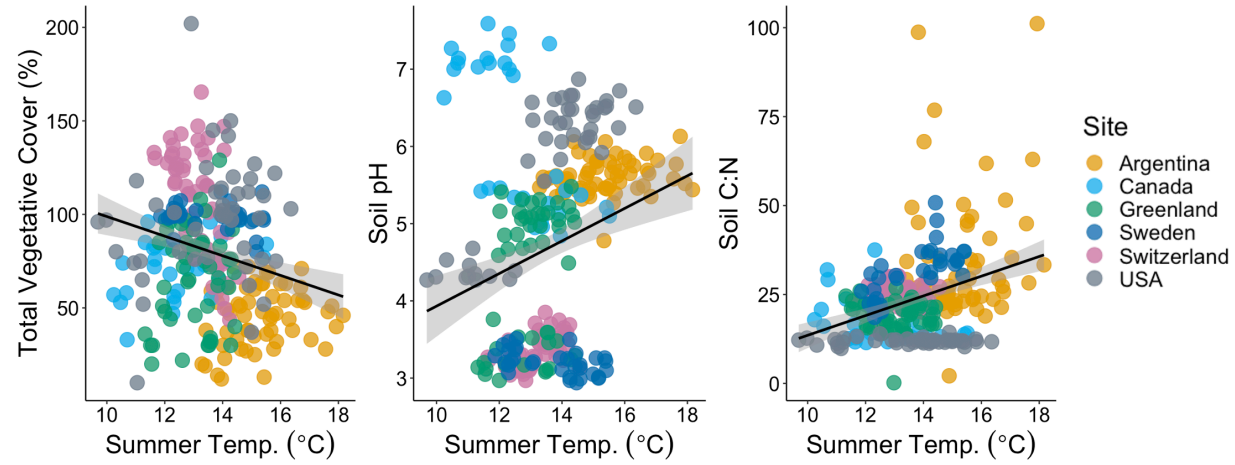


Figure S3. Mean summer air temperature is correlated with total vegetative cover ($p < 0.001$, $F_{273} = 16.94$, $R^2 = 0.055$), soil pH ($p < 0.001$, $F_{273} = 17.46$, $R^2 = 0.0570$), and soil C:N ($p < 0.001$, $F_{273} = 36.09$, $R^2 = 0.114$) in directions that create conditions that exacerbate P-limitation.

Table S1. Model results from linear regressions and t-tests analyzing the relationship between N-availability (transformed using natural log) and warming treatments, removal treatments, elevation (high or low), total vegetative cover, mean growing season air temperature, soil pH, and soil C:N.

Parameter	<i>F</i>	Degrees of Freedom	<i>p</i>	R ²
Total Vegetative Cover	11.87	320	0.001	0.033
soil pH	7.20	320	0.008	0.019
soil C:N	21.23	320	< 0.001	0.059
Mean Summer Temp.	25.8	320	< 0.001	0.072

t-Tests

Parameter	<i>t</i>	Degrees of Freedom	<i>p</i>	Response Ratio*
Warming	1.49	311.62	0.138	0.86
Removal	-1.25	295.5	0.212	1.14
Elevation	-2.28	293.5	0.023	0.79

* Response ratio for warming treatment = mean ln(N) in warmed plots / ambient plots

Response ratio for removal treatment = mean ln(N) in removal plots / control plots

Response ratio for elevation = mean ln(N) in high elevation plots / low elevation plots

Table S2. Model results from linear regressions and t-tests analyzing the relationship between P-availability (transformed using natural log) and warming treatments, removal treatments, elevation (high or low), total vegetative cover, mean growing season air temperature, soil pH, and soil C:N.

Linear Regressions

Parameter	<i>F</i>	Degrees of Freedom	<i>p</i>	R ²
Total Vegetative Cover	45.76	273	< 0.001	0.14
soil pH	8.26	273	0.004	0.026
soil C:N	20.12	273	< 0.001	0.065
Mean Summer Temp.	7.601	273	0.006	0.024

t-Tests

Parameter	<i>t</i>	Degrees of Freedom	<i>p</i>	Response Ratio*
Warming	-0.24	261.54	0.814	1.03
Removal	-0.25	272.65	0.805	1.03
Elevation	-6.87	243.32	< 0.001	0.43

* Response ratio for warming treatment = mean ln(N) in warmed plots / ambient plots

Response ratio for removal treatment = mean ln(N) in removal plots / control plots

Response ratio for elevation = mean ln(N) in high elevation plots / low elevation plots

WARMING REDUCES THE QUANTITY AND QUALITY OF LIVESTOCK FORAGE RESOURCES IN A COLORADO RANGELAND

Abstract

1. Rangelands provide numerous ecosystem services that support an estimated 30% of the global population. Sustainability of forage resource production in rangelands requires dynamic management of grazing pressure in order to adapt to changes in the quantity and nutritive quality of vegetation due to the threat posed by climate change in order to prevent long-term degradation of rangeland resources.
2. In order to explore the impact of climate change on forage quantity and quality in a semi-arid rangeland in the Gunnison National Forest, Colorado, USA, we measured changes in crude protein content and the abundance of key forage plant species for cattle in response to warming and dominant plant species removal treatments.
3. Our results revealed that community weighted crude protein content declined by 12% in response to warming, while plant species removal and the interaction between warming and removal treatments had only marginal effects on crude protein content at the community scale.
4. Warming had no discernible impact on total abundance of palatable plant species, but we found a subtle decrease in the relative cover of the highest-value forage

species while the relative cover of unpalatable or poisonous plant species exhibited a slight increase with warming.

5. *Policy implications:* In order to prevent overgrazing and the long-term degradation of rangelands in a warmer world, managers should consider reducing livestock stocking rates to mirror declines in forage nutritional quality as well as changes in the more-commonly monitored changes to forage biomass.

Introduction

Rangelands make up 53% of the terrestrial land area and provide a myriad of important ecosystem services that support an estimated 30% of the global population (Sala *et al.*, 2017). Services provided by rangeland ecosystems span all four main categories of ecosystem services (Millennium Assessment, 2005), including provisioning services such as the production of forage and freshwater, regulating services such as carbon sequestration and erosion control, cultural services such as hunting and recreational opportunities as well as cultural heritage, and supporting services most closely tied to ecology such as nutrient cycling and primary productivity (Sala *et al.*, 2017). Despite this diverse portfolio of services supplied by rangelands, only the provisioning services that provide forage to support the production of goods like meat, leather, and wool, hold market value, creating a tendency to prioritize rangeland management strategies centered on delivery of forage production for livestock (Sala *et al.*, 2017). Ensuring the long-term sustainability of the supply of ecosystem services like forage production requires striking a balance between the consumption of benefits and

prevention of long-term resource degradation (Teague and Kreuter, 2020), a balance that is further threatened by climate change.

Warming in particular can affect the quantity *and* quality of forage resource production and can drive long-term changes in the structure of rangeland plant communities. Because climatic warming exacerbates aridity by reducing soil moisture in arid and semi-arid regions (Xu *et al.*, 2013), several warming experiments conducted in water-limited ecosystems found that warming decreases aboveground biomass across the entire plant community (Elmendorf *et al.*, 2012; Brookshire and Weaver, 2015; Winkler *et al.*, 2016; Li *et al.*, 2018). A common plant physiological adaptation to heightened aridity with warming is to allocate more resources into belowground biomass for greater access to limiting water and nutrients (Quiroga *et al.*, 2010; Gargallo-Garriga *et al.*, 2015; Zeng and Zhang, 2015). Furthermore, warming can restructure the plant community as the relative abundance of vegetative functional groups shifts to favor those best adapted to warmer, drier conditions (Klein *et al.*, 2007). Li *et al.* (2018) found that warming in dryer regions of the Tibetan Plateau favored forbs at the expense of grasses, while another study conducted in rangelands in the western US found that warming favored dominance of cheat grass, an invasive grass species whose dominance increases the frequency of brush fires, reduces native plant diversity, and has little to no value as fodder for livestock or wildlife (Blumenthal *et al.*, 2016). Studies also point to the importance of temperature in determining forage plant nutritive quality (Buxton and Fales, 1994), with higher temperatures associated with lower forage quality (Lee *et al.*, 2017), measured as plant nitrogen (N) content or crude protein content. Rising ambient

carbon dioxide (CO₂) concentrations will only exacerbate the decline of forage quality in a warmer world, as CO₂ enrichment is linked to an increase in plant C content relative to plant N content, which remains low (Izaurrealde *et al.*, 2011; Dumont *et al.*, 2015; Augustine *et al.*, 2018).

The consequences of warming for forage quality and quantity demonstrate the direct effects of climate change, but climate change can also indirectly impact forage resource production due to shifts in plant species interactions. Several studies have suggested that climatic tipping points exist where plant facilitation in moderately stressful conditions (e.g. in semi-arid alpine ecosystems where productivity is limited by water resources) can shift to competition following extreme weather events (Grant *et al.*, 2014), with negative consequences for productivity (O'Brien *et al.*, 2017). Biodiversity loss can also result in a loss of facilitative dynamics such as microclimate amelioration (Wright *et al.*, 2017); in semi-arid ecosystems that experience high degrees of solar radiation during the growing season, dominant species can provide shade which supports the growth of other plant community members and reduces soil moisture losses to evaporation by providing ground cover. The negative impacts from the loss of a facilitative plant species from a community can be greater than any positive benefits stemming from the release from plant-plant competitive dynamics in physiologically stressful environments, with net negative consequences for ecosystem function (Bertness and Callaway, 1994; Rewcastle *et al.*, in press). Therefore, to understand the full extent of climate change impacts on forage resources, it is important to investigate both the effects of abiotic

changes like warming and the effects of shifts in plant species interactions on the quality and quantity of forage resources.

While numerous models and rangeland management strategies adapt grazing pressure in rangelands to account for changes in forage productivity (Díaz-Solis *et al.*, 2009; Kowal *et al.*, 2019), few also incorporate changes to forage resource quality (Jennewein *et al.*, 2021). If meadows in a warmer world contain less nutrition per unit biomass, livestock will require more expansive ranges to meet dietary requirements and maintain livestock productivity. Management strategies would need to be adjusted in a similar way to adaptations that are made to compensate for reduced forage biomass on the landscape. Therefore, existing rangeland management tools, like dynamic stocking rates based on variable forage productivity, can be employed to adapt to changes in forage resource quality so long as the concept of forage productivity is broadened to encapsulate the nutritional content of key forage species (Rouquette, 2016).

Warming experiments can be used to understand how the abundance and physiological properties of key forage species will respond to climate change. Here, we use a field experiment that implements warming and dominant species removal treatments to understand how the direct and indirect impacts of climate change impact the quantity and quality of cattle forage production in a public, semi-arid rangeland in the Colorado Rocky Mountains, USA. We hypothesize that warming and plant species removal will negatively affect forage quality and quantity due to increases in physiological stress stemming from the impact of climate change treatments (Bai *et al.*, 2013; Wright *et al.*, 2017). We also predict that warming will reduce forage biomass by

restructuring the relative abundance of plant functional types as each growth form responds differently to warming (Sebastiá, 2007). Assessing the impact of warming and plant species loss on forage resource quantity and quality will allow rangeland managers to adopt management strategies to protect the production of ecosystem services in rangelands in the face of climate change.

Methods

To understand how warming and shifts in species interactions will impact the quantity and quality of forage resources, we investigated the plant community response to experimental warming and dominant plant species removal in a subalpine grassland located in the Gunnison Ranger District of the Gunnison National Forest, Colorado, USA (38.71 N, -106.82 W, 2740 m asl). Climate at this site is characterized as semi-arid, and management of federal lands in the region are classified under plans for the Gunnison National Forest. Gunnison County received 55.88 mm of precipitation during the summer of 2019, and average temperature in the region was 16.22 °C for the 2019 growing season (June - August). The dominant plant species at this site was *Wyethia x magna* (mule's ears) a perennial forb, with the subdominant plant community comprised of numerous other forbs, grasses, and *Artemisia tridentata* (sage brush). Mayoworth loam was the dominant soil type in this area.

Description of rangeland management practices

While we constructed a fence around the two-acre area containing our experimental plots to prevent livestock from damaging the experimental infrastructure

and equipment, this location has been managed as an active rangeland since the late 1800s. Within the Gunnison Ranger District, private ranchers apply for permits annually to graze livestock on federal rangelands, with 988,265 acres experiencing active grazing in 2016 (USDA Forest Service, 2018). Ranchers pay a fee of \$1.35 per animal unit month (AUM), a measure of the forage required to support an average sized cow for one month, to graze livestock in the area. This fee was established as a minimum fee by an executive order issued by President Reagan in 1986 (E.O. 12548), and the USFS has not raised this fee since its establishment. In the Gunnison Basin, rangeland vegetation condition is rated as “excellent” in 12% of the land area, and 81% of the area is rated as “good” condition, with condition assessed by the abundance of desirable plants (Cook *et al.*, 2017).

Rangelands within the Gunnison Ranger District supported an estimated 105,126 AUM during the 2016 grazing season (USDA Forest Service, 2018).

Experimental design

We established the Warming and species Removal in Mountains (WaRM) experiment at this site in 2014 (Prager *et al.* in review; Sundqvist *et al.* 2020). Warming and dominant plant species removal treatments were applied in a full-factorial design in 2 m x 2 m plots ($n = 8$) to investigate the direct (ecosystem response to abiotic warming) and indirect (effects triggered by shifts in plant community dynamics) of climate change. We applied warming treatments using hexagonal open-top warming chambers (OTCs) constructed from trapezoid-shaped plexiglass panels with a ground-level diameter of 170 cm (Prager *et al.*, in review; Sundqvist *et al.*, 2020). The dominant species at this site, *W. x magna*. was removed by clipping aboveground biomass to soil surface. Warming and

removal treatments were first implemented in 2014. During the first two years of treatment application, we meticulously applied a small amount of glyphosate herbicide to the remaining base of the stems using a paintbrush in an attempt to kill belowground biomass and prevent regrowth of the removed individuals (Rewcastle *et al.*, in press). When it regrew in removal plots, *Wyethia* was removed removed by clipping aboveground biomass to the soil surface. To measure air and soil temperature in each plot throughout the growing season, we inserted one ibutton temperature logger in each plot 5 cm beneath the soil surface and attached a second temperature logger to a pin flag so that the logger was positioned 10 cm above the soil surface (Thermochron DS1921G iButton, Maxim Integrated Products, Inc., San Jose, California, USA). The air temperature logger was covered in reflective emergency blanket material to protect the logger from UV radiation (Prager et al in review). Both air and soil temperature loggers recorded temperature readings at 90-minute intervals throughout the entire growing season, from June 11th, 2019, to September 23rd, 2019.

Assessing forage quality: crude protein content

During the peak of the 2019 growing season, when plant biomass in this location was greatest, we conducted plant community surveys by visually estimating the percent of the plot area occupied by each individual plant species. Visual plant community surveys serve as a method of quantifying forage resource production and provide a proxy for plant species abundance and biomass without destructively sampling aboveground biomass. To quantify how forage resource quality was affected by warming and removal treatments, we measured leaf nitrogen content for the nine most common plant species.

To determine which species were most abundant at our site, we aggregated plant cover in the eight control plots and selected the nine species with the greatest cumulative percent cover. Tissue samples for nitrogen content measurements were collected from the following nine species: *Achillea millefolium*, *Alopecurus pratensis*, *Delphinium nuttallianum*, *Festuca thurberi*, *Poa pratensis*, *Potentilla pulcherrima*, *Senecio sp.*, *Taraxacum officinale*, and *Wyethia x magna*. We converted nitrogen content to an estimate of crude protein content using a 6.25 nitrogen-to-protein conversion rate. While many arguments have been made regarding the validity of this conversion rate, with some stating that it overestimates protein content in many grass species, we employ this ratio here simply to compare relative changes in the nutritive quality of forage species with warming (Conklin-Brittain *et al.*, 1999; Mariotti *et al.*, 2008). In each plot, we harvested one mature, un-damaged leaf from a single adult individual of each of the nine focal species. In a few instances, for plant species with especially small leaves, multiple leaves were harvested from a single individual to obtain enough biomass for nitrogen content analyses. Leaves were transported back to the laboratory at the Rocky Mountain Biological Laboratory (Gothic, Colorado, USA) and immediately placed in paper coin envelopes and dried in a forced-air oven at 60 °C for 48 hours. In October 2019, dried leaf samples were individually ground to a fine powder using a ball-mill grinder (Mini-Beadbeater-96, BioSpec Products, Inc., Bartlesville, OK, USA), and leaf C and N content were measured on ground leaf material using a Leco CHN 628 analyzer (LECO Corporation, St. Joseph, MI, USA). C and N content are reported as mg C or N per g of dry leaf tissue. Plant community surveys and leaf sampling for measurement of nitrogen

content were collected from within a 70 cm diameter circle in the center of each plot to avoid edge effects that might occur along plot perimeters.

Assessing forage quantity: classifying plant species abundance by species forage value

To capture a broader picture of how both the quantity and quality of livestock forage resources are impacted by climate change, we classified all plant species present at this site according to the livestock palatability/forage suitability of each species (Raufirad *et al.*, 2016; Nakano *et al.*, 2020). To accomplish this classification, we referred to descriptions of plant species palatability for livestock and wildlife compiled in a United States Forest Service report on plant species management in the Upper Gunnison Basin region (Johnston *et al.*, 2001). Species were categorized on a scale from 0 to 3, with plant species described as “poisonous” for cattle ranked as forage quality 0, species described as “low forage preference” ranked as forage quality 1, species of “moderate forage preference” ranked as forage quality 2, and plant species described as “good forage” or “high forage preference” for cattle ranked as forage quality 3. All plant species identified within our experimental plots were classified using this system, where information was available. Appendix Table S1 provides a list of the forage quality classification for each species included in this study.

Statistical analyses

To understand the effect of warming and plant species removal on forage quality at the community-scale, we calculated the community weighted mean (CWM) crude protein content within each plot. To calculate the CWMs, we weighted measurements of

crude protein content of each of the nine focal species within each plot by the relative abundance of that species within that plot, i.e., by the percent cover of each individual species divided by the cumulative cover of all nine focal species within each plot. We then analyzed differences between crude protein CWM measured in each plot according in response to the climate change treatments using an ANOVA. Finally, to identify which plant species specifically exhibited shifts in crude protein content in response to warming and species removal, we conducted a series of ANOVAs analyzing treatment differences in crude protein content within each species.

In order to identify the effects of warming on the quantity of plant cover produced in each forage resource quality class, we conducted a two-way ANOVA to assess the degree to which forage quality class, the warming treatment, and the interaction between these two variables affected the relative abundance of plant species within each forage quality class. We also used a Tukey's HSD post-hoc test to highlight specific forage quality classes that exhibited significant shifts in relative abundance with the warming treatments. For this analysis of changes to plant cover, we limited our analysis to a subset of the plots that did not receive the removal treatment ($n = 8$), allowing us to isolate the effect of warming on the abundance of plants of in each forage quality class. We also conducted a two-tailed Welch's t-tests to understand the effect of warming on the total cover of plant species that are palatable to cattle, excluding plant species in quality class 0 that are poisonous to cattle. We analyzed the effectiveness of using OTCs to raise soil and air temperatures above ambient conditions by performing a one-tailed t-test with the alternate hypothesis that temperatures in warmed plots were greater than those in ambient

control plots to analyze differences in mean growing season soil and air temperature data collected using the iButton temperature loggers. All statistical analyses were performed in RStudio (R version 4.0.5 “Shake and Throw”) (RStudio Team, 2020).

Results

We found that warming was associated with a significant decrease in mean plant crude protein content at the community scale ($F_{1,28} = 5.81, p = 0.023$). Community weighted mean crude protein content was 12.0 % lower in warmed plots than in ambient plots (Figure 1), indicating a decline in forage quality in response to warming treatments. Dominant plant species removal resulted in a subtle, marginally significant increase in crude protein content ($F_{1,28} = 2.98, p = 0.095$), while the interaction between warming and removal treatments had a marginally significant, negative effect on crude protein content at the community scale ($F_{1,28} = 3.64, p = 0.067$). Use of OTCs to implement a warming treatment was effective in raising the mean growing season air and soil temperatures (air: $t_{29,36} = 6.75, p < 0.0001$; soil: $t_{13,81} = 1.85, p < 0.0001$). Mean air temperature in warmed plots was 9.3%, or 1.36 °C, higher than in ambient plots, and mean soil temperature was 6.9%, or 1.10 °C, higher than soil temperatures in ambient plots.

Individual ANOVAs used to highlight the effects of warming and species removal on leaf crude protein content within a single species revealed no discernible effects of removal or the interaction of warming and removal on crude protein content of an individual species. We then removed the removal treatment from species models and

conducted two-tailed Welch's t-tests to analyze the effect of warming on crude protein content within individual species. Crude protein content decreased with warming in leaves of *T. officianale* ($t_{22.49} = -3.19, p = 0.002$) and *W. x magna* ($t_{11.17} = -2.60, p = 0.012$), and marginal declined in *F. thurberi* leaf tissue with warming ($t_{12.71} = -1.58, p = 0.069$) (Figure 2, Table 1).

Warming tended to reduce the cumulative cover of palatable plant species, though this effect was statistically insignificant ($t_{13.94} = -1.69, p = 0.114$, response ratio = 0.80) (Figure 3a). While we were unable to detect an overall effect of warming on plant community structure from the perspective of the relative cover of plants within each forage quality class ($F_{1,60} = 0.015, p = 0.903$), we found a marginally significant interaction between warming and forage quality class on the relative cover of plant species within each forage quality class. More specifically, results from Tukey's HSD post-hoc test indicated that relative cover of the most high-value forage species, forage quality class 3, subtly declined with warming, while the relative cover of the unpalatable plant species in forage quality class 0 exhibited a slight increase in response to warming (Figure 3b).

Discussion

Our results indicate that the quantity and quality of forage resource production for cattle in this semi-arid rangeland are threatened by rising temperatures. After only six years of moderate warming, we found support for our first hypothesis as crude protein content in three of the nine most common plant species decreased in warmed plots, a

marked decline in forage quality. Removal of the dominant plant species, however, did not meaningfully impact the nutritive quality of forage species. We found a marginal reduction in cover of plants in the most high-value forage species, partially supporting our second hypothesis. Together, these results paint a discouraging picture of the future of forage resource production in arid rangelands and highlight the need for adaptive rangeland management strategies that protect the long-term stability of forage production in light of declining forage quality and quantity in a warmer world.

Both the decline in forage quality and loss of cover from high-value forage species following warming can likely be attributed to increasing aridity with warming experienced in this moisture-limited system. Aridity can decouple the biogeochemical processes that establish ratios of key soil nutrients, resulting in an increase in soil C:N ratios that mirror the decline in leaf N content that we found with warming (Delgado-Baquerizo *et al.*, 2013; Doiron *et al.*, 2014; Jiao *et al.*, 2016). Warming that results in drying of the topsoil can also result in lower plant nutrient uptake (Querejeta *et al.*, 2021). Aridity has also been linked to greater allocation of photosynthetic carbon to roots relative to shoots in perennial grasses (Gargallo-Garrig *et al.*, 2015) and that grasses in general become less abundant as forbs increase in abundance following warming in water-limited ecosystems (Li *et al.*, 2018). As grasses encompass many of the high-value forage species on the landscape, shifts that favor resource allocation belowground in grasses specifically due to warming and increased aridity may explain the reduction in abundance of the species in the highest forage quality class in our experiment. Without adjustments to cattle stocking rates or the use of other rangeland management strategies

that reduce grazing pressure, over-grazing will compound the effects of warming to alter rangeland plant communities as a whole (Hunt *et al.*, 2014; Kowal *et al.*, 2019; Oñatibia *et al.*, 2020).

While we did not explicitly test the interactive effects of warming and grazing occurring simultaneously, other studies have observed convergent effects on rangeland degradation when warming, increasing aridity, and livestock grazing occur simultaneously, especially in drier climates (Köchy *et al.*, 2008; Gaitán *et al.*, 2018; Oñatibia 2020). Maintaining historical stocking rates despite declining forage production can exacerbate other threats to this ecosystem service. Invasive species are prone to colonization of disturbed areas, compromising native forage communities and increasing risk of fire (Blumenthal *et al.*, 2016). If estimated dryland forage production in this region were to be adjusted to account for the 12.0 % decrease in plant nitrogen content with warming, rangelands in the Gunnison Ranger District would be able to support 12,615 fewer AUM, or approximately 2,523 fewer head of cattle over the entire five month grazing season. Alternatively, providing supplemental fodder and importing livestock feed could be used without adjusting stocking rates to compensate for shortfalls in the nutritive quality of forage resources with climate change (Wreford and Topp, 2020). This field study, while small in physical scale, highlights the potential for even modest changes in growing season temperatures to result in significant losses in the production of forage resources. As we enter a future defined by climate change, our results call for the use of adaptive management strategies to protect the long-term health of rangelands.

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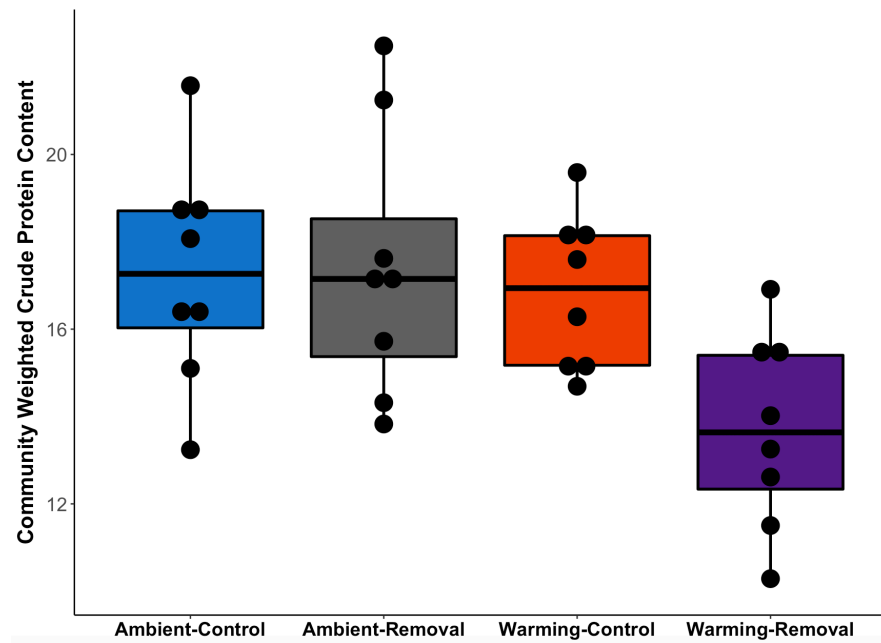
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Figures and Tables

	<i>t</i>	Degrees of Freedom	<i>p</i>	Response Ratio
<i>A. millefolium</i>	-0.53	23.67	0.299	0.95
<i>A. pratensis</i>	-0.17	19.21	0.435	0.98
<i>D. nuttallianum</i>	-0.37	17.98	0.359	0.96
<i>F. thurberi</i>	-1.58	12.71	0.069	0.85
<i>P. pratensis</i>	-0.26	18.99	0.397	0.93
<i>P. pulcherrima</i>	-1.28	13.00	0.111	0.91
<i>Senecio sp.</i>	-0.76	19.39	0.230	0.93
<i>T. officinale</i>	-3.19	22.49	0.002	0.77
<i>W. x magna</i>	-2.60	11.17	0.121	0.80

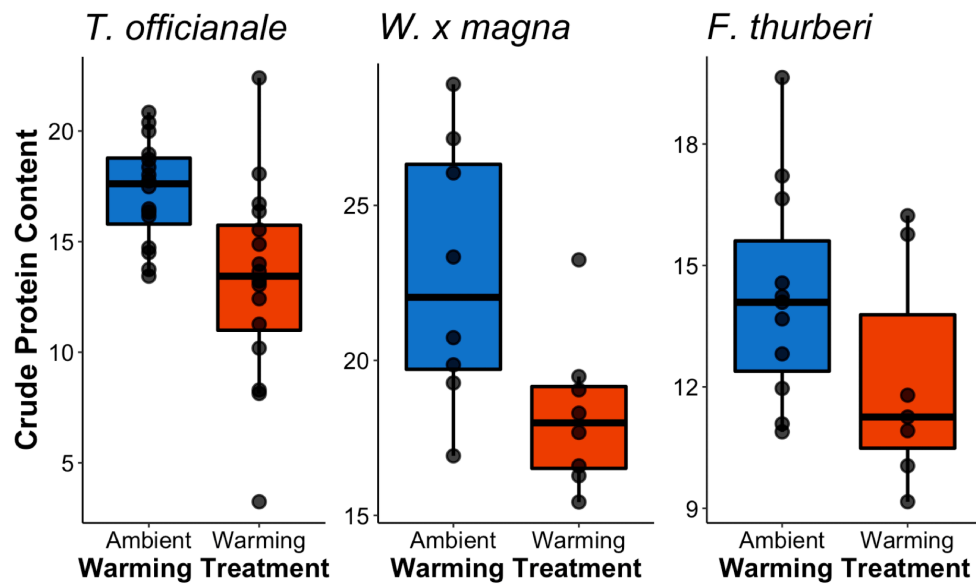
Table 1. Results from individual t-tests analyzing the effect of warming on crude protein content for the nine most common plant species in our experiment. Response ratios represent mean leaf crude protein content in warmed plots divided by crude protein content in ambient plots to demonstrate the relative magnitude of warming effects.

Figure 1



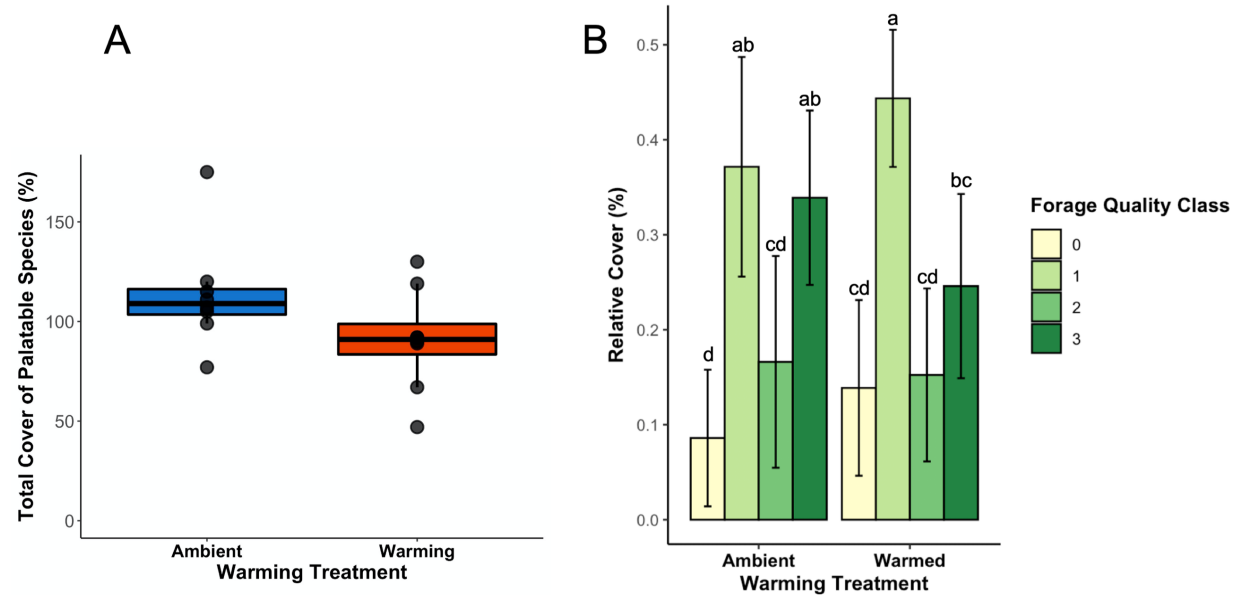
Warming resulted in a significant decrease in community weighted mean crude protein content, while the interaction between warming and removal treatments resulted in a marginally significant decrease in crude protein content. Removal of the dominant plant species resulted in a marginal increase in crude protein content.

Figure 2



Of the nine most abundant species for which leaf crude protein content was measured, crude protein content of *T. officianale* and *W. x magna* decreased significantly with warming, while crude protein content of *F. thurberi* marginally decreased with warming.

Figure 3



A) Warming slightly reduces the cumulative cover of palatable species and B) subtly reduces the cover of the highest value forage species for cattle, species in forage quality class 3, and increases the relative cover of the unpalatable/poisonous plant species in forage quality class 0. Different letters above the bars representing cover of plant species in individual forage quality classes in each treatment indicate significant differences in cover.

Appendix

Species	Forage Quality Class
<i>Achillea millefolium</i>	1
<i>Alopecurus pratensis</i>	3
<i>Delphinium nuttallianum</i>	0
<i>Festuca thurberi</i>	3
<i>Poa pratensis</i>	3
<i>Potentilla pulcherrima</i>	2
<i>Senecio sp.</i>	2
<i>Taraxicum officianale</i>	3
<i>Wyethia x magna</i>	1
<i>Adenolinum lewisii</i>	0
<i>Agoseris sp.</i>	2
<i>Antennaria rosea</i>	1
<i>Artemesia tridentata</i>	1
<i>Boechera stricta</i>	Forage quality data unavailable, fairly low-abundance
<i>Bromopsis inermis</i>	0
<i>Calochortus gunnisonii</i>	Forage quality data unavailable, fairly low-abundance
<i>Capsella bursa-pastoris</i>	Forage quality data unavailable, fairly low-abundance
<i>Castilleja miniata</i>	1
<i>Chrysothamnus viscidiflorus</i>	1
<i>Elymus elymoides</i>	2
<i>Elymus glaucus</i>	2
<i>Eremogone congesta</i>	1
<i>Erigeron sp.</i>	0
<i>Erigeron speciosus</i>	1
<i>Eriogonum umbellatum</i>	1
<i>Galium septentrionale</i>	1
<i>Geranium viscosissimum</i>	1
<i>Helianthella quinquenervis</i>	2
<i>Ipomopsis aggregata</i>	3
<i>Iris missouriensis</i>	1
<i>Lathyrus leucanthus</i>	2
<i>Lithophragma sp.</i>	Forage quality data unavailable, fairly low-abundance
<i>Mertensia fusiformi</i>	2
<i>Muhlenbergia montana</i>	3
<i>Phacelia sericea</i>	1

<i>Rosa woodsia</i>	2
<i>Sedum lanceolatum</i>	Forage quality data unavailable, fairly low-abundance
<i>Symphoricarpos rotundifolius</i>	2
<i>Valeriana edulis</i>	1
<i>Vicea americana</i>	3
<i>Viola labradorica</i>	Forage quality data unavailable, fairly low-abundance

Table S1. Forage quality classification for all species present at our field site. Species are ranked according to information provided by the United States Forest Service report prepared by Johnston *et al.*, 2001. Classification “0” indicates poisonous or unpalatable species, “1” indicates species described as “low” or “poor” forage quality, “2” indicates species of “moderate” forage quality, and species ranked as forage quality class “3” are “excellent” or “high-value” forage species that are dietary staples for livestock in the region.

CONCLUSION

Evidence from the three studies included in this research indicate that climate change, both through rising temperatures and the resulting shifts in plant species interactions, will have marked consequences for numerous aspects of nutrient cycling in mountain ecosystems worldwide. While many of the effects of climate change will be localized and context-dependent, my results show that global paradigms dictating the spatially generalizable impacts of both warming and plant species loss on pools and fluxes of nitrogen and phosphorus do exist. This research also highlights the promise of integrating high-resolution data stemming from ecological climate change experiments at the plot scale with the regional land management decision making process in order to protect the future of ecosystem services in mountain ecosystems in the face of global change. While this research has uncovered broad patterns of ecosystem responses to climate change, future research investigating the ecological mechanisms that drive and mediate shifts in ecosystem functions and services could strengthen our ability to predict the future of mountain ecosystems in a warmer world.

The first chapter revealed that the loss of a dominant plant species across an elevational gradient resulted in a consistent decrease in the variation in, and to some extent, the magnitude of potential N-mineralization rates, an important flux of nutrients to the soil system. The second chapter expanded the geographical scope of this investigation of climate change impacts on nutrient cycling, demonstrating that warming has a direct impact on soil N-availability across a global network of climate change experiments in mountains, while the impact of warming on soil P-availability was mediated by the

temperature-associated changes in soil properties. The third and final chapter revealed a substantial reduction in forage resource crude protein content in response to warming, a result that highlights the need to employ rangeland management strategies that reduce grazing pressure to prevent long-term degradation of rangeland resources in a future characterized by climate change. Together, this research lends insight to the consequences of future climate change for nutrient cycling and forage resource production in mountains, but future research should begin to unravel the ecological processes that determine the context-dependency of these results to pinpoint specific ecosystems and ecosystem services that might be especially vulnerable to the effects of climate change.

First, while the second chapter detailed the net impact of climate change on the plant-available pool of essential nutrients, future studies should investigate which nutrient fluxes are responsible for the net changes documented in this research. Is the reduction in available nutrients in the face of climate change the result of declining nutrient inputs or an acceleration of nutrient losses? If climate change reduces the size of the available nutrients pool, can we trace the movement of these nutrients into plant or microbial biomass? Isolating the specific nutrient transformations that drive fluctuations in nutrient pools will allow ecologists to focus on climate change impacts in ecosystems in which these sensitive nutrient fluxes play critical roles in nutrient cycling locally.

Second, this research solely focuses on the effects of atmospheric warming and the indirect effects of warming mediated by changes in species interactions. We know that numerous global change drivers threaten mountain ecosystems simultaneously, and

we must dedicate future research to investigating the interactions and synergies among multiple aspects of global change. How will warming, drought, severe flooding, shifting fire regimes, and heightened human presence in mountain regions around the world act in tandem to alter the structure and function of alpine ecosystems? Investigating the interactive effects of global change will be essential to protecting the mountain ecosystem services on which many rely.

Finally, climate change manifests changes to forage resource production in numerous different ways. While the third chapter documented changes to the quantity and quality of forage resource production with warming, other studies have shown that warming also affects the phenology of forage resource production, advancing the onset of the grazing season and increasing grazing season length. Future studies should explicitly link the effect of warming and livestock grazing on forage production and rangeland phenology to gain a more comprehensive understanding of the capacity of rangelands of the future to support current levels of livestock production.

Ultimately, the research described in this dissertation has given me the scientific tools and intellectual appetite to support a career spent harnessing applied ecological research in service of accomplishing land management goals. Skills acquired in pursuit of my doctoral degree fall into three main categories: 1) Environmental gradients can be used to envision the future structure and function of ecosystems with climate change, 2) Existing data stemming from ecological climate change experiments can be reframed to not only assess changes to the production of ecosystem services, but can quantify the magnitude by which land management strategies must be adjusted in order to respond to

future climatic conditions, and 3) While globally consistent net climate change effects exist, the nuance lies in the pathways by which these changes emerge. When designing future conservation strategies, it is important to hold space for numerous global change drivers and their multiplicative effects in order to build dynamic, adaptive management plans that account for simultaneous threats. While my ideal career would allow me to channel these lessons into public land management or the development of climate change adaptation strategies, these themes will undoubtedly serve me in numerous potential careers at the interface of applied science and adaptive decision making.

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