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# What Drives Species Richness in Colorado's Alpine Tundra

Michael Kintgen  
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MS ENVIRONMENTAL BIOLOGY  
CAPSTONE PROJECT

by

Michael T. Kintgen

A Project Presented in Partial Fulfillment  
of the Requirements for the Degree  
Masters of Science  
in Environmental Biology

REGIS UNIVERSITY  
May, 2018

MS ENVIRONMENTAL BIOLOGY  
CAPSTONE PROJECT

by

Michael T. Kintgen

has been approved

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## CHAPTER 1. LITERATURE REVIEW: WHAT FACTORS DRIVE SPECIES RICHNESS IN ALPINE ENVIRONMENTS?

Aridity is often considered a limiting factor in the evolution of plant species diversity; however, in certain alpine environmental situations, it may drive speciation and increase diversity (Korner, 2003). Limited research has been conducted on measuring species diversity as it compares to precipitation gradients in alpine biomes. Only two studies have specifically addressed precipitation gradients and how they affect species richness. Both studies were completed within Nahuel Huapi National Park in Patagonia, Argentina with 220 species found in the more arid part of the park and only 149 recorded in the more mesic areas (Ferreyra et al., 1998 a; Ferreyra et al., 1998b). Another study in Alberta examined the biodiversity of the region's vascular timberline flora. In this study, Harris (2002) mentions that species diversity and precipitation are correlated, but also examines how close some of his study sites are to current ice sheets.

Researchers have looked at other drivers than aridity concerning alpine flora and its richness around the world, including the origins of the various regional alpine floras, how elevation and aspect, (Kazakis et al. 2007), nutrient levels (Bowman and Damn, 2002), and snow depth and length of snow cover affect diversity (Bowman and Damn, 2002). Some of this work has even lead to the discovery of new species (O'Kane 2007). More research needs to analyze precipitation gradients and their influences on alpine plant species richness. This will provide a better understanding of these unique and fragile environments in the face of climate change and other anthropogenic effects on the environment.



## **Aridity**

Of all the alpine research investigating the origins and diversity of alpine species, only Ferreyra and her colleagues (1998a and b) in Patagonia and Harris (2002) in Alberta explored precipitation gradients as a potential factor contributing to species diversity. Studying twenty sites, Ferreyra et al. (1998) found that the more arid eastern portion of the Nahuel Huapi National Park was richer in species, with nearly twenty on Mount Meta while only nine species existed in the coldest and wettest sites on both more mesic Monte Tronador and Mt Lopez areas.

Harris (2002) compared the vascular timberline flora at six sites in the Rockies of Alberta along a 600km stretch. The sites were selected due to the detailed species lists that are available for each of the six sites and the availability of climatic data. Additionally, 40,000 herbarium specimens were examined to augment data collected in the field. Harris (2002) found that the two wettest sites had the highest plant diversity along with the transition zone of Plateau Mountain which was not glaciated due to its location near the boundary of extensive Wisconsin glaciation in the province. The least diverse site is located near the current Columbia Ice sheet. He proposes that since the site was perhaps more recently ice-free than the other sites, and more species have not had time to recolonize the site (Harris, 2002).

In examining Harris' work, all three sites with the highest diversity are located in the southern part of Alberta where effects from the late Wisconsin glaciation were less drastic, and he suggests that Plateau Mountain was an ice-free nunatak and provided a refuge for local alpine species during the glaciation (Harris, 2002). While it appeared that the wetter sites had

greater diversity than the drier sites further north, this is only partially true, because the alpine flora of Alberta drops in diversity north of the transition line located near Plateau Mountain. This is due to the confounding effects of glaciation (Harris, 2002). Additionally, Harris did a north to south site selection, while Ferreyra et al. (1998a and b) selected a west to east site selection following the local precipitation gradient.

## **Glaciation**

The extent of glaciation and time since the regional ice retreat has also been explored for its effects on plant diversity (Harris, 2002, Takhtahan, 1986). From the Canadian border, north, the northern areas of the Rockies were more heavily glaciated and have a lower species count due to the destruction and subsequent recolonization of the floras in the last 10,000 years (Takhtajan, 1986).

Research shows there are more endemic species in the Southern Rockies than the Northern Rockies; this is due to the less dramatic effects of glaciation in the Southern Rockies. Overall two to seven-percent of the total alpine flora of the Rockies is endemic (Bowman et al., 2002). Speciation and endemism can arise through geographic isolation; the longer the isolation, the more speciation occurs. Hadley (1987) hypothesized that the breaks in the Rocky Mountains such as the Wyoming Basin and the Colorado Plateau posed potential migration barriers for alpine species. These breaks have existed only for a geologically short time since the end of the Pleistocene Bowman et al. (2002). The low percentage of endemic species throughout the Rockies, however, demonstrates that these physical barriers did not lead to drastic speciation on each side.

## **Origins of the alpine floras**

Several researchers have studied the origin and number of species within alpine floras in the Western United States. Species origin and richness can help determine if aridity is truly a driving factor in increasing plant diversity in alpine habitats. Chabot and Billings (1972) explored the origins and ecology of the alpine flora in the Sierra Nevada of California, while Hadley (1987) studied alpine plant distributions in the Central and Southern Rockies. The most recent of these studies in the Rocky Mountain region was conducted by Fowler, Nelson, and Hartman (2014), who tallied the vascular alpine flora of the Southern Rockies without discussing proposed reasons for the species diversity. While this study was desperately needed due to changes in nomenclature and updated herbaria records for previously under-collected alpine areas, it only reviews species counts for the region, not by habitat. Among studies concerning alpine species origin and possible reasons for diversity and aridity, the Sierra Nevada alpine flora is very interesting due to its isolation and relatively young age (Chabot et al., 1972).

Within the flora of the Southern Sierra, arctic, northern alpine and Rocky Mountain alpine flora have a smaller contribution to the alpine flora than far Western North American floras, suggesting that the alpine flora evolved largely from the surrounding lowland xeric vegetation (Chabot et al., 1972). Hadley's (1987) work, located in the Central and Southern Rockies looked at size of alpine areas and their isolation from areas further north closer to the arctic. He chose two geological barriers, the Wyoming Basin and Colorado Plateau, as potential factors in species diversity with the hypothesis that the larger and less isolated the alpine area, and the more species diverse it would be due to disruption to species migration. Hadley (1987) specifically analyzed areas adjacent of the Wyoming Basin and

Colorado Plateau as potential barriers. He found that his hypothesis was not supported; instead, Central Colorado south of the Wyoming Basin is more species rich, despite being further from the arctic. Later it was determined that the alpine regions of Central Colorado are the most diverse in the Central and Southern Rockies with 499 taxa (Fowler et al., 2014). Colorado's higher species diversity and its position south of the Wyoming Basin refutes Hadley's hypothesis that at least one of the physical barriers studied had an effect on species richness.

### **Elevation and aspect**

In regions, other than the Rockies, such as Crete, Greece elevation gradients drive species richness, with fewer species at higher elevations (Kazakis et al., 2007). In the Rockies, there is no evidence demonstrating that elevation plays a large role in species diversity (Bowman and Damn, 2002). The difference in these two regions' floras may be linked to several factors. The alpine flora of Crete is on an island located in the Mediterranean Sea and most Cretan alpine species evolved from the lowland Mediterranean flora, which is naturally not well-suited to high elevation and cold winters. Other flora arrived as the few previously alpine-adapted species from neighboring mainland areas, mainly the Balkans (Kazakis et al., 2007). The majority of Rocky Mountain alpine flora, on the other hand, is composed in part of arctic species or has evolved from arctic species. If it is not of arctic origin, then it most likely evolved from the regional high elevation flora already primed to tolerate cold, high elevations. It was thought that since the southern exposures were the warmest, they would have the highest diversity, while the cooler north facing aspects would have the lowest (Kazaksi et al., 2007). Aspect was also explored on Crete, and while the richest aspect was not specifically named, it was noted that the north side was not the poorest

and the south side the richest, as might be expected. This is based on temperature as a control for species diversity. These results suggest slope aspect is not a driving factor in speciation, at least in Crete.

Several researchers in South Africa explored the number of endemics in the Drakensberg Alpine Center, the only true alpine area in South Africa (Carbutt et al., 2006). They tallied the number of endemics and briefly discussed the possible reasons that the species might be endemic. They proposed that species are narrow endemics or species found only in very limited areas or environments due to the following reasons: localized seed dispersal, specific habitats only found at high elevations, interrupted habitats which affect gene flow, the inability to tolerate heat, and the fact that alpenes can compete better in cold temperatures than the surrounding tropical flora (Carbutt, et al., 2006). While Carbutt et al. (2006) discuss extensively which species are endemic, they do not explore the idea of precipitation gradients, habitats, or any other potential effects on species richness.

### **Nutrient levels and disturbance**

Bowman and Damn (2002) studied the causes and consequences of alpine vascular plant diversity in the Rocky Mountains but did not assess precipitation gradients as a driver of diversity. This may be largely due to their work on Niwot Ridge, although they did an extensive literature review examining latitude and its effects on diversity. They discuss factors such as winter snow distribution and how variation in microclimate affects species diversity.

Bowman and colleagues cite Brunsfeld's work from 1981 that shows in east-central Idaho there were five times more arctic species in moist meadows than dry meadows. It was also noted that species with a smaller distribution or endemics were more likely to be found in dry sites (Brunsfield, 1981).

They also explore the plant driven effect on both soil conditions and disturbance, which in turn drives site diversity through nitrogen cycling or encouraging disturbance by mammals (Bowman and Damn, 2002). Bowman and Damn (2002) mention, in general, diversity decreased with increased soil resource supply and increased aboveground production of biomass. Findings on Niwot Ridge, Colorado showed that fertilizing a nutrient-poor rather dry site increased diversity, while fertilizing a more fertile and wet site decreased diversity (Bowman and Damn, 2002). This makes sense, as adding fertility to an infertile site should increase diversity, while in the wet meadow, it most likely caused several more robust species to take over and outcompete less vigorous species. Bowman and Damn (2002) also discuss the intermediate disturbance hypothesis based on work conducted by other researchers notably Fox in Central Alaska (1981, 1985), who suggests that moderate levels of soil disturbance creates the greatest level of diversity in alpine plant species. Moderate disturbance allowed open sites for different species to colonize, sites otherwise filled with stable vegetation. The disturbance occurs on a small enough scale and infrequently enough that it does not destroy all the existing vegetation.

Further support by Korner and Chaplin (1994), states that that species diversity is highest on a local level in areas of moderately unstable soils, while stable areas develop a heavy organic layer and have poor species richness in both the arctic and alpine. Several researchers mention that within the Colorado alpine zone most of the endemic species are found on scree or in fellfields, both habitats that are typically more arid than other alpine habitats (Bowman and Damn, 2002; Weber and Wittman, 1996).

### **Snow depth**

Multiple studies have investigated how snow distribution contributes to species richness

(Vesterngren 1902; Komarkova 1979; Harrison 1986; Walker et al. 1993; Bowman and Damn 2002). While this addresses the issue of moisture and species diversity found within habitats with varying snow cover, it does not explore precipitation gradients. Komarkova (1979) notes many rare species grow only in snow bed areas in the Front Range of Colorado; however, most of these rare species mentioned are arctic or boreal alpine and need more moisture to survive and do not represent regional endemics that may only be found on a particular mountain range (Bowman et al., 2002). In New Zealand, Harrison (1986) explored the effect snow fences had on the snowpack of the Old Man Range with the goal of observing if they caused snow drifts to linger and therefore increase late summer river flow in the Fraser River. While this would seem to be unrelated to alpine plant diversity, it was found that at all sites, plant diversity increased as a result of the snow fences (Harrison, 1986). Harrison (1986) does not offer a possible explanation for the increase, only mentioning that the dominant plant *Dracophyllum muscoides* declined and bare ground and organic litter increased.

### **Discovery of new species in arid areas**

Lastly, survey work on the Patagonian precipitation gradient projects led to the discovery of a new species, *Senecio carbonesis*, further documenting that there might be more undiscovered species in other arid alpine areas (Ezcurra et al, 1995). In 2007, a new alpine species of *Physaria* was described from the San Juan Mountains of Southwest Colorado growing on barren and very windy areas of Leadville limestone (O’Kane, 2007).

Colorado, or somewhere in the Western United States, would provide an excellent site to explore the concept of precipitation gradients and alpine plant diversity as it is a steppe region like Patagonia. The limited findings presented above support that arid alpine areas are more diverse than mesic areas however, more research needs to be conducted to explore

this influence on alpine flora. New research would give better understanding of these habitats before these before they change or are further impacted by humans.



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## CHAPTER 2. GRANT PROPOSAL DOES ARIDITY DRIVE SPECIES RICHNESS IN COLORADO'S ALPINE TUNDRA?

### Abstract

Little is known about what truly drives vascular plant species richness in alpine habitats. Factors such as origins of the current flora, elevation, slope aspect, the effect of Pleistocene glaciation, nutrient levels, and the intermediate disturbance hypothesis have been studied. Despite a large amount of research, few patterns have emerged. Aridity is one factor that has been studied in Patagonia, where it was found that increasing aridity correlated to a higher species richness. This project will examine how precipitation gradients in Colorado affect species richness similarly to what was found in Patagonia. A full species assessment will be conducted on five mountains covering the precipitation gradient in Colorado from driest to wettest. Work will be conducted in randomly selected plots in fellfields at the same elevation, aspect, and slope. Herbarium specimens, tissue samples and soil samples will be collected to determine species richness and assess if aridity affects species diversity. I expect to find that the more arid alpine areas have a higher plant species diversity than wetter areas.

### Background/Rationale/Significance

Alpine habitats are some of the most delicate habitats on earth. Harsh conditions make life tenuous for plants and animals. The disruptions these areas are experiencing from anthropogenic pressures and climate change increase the importance of the work needed to fully understand what drives speciation in alpine areas (Körner, 2003). This study will contribute to the limited body of work that has addressed drivers of speciation in alpine environments. It will help to answer the question of why some alpine areas are more species rich than others. Species richness is the measure of number of species in an area. Aridity is often considered a limiting factor in the evolution of plant species diversity; however, in certain alpine environmental situations, it may drive speciation and increase diversity (Körner, 2003). Aridity is the lack of precipitation resulting in a semi-arid or arid climate. Diversity is the

measure of variation in living organisms in an ecosystem. Work done in the Southern Andes of Patagonia, Argentina suggests that more arid areas have greater species diversity than mesic areas experiencing greater precipitation (Ferriera et al. 1998a). No comparable work has been done in North America.

Multiple factors have been explored that may drive species richness in alpine areas around the world. These range from the origins of the flora, to elevation and slope, aspect, or the effects of glaciation. Other researchers have examined nutrient levels and the intermediate disturbance hypothesis (Bowman and Damman, 2002; Fox 1981, 1985; Körner and Chaplin, 1994). Snow depth has also been investigated as a species driver by multiple researchers on several continents (Vestergren 1902; Komarkova 1979; Harrison 1986; Walker et al. 1993; Bowman and Damman 2002).

Understanding origins of alpine flora is something that has interested scientists for many years and is certainly a driving factor in species diversity amongst alpine flora. Historically it was proposed that all alpine flora originated from the flora in the arctic (Körner, 2003). Later work in the Sierra Nevada of California proposed that the Sierran alpine flora evolved from the surrounding lowland dryland vegetation as opposed to a more mesic moisture-loving flora from the arctic and alpine area further north (Chabot and Bilings 1972).

While it might be assumed that elevation exerts a strong driving influence on species diversity, findings have not been consistent across alpine regions. Work in Crete has shown that elevation but neither slope nor aspect affected the diversity of alpine flora (Kazakis et al. 2007). In South Africa, however, elevation contributed to the evolution of endemic species as the surrounding lowland flora was not adapted to the higher cooler elevations of the Drakensberg (Carbutt and Edwards, 2006). In the Southern Rockies, Bowman and Damman (2002) mention elevation does not affect species diversity.

Pleistocene glaciation has been explored by many scientists and botanists in particular for its effect on alpine flora (Harris, 2002; Takhtajan, 1986; Bowman and Damman, 2002). Takhtajan (1986) proposes that the Canadian Rockies have lower species richness due to the destruction from glaciation and subsequent recolonization by the flora in the last 10,000 years. Harris (2002) found that the least diverse study site in the Canadian Rockies was closest to the current ice sheets. The Southern Rockies has a higher percentage of endemic species than the Northern Rockies, showing the effect Pleistocene glaciation had on the Northern Rockies and its

species diversity (Bowman and Damn, 2002).

Nutrient levels have been investigated in Colorado as a driver for either the positive or negative influence they had on species diversity. Findings on Niwot Ridge showed that fertilizing a nutrient-poor rather dry site increased diversity, while fertilizing a more fertile, wet site decreased diversity (Bowman and Damn, 2002). This makes sense, as adding fertility to an infertile site should increase diversity, while in a wet meadow it most likely caused several more robust species to take over and outcompete less vigorous species. Bowman and Damn's (2002) work also mentions that increased biomass does not necessarily equate to an increase in diversity. If nutrients are not the only factor exerting influence, then there must be additional factors such as precipitation and water availability that affect species diversity.

The intermediate disturbance hypothesis could drive higher species richness and diversity. The intermediate disturbance hypothesis states that if disturbance is infrequent enough to allow vegetation to establish, it creates voids that are filled by early successional species in areas that are largely filled with species favoring more stable conditions (Fox, 1981, 1985; Körner and Chaplin, 1994; Bowman and Damn, 2002). In Colorado, most of the alpine endemic species are found on screes or in fellfields; both habitats are typically more arid and experience higher degrees of disturbance than other alpine habitats (Bowman and Damn, 2002; Weber and Wittmann, 1996).

Snow depth has been studied extensively by researchers in North America, New Zealand and Europe (Vestergren, 1902; Komarkova, 1979; Harrison, 1986; Walker et al., 1993; Bowman and Damn, 2002). In Colorado, it was found that many rare species grow only in snow bed areas in the Front Range. On further investigation, most of these rare species are arctic or boreal alpine species that need more moisture to survive than Southern Rocky Mountain endemics. They do not represent regional endemic plant species but wide-ranging species at the southern limit of their ranges finding refuge in cool moist microclimates. Harrison (1986) found that plant diversity in New Zealand increased as the result of snow fences and the area covered by the dominant plant *Dracophyllum muscoides* (Ericaceae) decreased.

Research in Argentina's Southern Andes and Colorado's San Juan Mountains has helped shed light on aridity as being a possible driver in increasing species diversity. In Argentina's Nahuel Huapi National Park, studying species richness across the park's precipitating gradient led to the discovery of *Senecio carbonensis*, a rare and endemic species native in the drier

areas of the Park (Ezcurra et al 1995). In 2007, a new species of *Physaria* scrotiformis was described in the San Juan Mountains of Southwest Colorado (O’Kane 2007). These two rather recent discoveries point to the importance of arid areas and that new discoveries are not just occurring in the tropics or distant mountain ranges that have been poorly explored by science, but in mountain ranges with a long history of botanical exploration.

Aridity has not been studied extensively and could prove to be an overlooked factor in explaining diversity in alpine ecosystems. My project will look specifically at aridity in Colorado and its influence on species richness in alpine ecosystems. The other factors explored above point at some possible explanations, but no sound patterns have emerged.

I hypothesize that more arid alpine areas in Colorado will have greater plant species diversity than areas receiving more precipitation. Areas such as the Park Range, receiving upwards of (1524mm) of precipitation, will have fewer species present compared to areas receiving less precipitation, such as the Mosquito Range.

This project aligns with Regis University’s goal of contributing to the body of human knowledge not only through the information collected in the Colorado alpine tundra, but in furthering the call to action to preserve the natural world in a time of intense habitat destruction worldwide. Information gained from this project will provide a better understanding of what drives species diversity in some of the most endangered habitats on earth.

### Purpose and Specific Aims

The primary aim of this project is to determine if aridity is a driving factor in determining plant species richness in alpine environments. This complements research in the Southern Andes in Patagonia, Argentina, where it was found that more arid areas have greater species diversity than mesic areas experiencing greater precipitation (Ferreyra et al. 1998 a and b). Ferreyra et al. (1998 a and b) did not focus on fellfields but rather a variety of alpine habitats except for areas affected by ground water seepage or stream sides. Ferreyra and colleagues’ work was on a very strong precipitation gradient varying from 3000mm at the western end to 800mm at the eastern end. Nowhere in Colorado is there such a strong precipitation gradient; most precipitation ranges from 762 mm to over 1524 mm.

Hypotheses:

1. More arid areas will have higher plant species diversity than wetter areas.
2. Extreme aridity will decrease species richness just as extremely high precipitation rates will decrease species diversity. I expect there to be a precipitation range where species diversity is highest.
3. No areas of Colorado receive enough precipitation to be on the same scale as Patagonia, I expect to see a pattern at a different scale than was found in Patagonia.

## Methods

I will explore five sites in Colorado's alpine environments at a uniform elevation of 12,000 feet, on the same aspect and degree of slope, spanning a range of Colorado's precipitation gradient from drier to wetter. Information from PRISM climate data for Colorado will be used to determine the site in advance. Work will be done on fellfield sites which tend to be the driest alpine sites, and the vegetation has a stronger response to natural precipitation than moist meadows or other areas that may have water drainage flowing through them. 10 plots will be set up at each site. Plots will be one-meter square and 10 meters apart along a transect.

Field work will be completed during the 2017 growing season after all the proper permits are obtained, during which I will collect and record species from randomly selected plots on the precipitation gradient. Number of species, and abundance of each species will be noted in each plot. All species of vascular vegetation (flowering plants, grasses, sedges and ferns (if present)) will be photographed and both herbarium and tissue samples collected. Tissue sampling is an additional step to herbarium work and supports the Global Genome Initiative as outlined by the Smithsonian Institute. Herbarium specimens and photographs create a voucher, allowing the identity to be verified later if any questions arise. Herbarium vouchers will be collected for several reasons. They will allow species identification to be revisited if there are any questions about identity. If any new species are suspected the voucher provides a sample to examine. These samples collected allow vouchering of what is present at the sites, can be used to compare against historical records, and will serve as a baseline of what is present currently and if it changes in the future due to climate change. Data will be accessible through a public online portal. Soil samples will be collected for soil analysis

between sites to control for the influence of soil composition (Ferreyra et al. 1998 a and b).

Percentage of vegetation coverage will also be calculated along with life form as outlined by Ferreyra et al. (1998 a and b). Ferreyra et al. (1998 a and b) outlined the following life forms in their paper, which are consistent with Colorado's alpine flora:

- Annual
- Perennial
- Perennial graminoides
- Grasses
- Sedegs
- Rushes
- Suffruticose plants
- Shrubs

Collected herbarium and tissue samples will be deposited at the Kathryn Kalmbach Herbarium (KHD) at Denver Botanic Gardens.

Data analysis will be done by identifying all the herbarium specimens and determining which areas have the highest species diversity. Precipitation through PRISM will then be consulted again, to determine if in fact the driest area has the highest diversity. (Ferreyra et al., 1998 a and b). This will also allow it to be determined if there is a precipitation range where species diversity is highest. The number of species can be compared at each site against those in Patagonia to see if the scale is the same or different.

For statistical analysis I will use vegan (R package) and a linear regression. ANOVA if there are differences in the soil samples to control for the influence of soil composition. I will also do a multivariate ordination analysis for the variation between plots at each site. Ordination will also allow it to be determined if there are changes in community composition along the precipitation gradient.

## Work Plan

Field work will be undertaken in the Summer of 2017 from late June to late July to align with the peak bloom time of most alpine plants. During this time herbarium, soil samples and tissue samples will be collected, list of species compiled, and percentage of vegetation coverage



calculated. Sites will be revisited twice during the 2017 growing season after July to collect the full spectrum of species present at each site. Herbarium samples will be identified and processed during the summer of 2017 at Denver Botanic Gardens herbarium. During the fall/winter of 2017/2018 data collected in the 2017 field season will be compiled and analyzed. Species identification will be confirmed at the Denver Botanic Gardens herbarium. A final research paper will be completed by May 2018.

### Budget

| Items                                       | Funds request<br>from URSC | Funds requested<br>from other<br>sources | Source of other<br>funds | comments                        |
|---|----------------------------|--|--------------------------|---------------------------------|
| <b>Equipment<br/>(Non-<br/>consumable)</b>  |                            |  |                          |                                 |
| Herbarium plant<br>press                    |                            |  |                          | Already<br>possess              |
| PVC Plot for<br>quadrants                   |                            |  |                          | DBG<br>herbarium will<br>supply |
| trowel for soil<br>and herbarium<br>samples |                            |  |                          | Already<br>posses               |
| Field Vehicle                               |                            |  |                          | Already<br>possess              |

|   |               |                |   |                 |
|---|---------------|----------------|---|-----------------|
| Tent and back packing supplies  |               |                |   | Already possess |
| <b>Supplies (Consumable)</b>  |               |                |   |                 |
| Herbarium paper and herbarium supplies  |               |                | Denver Botanic Gardens herbarium                            |                 |
| <b>Fuel (5 sites x 2 visits x 200-400 miles round trip x 20 miles a gallon x\$2.50)</b> | <b>\$550</b>  |                |   |                 |
| <b>Food x \$20 a day x 3-4 people x 20 field days</b>                                   |               | <b>\$1,400</b> | <b>Colorado Native Plant Society Grant due Feb 20, 2017</b> |                 |
| <b>Zip lock Plastic bags for collecting soil samples</b>                                | <b>\$4.99</b> |                |   |                 |

## Budget Justification

### Non-Consumables

**Herbarium** plant press- Needed to produce high quality herbarium specimens.

**PVC plot**-Needed to outline study plots to collect data and specimens. Recommended by Denver Botanic Gardens research staff over tape measures

**Trowel**- Need to collect herbarium species and soil samples.

**Field Vehicle**- Needed for transportation to get to field sites.

**Tent and back packing supplies**- Needed for possible overnight stays as some sites are quite remote.

### Consumables

**Herbarium paper and supplies**- Needed for preparing high quality herbarium specimens that will be used as a scientific resource for years to come. Blotting paper, acid free archival paper, glues etc.

**Fuel**- needed to drive vehicle to research sites across Colorado's Alpine Tundra. A bit of extra money was estimated to cover the potential of higher fuel costs, or an extra trip

**Food**- will be needed during the field work session which may last several days in Colorado's high Country. About 20 field days are expected. A little bit of extra money was estimated to cover any unforeseeable food needs.

**Zip lock bags**- Needed for collecting soil samples

\*As this project links with Denver Botanic Gardens Kathryn Kalmbach herbarium, they will help supply the materials needed to take herbarium samples and tissue samples.

## Relevance to Current Coursework

This proposed study supports the main reason for me deciding to undertake a master's at Regis to work with Dr. Kleier. It supports not only what I am working on as curator of Alpine Collections at Denver Botanic Gardens but it also ties in nicely to the courses I am taking at Regis involving Forest Ecology and Grant Writing Seminar. Forest Ecology has been great for widening my understanding of ecology and Grant Writing seminar has helped me write stronger, more scientifically structured papers. The skills I am learning in Grant Writing will be invaluable for writing the research paper

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## CHAPTER 3. JOURNAL MANUSCRIPT: WHAT DRIVES SPECIES RICHNESS IN COLORADO'S ALPINE TUNDRA?

### Abstract

Despite years of research, drivers of vascular plant species richness in Colorado's alpine tundra habitats are largely unknown. Factors such as slope aspect, Pleistocene glaciation, nutrient levels, latitude and longitude, snow depth, and disturbance have been studied. Despite this research, few patterns have emerged. Research in Colorado has been conducted on a few well studied mountains. Aridity is one factor that has not been well studied but shows promise in explaining species richness. In Patagonia and the Swiss Alps, increasing aridity correlates with higher species richness. Here, a full species assessment was conducted on nine mountains previously under researched or not researched in fell field and dry meadow communities. These nine sites covered the precipitation gradient in Colorado from driest to wettest conditions (425mm-1941mm) found above 3657 meters. We found that the abiotic factors of increased precipitation, substrate pH, rather than aridity offered a better explanation of what drives higher species richness. Additionally, we discuss an ecotone between fell fields and dry meadows that can form between these two communities or where topography creates intermediate communities with conditions and species composition shared by both communities. We define a new addition to alpine vegetation communities, pseudo-fell field. This community develops where environmental conditions are similar to true fell fields and include both traditional fell field species, but the overall species composition is unique to this community. If we are able to more accurately characterize in-situ community types, researchers will better understand Colorado's alpine environments and how future changes will impact them.

## Introduction

Temperature and precipitation are the primary drivers of plant species diversity globally. Interestingly, latitude and elevation above sea level mirror one another when examining their effect on species diversity. Both species richness and species diversity decrease with increases in latitude and elevation (Körner 2003). While species counts in alpine environments may be lower than ecosystems at lower elevations, the small size of the individual plants and habitat heterogeneity allow for a high species richness in a small area (Körner 2003). Researchers are predicting the effect of climate change on alpine species diversity often solely using temperature without taking into account additional factors that drive richness in alpine environments (Körner 2003; Klanderud and Birks 2003). Alpine areas are particularly sensitive to climate change and abiotic factors such as precipitation, length of growing season, depth and duration of snow cover that change with warming climate also affect alpine ecological patterns (Körner 2002). Future predictions of climate change on alpine environments will be more accurate by improving the understanding of ecological patterns that drive richness in alpine environments.

The factors that drive alpine species richness have long been investigated, but no study has demonstrated a convincing driving factor worldwide. A long list of abiotic factors including latitude, origins of the flora, the effect of glaciation, size and proximity of alpine areas, elevation, substrate, and nutrient concentrations have been examined.

Macroenvironmental factors such as latitude have been examined in both the Rockies and the Alps (Bowman and Damn 2002, Virtanen 2002). Latitude was thought to be a factor that might explain richness, but degree of recent glaciation and size and proximity to other alpine areas are stronger factors in determining local species richness (Bowman and Damn 2002; Hadley 1987). Glaciation explains some of the current species richness in heavily glaciated areas

such as the Northern Rockies and Alps, however it does not offer a full explanation and little explanation in areas that were not heavily glaciated. The effects of Pleistocene glaciation have been measured with the idea that many alpine areas around the world were depopulated during glaciation and species repopulated these areas post-glaciation (Harris 2002). Working off glaciation in the Rockies, the size, proximity and barriers to migration such as the Wyoming basin and Colorado Plateau were explored as probable drivers of species richness (Hadley 1987). Similar to island biogeography, larger alpine areas in close proximity to other alpine locations have higher species richness (Hadley 1987).

Other researchers have supported the idea that past species richness and evolution during the uplift of the current mountain ranges pre-dating Pleistocene glaciation determines present distributions of alpine flora (Chabot and Billings 1972; Körner and Chapin 1994). Individual alpine areas have on average 200-300 species in any given area regardless of past origins (Körner 2002). More recent changes in the local flora were caused by glaciation than evolution and mountain building.

Localized environmental factors also influence alpine species composition. Elevation, slope aspect, snow cover, substrate and nutrient concentrations have all been examined. Elevation and slope aspect, which seem like strong potential drivers, are secondary to stronger drivers such as substrate and precipitation (Kazakis et al. 2007; Wohlgemuth 2002; Nagy and Grabherr 2009).

Of these three factors, snow depth has been studied the longest. Snow depth influences species richness by determining several factors, such as exposure to winter weather, water availability in the growing season, and the length of the growing season (Vestergren 1902;



Komarkova and Weber 1978; Komarkova 1979; Harrison 1986; Walker et al. 1993; Bowman and Damn 2002; Virtanen et al. 2002).

While snow depth offered a partial explanation for species richness, substrate type and pH offers additional information and has been explored in Europe and the Rockies (Bamberg and Major 1968, Wohlgemuth 2002; Virtanen et al. 2002). Substrate type and pH was found to be the strongest driver in determining species richness in the Alps (Wohlgemuth 2002). At smaller scales, nutrient concentrations were examined in the Southern and Middle Rockies (Bowman and Damn 2002). Nutrient concentrations in Colorado's alpine tundra showed positive effects on density and biomass, but not species richness (Bowman and Damn 2002). Despite the sizable amount of research, the above abiotic factors do not fully explain what drives species richness. Additional attempts explored the intermediate disturbance hypothesis (IDH) which can be caused by both abiotic and biotic factors such as landslides, frost heaving, and rodents. Under IDH local species richness is highest between high disturbance and low disturbance. If the disturbance is too frequent no species are able gain a foothold and if it is too infrequent aggressive tend to dominate the community. IDH from frost heaving and rodents has also failed to fully explain alpine floral diversity (Fox 1981, 1985; Körner and Chaplin 1994).

The above factors have failed to fully produce predictable patterns in species richness in the alpine worldwide. In the Southern Andes and the Alps, species richness and precipitation showed an inverse relationship across a precipitation gradient (Ferryera et al. 1998a, Ferreyra et al 1998b, Wohlgemuth 2002). Aridity has not been well studied outside the Alps or Southern Andes but may explain alpine species richness in North America.

In the Patagonian alpine, an environment similar to the North American alpine, higher species diversity is associated with lower precipitation (Ferreyra et al. 1998a). The alpine regions

of North America and those of Patagonia share a similar climate due to their similar latitudes, weather patterns and history of glaciation during the Pleistocene (Ferreyra et al. 1998a, Greenland and Loslenben 2001). Colorado's alpine tundra tends to be drier (425-1941mm) than in Patagonia (1034-2007 mm) although the precipitation ranges overlap (PRISM 2014, Ferreyra et al. 1998a). Precipitation can limit species diversity at either end of its range (Miehe 1988). If it is too dry, there is not enough available water and individuals and species compete for this scarce resource. In higher precipitation environments, fewer species dominate as conditions favor large aggressive species (Körner 2002). The importance of abiotic factors in the alpine means that four factors: snow cover (Harrison 1986; Walker et al. 1993; Bowman and Damn 2002), substrate (Körner 2002; Virtanen 2002; Wohlgemuth 2002), slope and wind (Bowman and Damn 2002) interact to create sharp differences in moisture heterogeneity across the alpine.

Given the ecological similarity between Patagonian and Colorado alpine tundra with moisture heterogeneity across the alpine, this study examined species richness across a precipitation gradient in the Colorado alpine to test Ferreyra et al.'s (1998a) results in an abiotically similar ecosystem. This work will be important for determining how climate change will affect species richness in the Southern Rockies. If we know the abiotic factors that influence alpine ecosystems, then we can better predict how climate change will affect them. For example, snow depth has been shown to drive species richness in Colorado; a factor that could be more variable with climate change (Bowman and Damn 2002; Williams et al. 1996).

Alpine environments are broken into various habitats: dry meadow, wet meadow, fell field, scree, and boulder field are some of the most common (Gellhorn 2002). In this study we examined fell fields and dry meadow. Fell fields and dry meadows differ in important ways,

namely in topography which influences wind exposures, and the resulting snow depth and moisture availability (Gellhorn 2002). Fell fields form on the windblown shoulders and ridges of mountains and are often the windiest and driest of the alpine habitats (Gellhorn 2002). Due to high winds, fell fields have little snow cover in the winter and thus have a higher likelihood of frozen soil where plants are subject to greater frost damage in the spring (Shimono and Gaku, 2005). Soils in fell fields are poorly developed, rocky, and low in organic matter, and wind deflation from strong prevailing winds results in a gravelly pavement-like substrate (Gellhorn 2002; Shimono and Gaku 2005; Walker et al. 2001). Snow distribution patterns influence fell fields through nutrient deposition. For example, mesic alpine meadows have more available nutrients relative to fell fields which are generally nutrient poor as they receive little snow melt water (Theodose and Bowman 1997). Fell field indicator species in Colorado include *Dryas octopetala*, *Paronychia pulvinalis* and *Carex rupestris*. (Nagy and Grabherr 2009).

Dry meadows form where there is greater winter snow cover than fell fields (Gellhorn 2002). They are often downslope of fell fields and receive great moisture and more protection from winter cold and desiccating winds. The greater protection from the stressful elements encountered by fell field species allows denser and taller vegetation to develop. True dry meadows are dominated by dense aggressive grasses, *Kobresia*, sedges, and larger mat or clump forming forbs (Gellhorn 2002). These larger more aggressive plants outcompete many of the shorter cushion and mat forming plants found in fell fields.

The objectives of this project overall: (1) to better define fell fields, dry meadows and the ecotone that can exist at nine sites across a precipitation gradient in the Colorado alpine, (2) determine if aridity is a driving factor in species richness in the Rockies (3) bolster herbarium

specimen collections from poorly collected areas and contribute tissue samples of observed flora for the Global Genome Initiative (GGI). We predicted that areas receiving less precipitation would have a higher species richness.

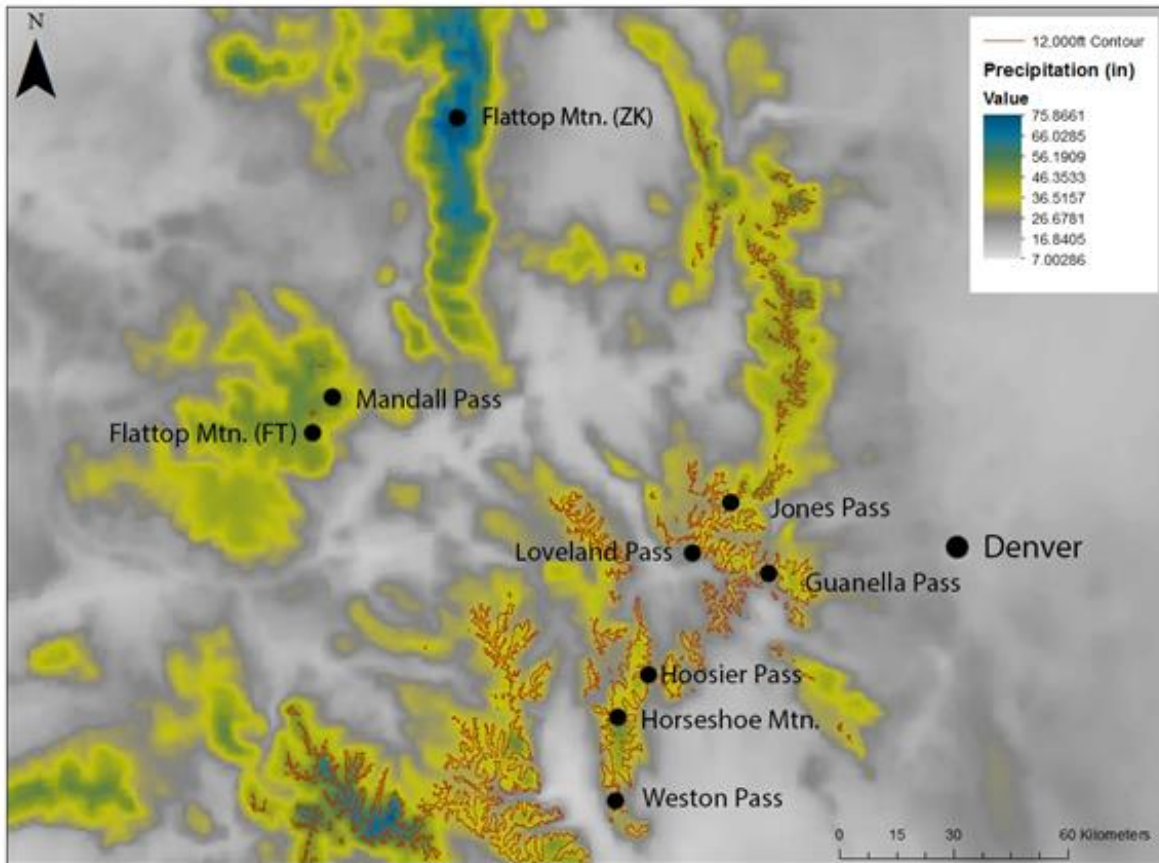
## Methods

### *Study Area*

Precipitation varies widely across Colorado's alpine tundra. The alpine areas in the Rockies of Colorado are largely connected, offering one of the largest continuous alpine areas in the United States (Hadley 1987) (Figure 1). High ridges and passes connect these alpine areas, with large valleys and parks (large open basins partially dissecting the ranges). The study area comprises many individual ranges: The Front, Mosquito, Ten Mile, Sawatch and Gore Ranges are some of the most important. The elevation of the peaks range from 3658-4267m and the passes lie at an elevation of 3505m or greater. The parent bedrock varies widely and can be igneous, metamorphic, or sedimentary in origin depending on the mountain range and its location. The Mosquito range is largely sedimentary with some igneous intrusions, while the others tend to be largely metamorphic.

Northern Colorado's alpine areas are more isolated, the Front Range and the Medicine Bow Range continue almost uninterrupted to the Wyoming border, and they are broken only by a few passes that are below tree line. To the west and northwest of the Front and Medicine Bow Ranges are two isolated alpine areas: The Flat Tops and the Park Range, are separated from the other alpine areas in Colorado. Large, wide parks(local term for the expansive open valleys) and deep valleys filled with vegetation from lower elevations separate the mountains.. Elevations in these Northern ranges are more moderate with peaks topping out between 3353-3800m, and

passes are much lower at 2438-3048m. The parent bedrock in the Flat Tops is largely igneous and the Park Range metamorphic.



**Figure 1.** Location of the nine alpine study sites in North Central Colorado. Thirty-year precipitation averages in North Central Colorado and locations of the study sites. The twelve-thousand-foot elevation contour is represented in red.

**Table 1** Characteristics of the 9 alpine sites surveyed in North, Central Colorado

| Study Site                     | Elevation<br>(m) | Latitude  | Longitude   | Precipitation (mm) 50-<br>year average                            | pH   | Date visited                         |
|--------------------------------|------------------|-----------|-------------|---|------|--------------------------------------|
| Guanella Pass east             | 3728             | 39.55251  | -105.699154 | 425.57mm  | 6.15 | June 23, and<br>August 21,<br>2017   |
| Hoosier Pass                   | 3651             | 39.3566   | -106.0395   | 736.74mm  | 6.2  | June 26, 2017,                       |
| Jones Pass                     | 3699             | 39.773778 | -105.889548 | 774.69mm  | 5.3  | July 6, and<br>August 21 2017        |
| Loveland Pass                  | 3720             | 39.659461 | -105.879334 | 816.21mm  | 5.05 | June 23, and<br>September<br>2017    |
| Weston Pass                    | 3672             | 39.129    | -106.1823   | 1073.08mm   | 6.75 | June 25, 2017,<br>August 15,<br>2017 |
| Horseshoe<br>Mountain          | 3693             | 39.1829   | -106.1855   | 1073.08mm   | 5.95 | June 30,<br>August 21,<br>2017.      |
| Flattop Mountain-<br>Flat Tops | 3586             | 40.0087   | -107.0841   | 1313mm  | 6.9  | July 9, 2017                         |
| Mandall Pass Flat<br>Tops      | 3600             | 40.082247 | -107.097017 | 1196.77mm   | 7.05 | July 8, 2017                         |
| Flattop Mountain<br>Zirkel     | 3669             | 40.807377 | 106.635512  | 1941mm<br>*insufficient data from<br>PRISM for 50-year<br>average | 5.9  | July 15, 2017                        |

### *Climate*

The study area receives year-round precipitation, with the majority of the precipitation falling as snow between the months of September and May. Snowfall is possible year-round, but precipitation generally falls as rain in the warmer months of July, August and early September, when a second pulse of moisture arrives during the North American Monsoon. Winters are long, cold and windy (Greenland and Loslenben 2001), the climate is highly variable between seasons and year to year in both temperature and precipitation. Due to the elevation and position far from the sea, temperatures change quickly. Precipitation can be very low some years, followed by above average years depending on La Niña or El Niño weather patterns in the Pacific. At Niwot Ridge the average December temperature within the cushions of a fell field (the focus of this study) was  $-15.5^{\circ}\text{C}$  (Walker et al. 1993).

### *Site Selection*

The nine alpine sites were chosen in North Central Colorado along a precipitation gradient. Sites were chosen using PRISM Climate data (Oregon State University 2016) and ArcGIS 10.6 (ESRI, 2017) . A raster at the 3576m elevation was created to show annual precipitation averages in the Colorado alpine. Nine sites were chosen in Central and Northern Colorado based on 50-year precipitation averages (Table 1). Using R (R Core Team 2017) and ArcGIS (ESRI, 2017) we pulled estimated annual precipitation for each site going back to 1952 (except for Flattop Mountain Mt Zirkel Wilderness). Fifty-year precipitation averages at the study sites ranges from 425-1313 millimeters annually (PRISM). Flattop Mountain in the Park Range was removed due to its geographic isolation and lack of long term climate data from PRISM. Sites were chosen along a precipitation gradient based on ease of access and known

presence of fell field vegetation. We attempted to select sites within 90 meters of the 3657-elevation contour.

### *Quadrat Selection*

Ten one-meter square plots were selected at each site. The plots were chosen by throwing twenty numbered pin-flags from a central point of the selected site. Each site ended up being about 10 by 10 meters when the pin-flags were thrown. A random number generator was used to select 10 of the numbered pin-flags. At each randomly selected pin-flag, the bottom left corner of a one-meter square quadrat was set and positioned toward magnetic north.

### *Data Collection*

Data were collected June 23-July 15<sup>th</sup>, 2017 to align with the peak bloom time for most alpine plants. All sites except the three northern sites were revisited once more in August or September to collect grasses that were not in bloom in June. The three northern sites were visited once in July due to their distance from roads. For each quadrat, we created a species list for all species present and estimated total vegetation cover, percent cover for each plant species, and percent dead mass in the cushion plants. We also noted whether each species was flowering, setting seed or vegetative. A photograph was taken of each species in each quadrat, and if there were sufficient specimens in bloom or seed, an herbarium specimen was collected along with leaf tissue samples for the Global Genome Initiative. Leaf tissue samples were stored in silica gel immediately upon harvest. Species outside the quadrats, but within the 10 by 10-meter study site, were identified to species levels and herbarium and leaf samples also collected if there were sufficient populations. In addition, we collected soil samples from the first randomly selected



plot at each research site to test pH of the substrate. We measured elevation at each site using a Garmin GPS unit.

### *Data Analysis*

Species were identified using, Wingate & Yeatts (2008) and nomenclature was updated using Ackerfield (2015). Any questionable identifications (particularly within *Poaceae* or *Cyperaceae*) were verified and corrected by Janet Wingate at the Kathryn Kalmbach Herbarium at Denver Botanic Gardens. Soil samples were analyzed for pH, at each of the nine sites to control for the possible effect of substrate on species richness. The soil samples were sorted with a number 12 soil sieve into coarse and fine particles. Twenty grams of soil of each the fine and coarse particle size was mixed with 20 ml distilled water. The soil and water were mixed into slurry, covered with cling wrap and left to set 15 mins. The pH of the slurry was measured with a handheld pH meter (Oakion ecotester). We measured the pH of both the fine and coarse particles. An average of fine and coarse soil particles was used for statistical analysis. Yearly precipitation was lifted from PRISM datasets for the past 50 years, yielding mean values for each site.

### *Statistical Analysis*

Total species richness from each site was analyzed as a function of substrate pH, elevation, 50-year precipitation and habitat using a generalized linear model (Poisson). A similar model was built using individual plot species richness as a response variable as a function of substrate pH, elevation, and 50-year precipitation average. Vegetation cover was analyzed as a response variable to substrate pH, elevation, 50-year precipitation average, and habitat. Models were evaluated based on AIC scores, residual variance, and residual degrees freedom; the best models for the best fitting set of response variables were selected and reported. We analyzed site

species richness separately from within-plot richness because site richness included species not found within plots but within the 10 by 10 meter study site. Therefore, site species richness represents a broader characterization of vegetation at the study site than plot species richness. A principal components analysis (PCA) examined the correlation structure of environmental variables.

We performed a cluster analysis to determine community types among our plots. We eliminated any species that were present in fewer than two sites for our cluster analysis. The “vegdist” function in the “vegan” package in R (Oksanen et al. 2013) was used to calculate Bray-Curtis distances between site species compositions. Hierarchical agglomerative cluster analysis with the “hclust” function the “stats” R package (R Core Team 2017) helped to classify plots. We plotted the hierarchical cluster and drew boxes around each cluster class by using the “rect.hclust” function in the “vegan” package (Oksanen et al. 2017).

Non-metric multidimensional ordinations (NMDS) were produced based on a distance matrix of the percent cover of all species found at more than one site. Again, we removed any species that did not occur in at least one site, resulting in 49 species total. Principal component scores, calculated earlier, were added to the environmental data. Using the “vegdist” function in the “vegan” package (Oksanen et al. 2017), we calculated the Bray-Curtis distances between site species compositions. We ran ordinations in each dimension using the “ecodist” package (Goslee & Urban 2007). We found three dimensions would be sufficient using a stress <0.2 cutoff. Lastly, to complete the ordination we used the “distance” function in the “ecodist” package to find the Bray-Curtis distances and plot them against species composition distances to determine if there was a linear relationship. After words, we rotated the axes using the base stats

package (R Core Team 2017) so that the greatest amount of variation was explained by the first axis. These scores were plotted and we overlaid significant environmental predictors.

All analyses were completed in R version 3.4.4 (R 2017) using the vegan (Oksanen 2018), labdsv (Roberts 2016), ecodist (Goslee and Urban 2007) and cluster (Maechler et al. 2017) packages for cluster and ordination analyses. The ggplot2 package (Wickham 2009) was used to produce scatter plot figures.

## Results

### *General Site and Vegetation Characteristics*

In total we collected and identified 49 species comprised of 35 genera across all 90 research plots at 9 different mountain sites in north central Colorado. Herbaceous perennial forbs were the only vegetation type present at research sites. Mean vegetation cover was 31% across all research plots. Mean elevation for all nine research sites was 3669 meters and average substrate pH was 6.14. Out of 90 plots the most frequently observed species and the percentage of plots in which they were found are in Table 2; The most abundant families are listed in table 3 and represent some of the most abundant families in the Colorado flora (Ackerfield 2015).

**Table 2.** The five most observed species in the 90 plots and number of plots in which they were found

| Species                      | Number of occurrences (out of 90) |
|------------------------------|-----------------------------------|
| <i>Minuartia obtusiloba</i>  | 87                                |
| <i>Paronychia pulvinata</i>  | 56                                |
| <i>Arenaria fendleri</i>     | 51                                |
| <i>Oreoxis alpina</i>        | 49                                |
| <i>Trifolium dasyphyllum</i> | 41                                |

**Table 3.** The five most abundant families at the nine sites

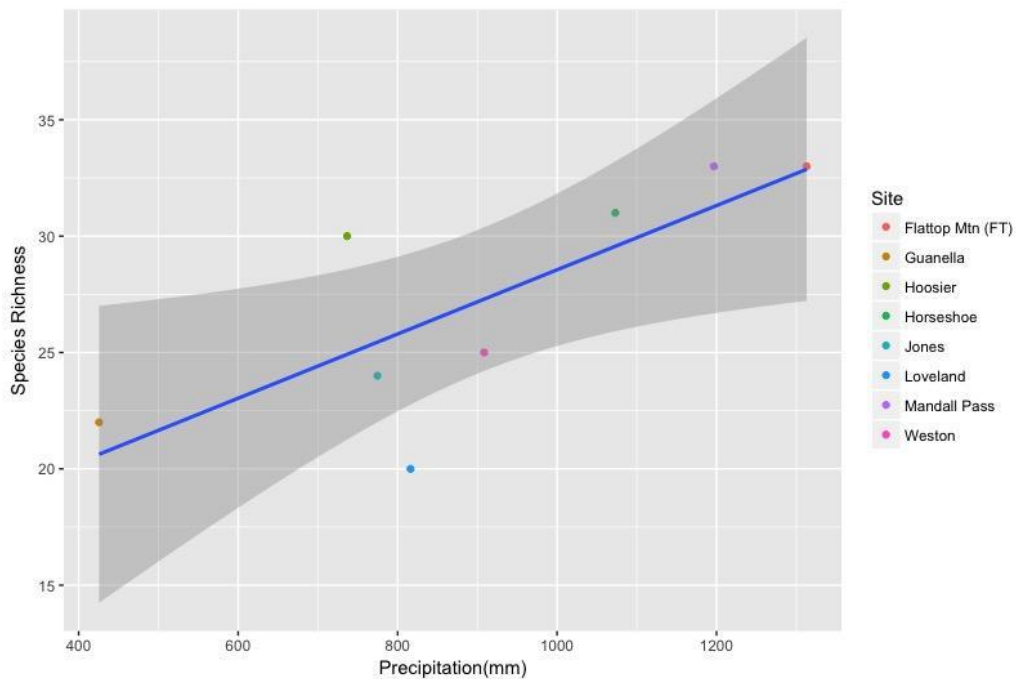
| Family                 | Number of Species |
|------------------------|-------------------|
| <i>Poaceae</i>         | 7                 |
| <i>Asteraceae</i>      | 6                 |
| <i>Caryophyllaceae</i> | 4                 |
| <i>Fabaceae</i>        | 4                 |
| <i>Cyperaceae</i>      | 4                 |

### *General Linear Model Results*

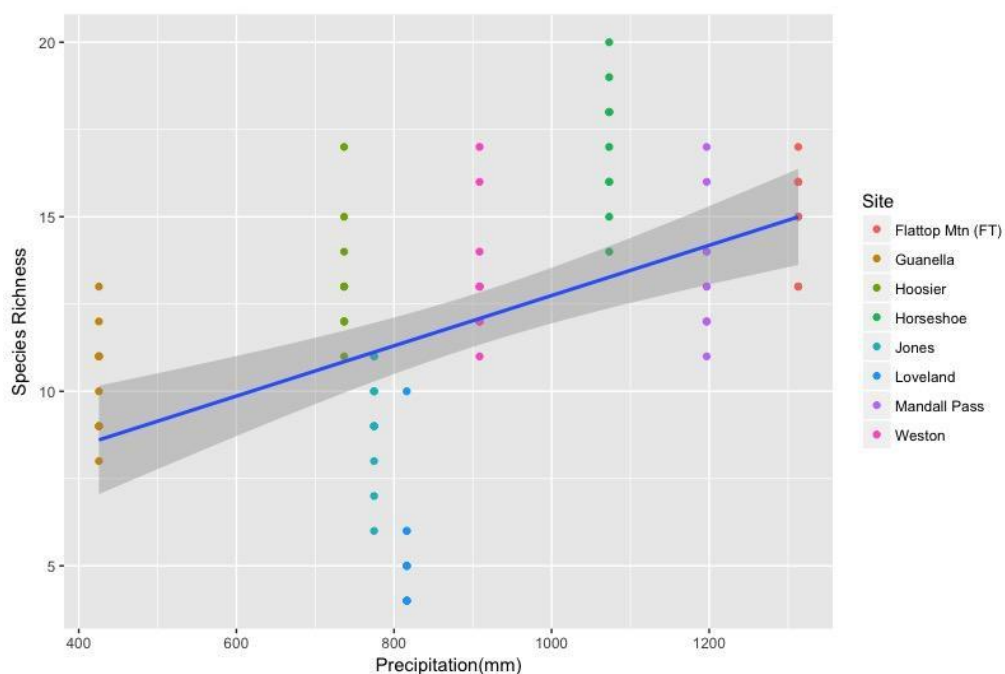
We found that two abiotic factors, substrate pH and annual precipitation, significantly drive species richness across the eight sites across the precipitation gradient in central and northern Colorado. Both precipitation and pH have a direct positive correlation with species richness and vegetation cover. Our generalized linear models indicate that precipitation has a significant positive correlation with both total site species richness and plot species richness; for every millimeter increase in precipitation, total species richness increases by 0.005 (95% confidence=7.2x10<sup>-5</sup> to 0.001) and plot species richness increases by 0.001 (95% CI=1.70x10<sup>-5</sup> to 0.006) ( $p = 0.0476$  and  $0.0431$ , respectively) (Figure 1 and 2). In other words, a five-hundred-millimeter increase in precipitation would yield an increase of 2.5 additional species. This is counter to our hypothesis that species richness would increase with a lower site precipitation. Substrate pH was also significantly positively correlated with plot species richness, ( $p = 2.3 \times 10^{-5}$ ) (Figure 4). An increase in (95% CI=1.57x10<sup>-1</sup> to 0.493)

Habitat type has a significant correlation with both species richness and vegetation cover. Fell fields and pseudo fell fields have a lower percentage vegetation cover than both ecotone and dry meadow communities; fell fields have 5.42% (95% CI=4.72% to 6.88%) less vegetation

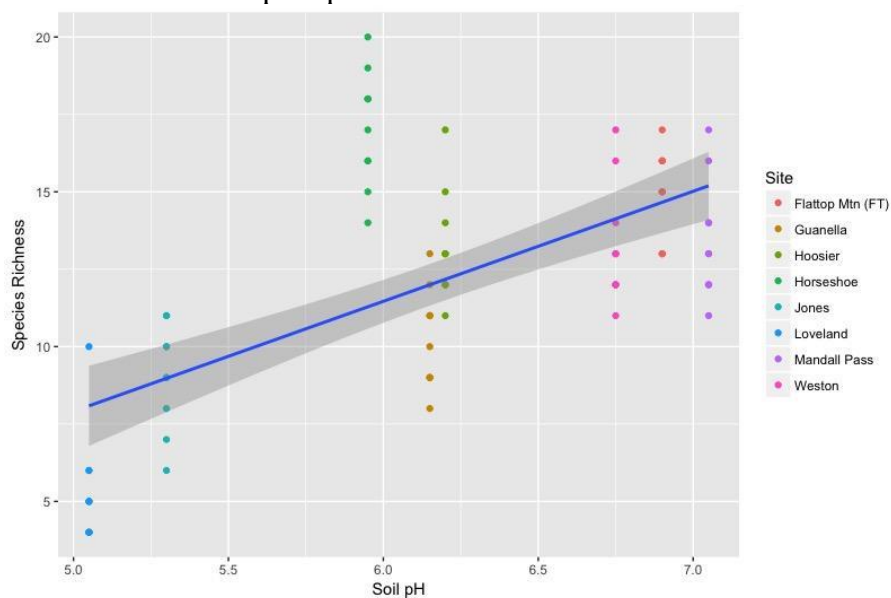
cover than dry meadows pseudo fell fields have 6.82% (95% CI= 5.87 to 7.18%) less than dry meadow communities ( $p = .005$  and  $2 \times 10^{-16}$ , respectively) (Figure 6). Species richness, however, does not follow the same pattern as vegetation cover relative to habitat type. Ecotone communities have a higher species richness than dry meadows ( $p = 0.005$ ) and pseudo-fell fields have a higher species richness than any of the other community types ( $p = 0.0007$ ) Fell fields do not have a significantly different plot species richness than the other community types ( $p=0.328$ ) (Figure 7).



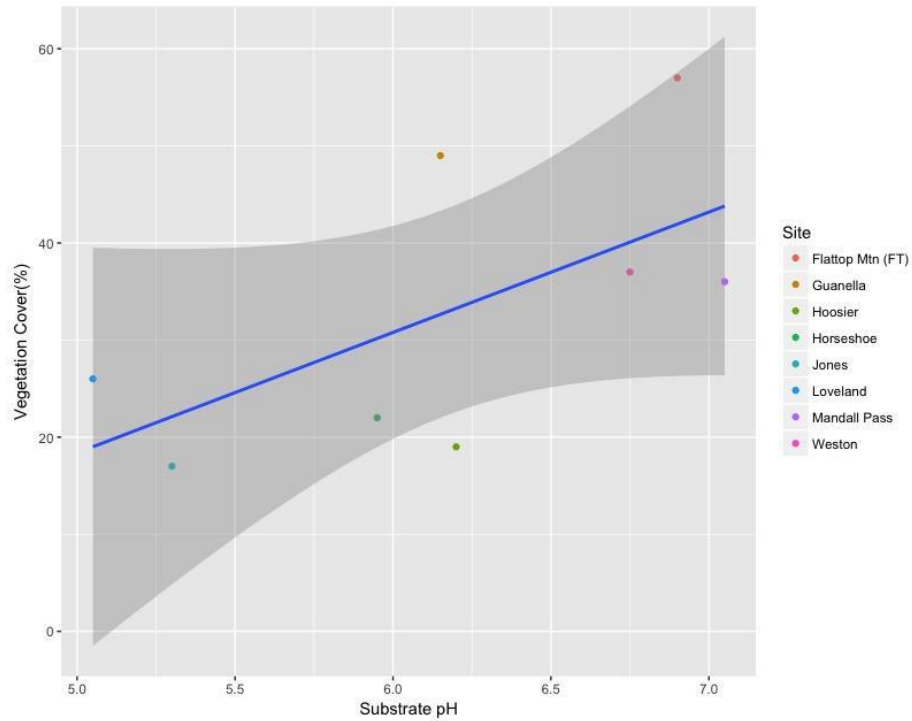
**Figure 2.** A linear regression showing the total species richness at each site as a function of site precipitation; 95% confidence interval in dark gray. Site species richness increases with increased precipitation ( $p=0.0476$ )



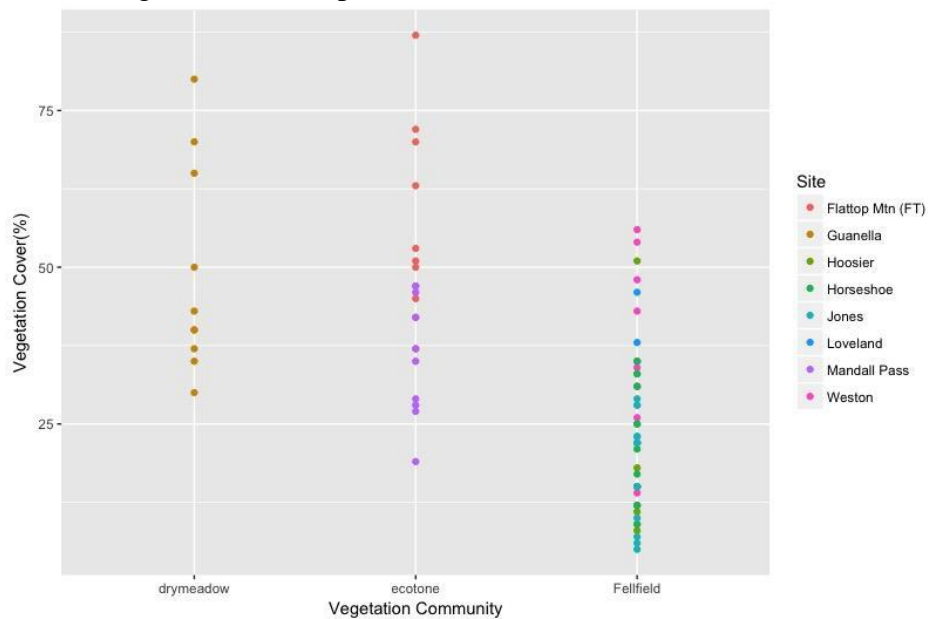
**Figure 3.** A linear regression showing plot species richness as a function of site precipitation; 95% confidence interval with dark gray shading (p-value 0.0431) Localized plant species richness increases with increased precipitation



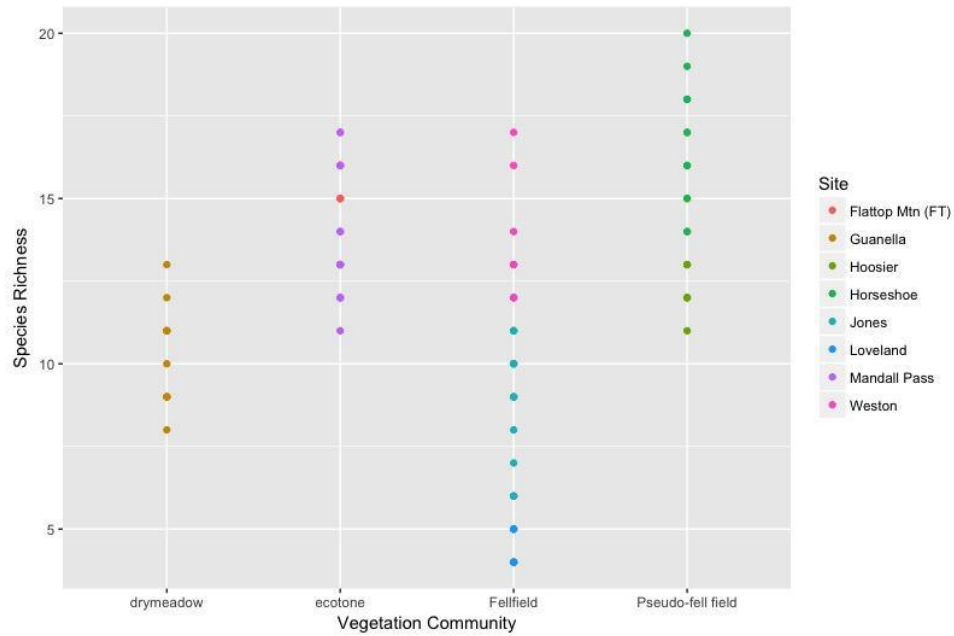
**Figure 4.** A linear regression showing the relationship between site soil pH and plot species richness. Soil pH has a direct positive relationship with plot species richness. Sites with a pH closer to neutral have a higher species richness ( $p=2.3e-5$ )



**Figure 5.** Linear regression with a 95% confidence interval showing the relationship between soil pH and mean vegetation cover at our study sites. Sites with higher soil pH (closer to neutral) have a higher mean vegetation cover ( $p=2.6e-8$ )



**Figure 6.** Scatterplot of vegetation cover as a function of plant community. Dry meadows and ecotones have significantly higher vegetation cover than fell field communities ( $p=1.12e-14$  and  $2e-15$ , respectively)



**Figure 7.** Scatterplot of total site species richness as a function of plant community. Ecotones and pseudo fell fields have higher plot species richness relative to dry meadows (p-value=0.05786 and 0.000717, respectively). Fell fields do not have a significantly different species richness relative to the other community types (p=0.328).

### Gradient Analysis

A cluster analysis was conducted in R on the vegetation composition of all 90 research plots. This analysis divided the species into vegetation communities which correspond to habitat types defined by visual observations in the field (see Table 3). Longitude, precipitation, latitude, species richness, elevation, and vegetation cover have significant correlation to difference in species composition. Five community types resulted from the cluster analysis. See Figure 8 for a visual representation of the vegetation community types, with environmental gradients overlaid. Group one was composed of *Silene acaulis* and *Paronychia pulvinata*, cushion-forming alpine species associated with fell fields and dry slopes. A larger suite of species including *Arenaria fendleri*, *Carex rupestris*, *Oreoxis alpina*, *Potentilla nivea*, and *Trifolium dasyphyllum* were representative of a second group of fell field species. A third community type including



*Eritrichium aretioides*, *Tetraneris acaulis*, and *Phlox condensata* represent species found in fell field communities or habitats with similar environmental conditions to true fell fields. An ecotone between fell field and dry meadow communities existed at several of the research sites. Species including *Smelowskia calycina*, *Minuartia obtusiloba*, and *Carex elynoides* compose this ecotone plant community. Lastly, some research sites had a vegetation community more closely described a dry meadow than a fell field. *Poa glauca ssp. rupicola*, *Castilleja occidentalis*, *Tetraneris grandiflora*, and *Carex cyperoides* compose this community. (Figure below showing the vegetation cover in the three communities). Vegetation communities were classified through a combination of vegetation analysis and in situ observation of physical factors. See Table 4 for a summary of sites and their vegetation community designation.

Longitude, precipitation, latitude, species richness, elevation, and vegetation cover have significant correlation to difference in species composition. The NMDS ordination had a stress value of 0.0581 and explained 87.45% of the variability in species composition across sites. We reported three axes in order to account for an acceptable amount of variance. Latitude and precipitation were most strongly correlated to species composition ( $r^2 = 0.19277$ ,  $p=0.001$  and  $r^2 = 0.13697$ ,  $p=0.0013$ , respectively). Latitude and precipitation gradients scaled in the same direction. Species richness ( $r^2=0.08307$ ,  $p=0.0009$ ) was perpendicular to both elevation and vegetation cover ( $r^2=0.03265$ ,  $p=0.001$  and  $r^2=0.03265$ ,  $p=0.002$ , respectively).

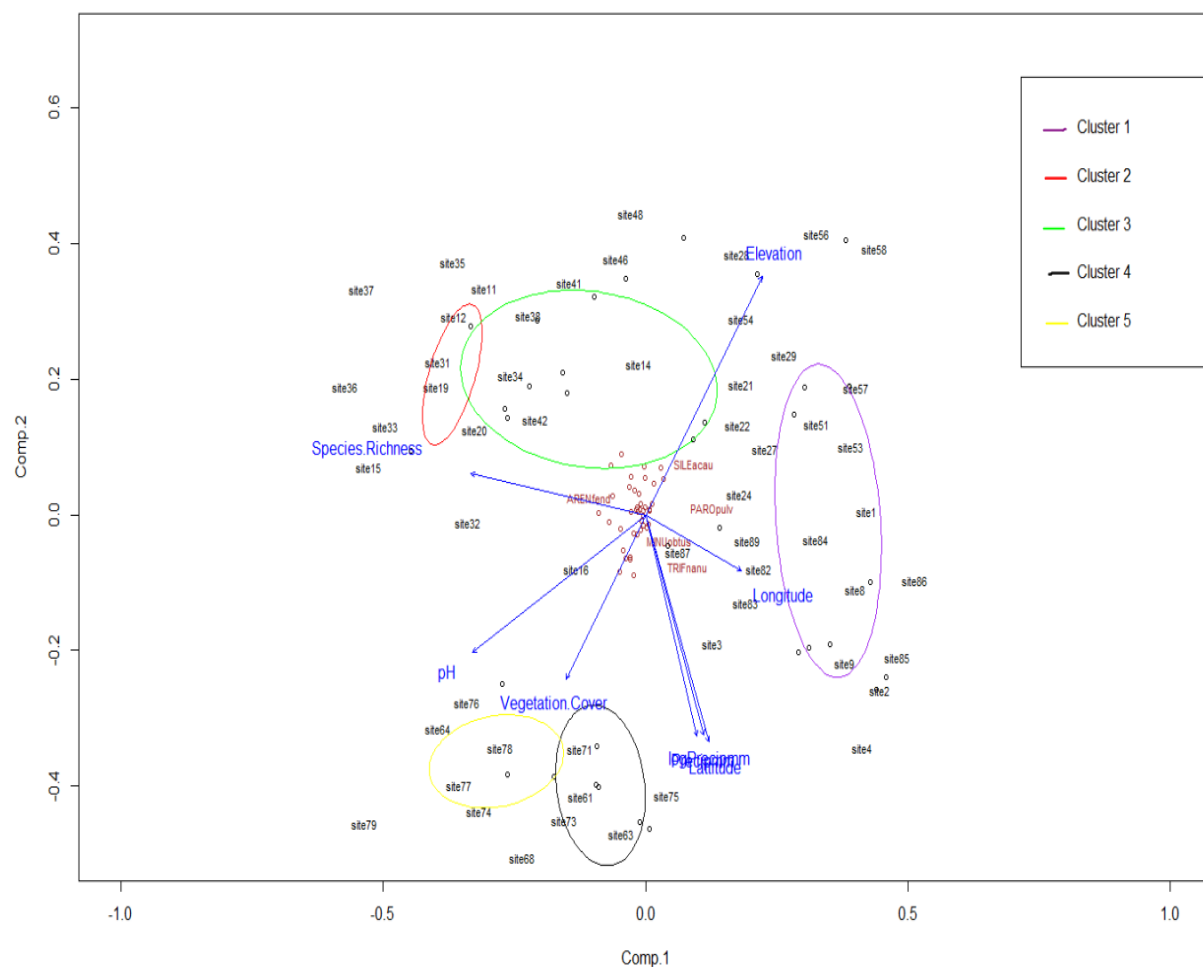
**Table 4.** Study sites and their community classification

| <b>Site</b>                | <b>Community Designation</b>     |
|----------------------------|----------------------------------|
| Loveland                   | Fell field                       |
| Guanella                   | Dry Meadow                       |
| Weston                     | Fell field                       |
| Hoosier Pass               | Pseudo fell-field                |
| Horseshoe                  | Pseudo fell-field                |
| Jones                      | Fell Field                       |
| Flattop Mountain Flat Tops | Ecotone of dry meadow/fell field |
| Mandall Pass               | Ecotone of dry meadow/fell field |
| Flattop Zirkels            | Fell field                       |

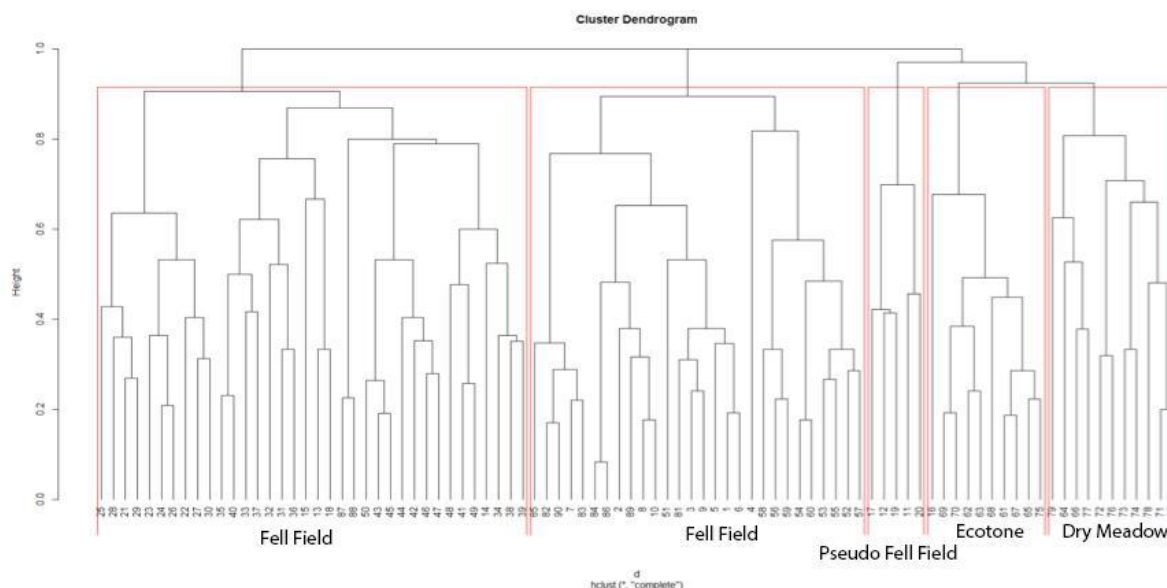
**Table 5:** List of species found at sites, which clusters they are most commonly found in, and their preferred habitat types. The cluster analysis showed that typical fell field, ecotone, and dry meadow species assemblages are grouped together.

| Species                                      | Vegetation Group | Habitat     |
|--|------------------|-------------|
| <i>Paronychia pulvinata</i>                  | 1                | Fell Field  |
| <i>Silene acaulis</i>                        | 1                | Fell Field  |
| <i>Arenaria fendleri</i>                     | 2                | Fell Field  |
| <i>Carex rupestris</i>                       | 2                | Fell Field  |
| <i>Eriogonum acutatum</i> var <i>xanthum</i> | 2                | Fell Field  |
| <i>Helictotrichon mortonianum</i>            | 2                | Fell Field  |
| <i>Oreoxis alpina</i>                        | 2                | Fell Field  |
| <i>Potentilla nivea</i>                      | 2                | Fell Field  |
| <i>Sedum lanceolatum</i>                     | 2                | Fell Field  |
| <i>Trifolium dasyphyllum</i>                 | 2                | Fell Field  |
| <i>Eritrichium aretioides</i>                | 3                | Fell Field* |
| <i>Frasera speciosa</i>                      | 3                | Fell Field* |
| <i>Kobresia myosuroides</i>                  | 3                | Fell Field* |
| <i>Oxytropis parryi</i>                      | 3                | Fell Field* |
| <i>Phlox condensata</i>                      | 3                | Fell Field* |
| <i>Tetraneuris acaulis</i>                   | 3                | Fell Field* |
| <i>Carex elynoides</i>                       | 4                | Ecotone     |
| <i>Erigeron pinnesectus</i>                  | 4                | Ecotone     |
| <i>Luzula spicata</i>                        | 4                | Ecotone     |
| <i>Minuartia obtusiloba</i>                  | 4                | Ecotone     |
| <i>Polemonium viscosum</i>                   | 4                | Ecotone     |
| <i>Smelowskia calycina</i>                   | 4                | Ecotone     |
| <i>Carex cyperoides</i>                      | 5                | Dry Meadow  |
| <i>Castilleja occidentalis</i>               | 5                | Dry Meadow  |
| <i>Poa glauca rupicola</i>                   | 5                | Dry Meadow  |
| <i>Potentilla diversifolia</i>               | 5                | Dry meadow  |
| <i>Potentilla ovina</i>                      | 5                | Dry Meadow  |
| <i>Tetraneuris grandiflora</i>               | 5                | Dry Meadow  |

\*Sites with fell field like conditions, but do not fit the classic definition of fell field. We term these pseudo fell-fields



**Figure 8.** Cluster analysis of species found at all 90 plots and cluster ellipses of vegetation groups. Biplot of environmental variables overlaid in blue. Distinct vegetation communities emerged along environmental gradients. Vegetation clusters are divided as follows: fell fields comprised of two true fell field vegetation groups (fell field 1 and 2), pseudo-fell fields (fell field 3), ecotone, and a dry meadow community



**Figure 9.** Dendrogram showing the five clusters into which the individual plots fell. The first two groups are fell fields, the third is a pseudo fell field community, and the fourth is the ecotone between fell field and fifth is the dry meadow assemblage

## Discussion

The goals of this study were to 1) characterize alpine vegetation across a precipitation gradient in the alpine of Colorado 2) determine if aridity is a driving factor in species richness and 3) booster herbarium specimen collections in poorly collected areas and contribute tissue samples of the observed flora to the Global Genome initiative (GGI). Our study provides evidence that higher precipitation and substrate pH drive higher species richness in Colorado's alpine tundra. Prior to our study the only convincing driving factors impacting species richness across all alpine habitats were snow cover, the size of the alpine area and distance to other alpine areas (Bowman and Damn 2002; Hadley 1987). Precipitation has increased on the Front Range of Colorado since 1951 (Williams et al. 1996). Climate prediction models with the addition of

precipitation and substrate pH will improve predictions on how alpine areas will be impacted by climate change.

### *Goal 1*

Fell fields, dry meadows, and the ecotone between the two were studied in this project. While fell fields are traditionally well-defined in literature, a wider definition of what constitutes fell field species composition is needed. Many of the species traditionally defined as fell field indicator species were present; however, some species traditionally defined as indicators were absent from each individual plots and more broadly at most of the nine sites. For example, *Dryas octopetala* is considered a fell field indicator species, but it was absent from our study plots (Nagy and Grabherr 2009). We offer updated definitions of fell fields below and discuss an ecotone that forms between fell fields and dry meadows in certain mountain ranges due to topography. Traditionally there is a well-defined boundary between various alpine communities in Colorado (Bowman and Damn 2002). The plant communities at many of our sites could be clearly described as fell field or dry meadows. However, we did find some sites that are true ecotones between several communities. Our survey of nine fell field sites indicated that *Arenaria fendleri*, *Minuartia obtusiloba*, *Trifolium dasyphyllum*, *Trifolium nanum*, and *Phlox condensata* are common forb inhabitants of fell field communities in central and northern Colorado.

*Dryas octopetala* is listed as a fell field indicator species in Colorado (Nagy and Grabherr 2009); however, it was not present in any of the plots or within the 10 x 10 meter plots sites. It was also not present near any of the study sites in the surrounding communities. At Loveland, Weston, and Horseshoe Mountain it was found on the mountain but in very different habitats

than fell field. Thus, we do not consider *Dryas octopetala* to be a fell field community indicator in Colorado.

### *Fell field/dry meadow ecotone*

Some of our sites, especially those in the Flat Tops, are really ecotones between fell fields and dry meadows. The flat topography of the Flat Tops does not lend itself to the formation of classic fell field communities, since areas are generally not scoured free of snow by the wind. Instead ecotones of dry meadows and fell fields form on the edge of cliffs and on hummocks on long and gentle ramp-like slopes leading up to the highest summits. Most slopes and summits are densely vegetated meadows or pseudo-boulder fields of small volcanic rock with relatively few species and low vegetation cover. These ecotones between dry meadow and fell field may be found elsewhere in the state. Additional study sites that did not fit the classic fell field description were Horseshoe Mountain, Hoosier Pass and Guanella Pass. We define Guanella Pass as a dry meadow, rather than the ecotone defined above, due to the presence of larger grasses, sedges and high percentage of vegetation cover in the plots.

Over the course of the study we observed a third community type, found in locations where environmental conditions are similar to fell fields but are not located on true alpine ridgelines. This community is composed of species commonly found in true fell fields (*Eritrichium aretioides*, *Phlox condensata*, etc.) but ultimately contains a unique array of plant species that is neither well represented by true fell field nor dry meadow species. Therefore, rather than characterizing this community as a dry meadow-fell field ecotone, we believe this constitutes a distinct vegetation community and name it the pseudo fell-field. For example, Horseshoe Mountain and Hoosier Pass, are located on windblown secondary ridgelines protected from the full force of prevailing westerly winds; both of these had many of the classic species

and characteristics of a fell field but also had nontraditional species. *Frasera speciosa* and *Bistorta bistortoides* are more typically found in dry meadows even though our ordination analysis placed *Frasera speciosa* in the last category of fell field (class 3).

### *Implications of Goal 1*

Stronger definitions of fell-fields, dry meadows, the ecotone between the two and the new definition of pseudo-fell field help scientists, botanists, and public land managers better understand these communities. Additionally, by adding to the understanding of where these communities existed in 2017 both short and long-term changes at these sites can be observed and documented. Several of the areas we visited in 2017 had not be scientifically documented as to community type and vegetation composition.

Our study was one of the first to complete a full species assessment at multiple sites in Colorado's alpine tundra with the aim of testing the effects of precipitation and substrate on alpine species richness. Much of the work cited in this paper was completed at Niwot Ridge (Bowman and Damn 2002; Greenland and Losleben 2001; Komarkova and Weber 1978, 2001; Theodose and Bowman 1997). Niwot Ridge cannot be overlooked for the important contributions it has made to our understanding of alpine ecology, however it is one site within a much larger contiguous alpine area. Mountainous areas have large variation to climate change on both horizontal and vertical scales (Diaz and Bradley; Weber et al. 1997). Thus, expanding the sites studied in the Colorado Rockies presents an ever-expanding picture of how alpine environments in Colorado will respond to change.



## Goal 2

### *Precipitation as a driver of species richness*

Precipitation is a driver in species richness in Colorado's alpine tundra. There is a direct positive relationship, as precipitation increases, species richness increases. Although our generalized linear model yielded a modest effect size (0.005 species/mm), in the biological context of a large precipitation range in North Central Colorado, we believe this effect has a significant bearing on speciation in alpine environs. For example, within the confines of this study, precipitation had a range of over 1516 mm, which, according to our model could yield an increase of over seven additional species. Indeed, we observed a total of 22 species at Guanella Pass which 425.57mm average annual and 33 at Flattop Mountain with 1313mm annual precipitation. It is not surprising the environmental variables played such an important roles in determining species composition as abiotic factors are the primary predictors of local plant community composition (Klanderud et al 2015). Our results differed from others in the Alps or Andes likely because Colorado is drier and more continental than the Andes or the Alps. Our driest site was much drier than the sites tested in the Southern Andes ( 1034mm in Argentina versus 425 mm in Colorado). Interestingly, several species were limited to the drier end of the precipitation spectrum, *Tetrandeum acaulis* and *Eriogonum acutatum* var *xanthum* were both limited to the drier sites in Central Colorado. *Tetrandeum acaulis* was found at four of the sites: Guanella, Weston, Hoosier, and Horseshoe Mountain. It was absent from Loveland Pass, which is not far from Guanella or Hoosier in airmiles. Loveland is wetter than the four sites and was also a classic Colorado fell field, while the other sites were dry meadow, or pseudo fell fields with a richer assortment of species. The distribution of *Tetrandeum acaulis* may be associated with precipitation or it could follows the calcareous (limestone, dolomite) of the Mosquito Range

and across the east-west running Hoosier Ridge and associated mountains to the Mount Evans Massif and Guanella Pass. Loveland Pass is just north of this east west trending range of mountains and maybe out of this species range. *Eriogonum acutatum* var *xanthum* was only found at the driest site. Other species such as *Oxytropis podocarpa* and *Oxytropis parryi*, were limited to the sites in the Mosquito Range: Weston, Hoosier and Horseshoe Mountain. Flattop Mountain in the Flat Tops and Mandal Pass, two of the wettest sites had the highest and second highest species counts at 33 (tied with Hoosier) and 32, respectively.

### *pH as a driver of species richness*

While we did not set out to prove that substrate pH is also a driver of alpine vegetation diversity, our results show substrate (parent rock type) is a statistically significant predictor of species richness in Colorado; there is a general increase in the number of species with an increase in pH, moving from acidic towards neutral. In the Swiss Alps, it was shown that substrate pH was the best predictor of species richness and composition (Wohlgemuth 2002). Additional studies throughout Europe's high mountains found that the calcareous soils (higher pH) had greater species richness than siliceous soils, after accounting for snow cover (Virtanen, et al 2002). Our results support these findings. Additionally, as discussed, both sites in the Flat Tops are not true fell fields; they are ecotones between dry meadows and fell fields and therefore have more consistent winter snow cover than fell fields. These sites also reported the two highest soil pH values. Since fell fields are exposed to desiccating winds and do not have the moderating effect of snow cover against temperatures, they are not as species rich as these ecotone communities.

### *Latitude (Isolation)*

The site with the highest annual average precipitation, Flattop Mountain in the Park Range, had the lowest total species richness of all sites. This may be due to the fact that it is an isolated alpine area located to the northwest of the main axis of alpine areas in Colorado. It was removed from the models because of its isolation. Hadley (1987) found that the total number of species richness decreased with increased distance from the central Colorado Rockies (Front Range, Mosquitos, and Sawatch Ranges). The Flat Tops are also an isolated alpine area, yet had more species in common with the sites in Central Colorado. The higher than average species richness found in the plots may be due to the fact that the study sites were located in an ecotone of fell field dry meadow and had species from both communities.

### *Implications of Goal 2*

Adding precipitation and substrate to the list of statistically significant factors, along with snow cover, and the size and proximity of alpine, broadens the understanding of how multiple abiotic factor work together in alpine environments to drive plant species richness. The sensitivity of alpine environmental to climate change have been stated by multiple authors (Lenoir et al. 2010; Pauli et al. 1996; Walker et al. 2001; Wilson and Nilsson 2009). Additionally, precipitation in alpine areas is predicted to change in its timing and form (Wolfe et al. 2003; Wookey et al. 2009). At two sites on Niwot Ridge in Colorado it increased between 228mm and 300mm between 1951 and 1994(Williams et al. 1996).

### *Goal 3*

The last goal of this project which is traditionally outside of many community ecological studies was to bolster herbarium specimen collections from poorly collected areas and contribute tissue samples of Colorado's alpine flora to the Global Genome Initiative. We contributed 176 herbarium specimens and 150 tissue samples to the Kathryn Kalmbach Herbarium at the Denver Botanic Gardens from this study. Three of the study sites were very poorly or not represented at all in regional and national herbaria in a database search SEINet data portal( (<http://swbiodiversity.org/seinet/index.php>, March 16, 2018). Collections from these areas help fill in species distribution and community composition information for future researchers and give a snapshot of what species were present in these communities in 2017(Funk 2003) Ultimately, records of the collections made over the course of this study allow for longitudinal monitoring of our study sites over time. Later work will have more information to assess the impact of climate change on community composition or species richness at all nine sites.

Herbarium specimens help serve an important role in ecological studies (Funk 2003). They allow correct and timely identifications and they serve as a record of which species are present at a site at that given point in time (Funk 2003). They show what morphological characteristics an individual or population may have, and they show phenology (what growth stage the plant was at on a given date) (Funk 2003). Herbarium specimen were used for several community composition studies in California proving that some species had moved up in elevation, while other species were senescing due to age and fire regimes (Kelly and Goulden 2008 & Schwilk and Keeley 2012). All of this data will be important for climate change studies going forward (Hufft et al. 2018). Ecologists are increasingly using herbarium specimens for

data for ecological studies, from the ever-growing number of herbaria databases (Hufft et al. 2018).

### *Future Implications with Climate Change*

Alpine areas are particularly sensitive to climate change (Körner 2002). In recent years, climate change has been shown to alter species diversity and distribution of alpine plants. In Norway warming temperatures over the past seven decades, have increased plant species richness at several alpine sites (Klanderud and Birks 2003). Studies in Norway show that changes in aridity are relatively unimportant compared to an increase in average temperature, which allows plants from lower elevations to move up into new sites that were previously too cold for their survival and reproduction (Klanderud and Birks 2003, Klanderud et al. 2015). In alpine environments, abiotic factors are the primary predictors of local plant community composition along regional bioclimatic gradients (Klanderud et al. 2015). The smaller size of alpine flora makes them less likely to outgrow one another, and in the harsh alpine environment factors such as temperature and substrate became primary drivers in species richness (Klanderud et al. 2015). The role of precipitation is complex and depends on the temperature at the various sites (Klanderud et al. 2015). Biotic factors such as competition from large meadow plants significantly predicts flora richness at lower altitudes, but abiotic factors are the primary drivers at higher elevations. At all elevations, precipitation consistently interacts to drive species richness regardless of what other factors are at play (Klanderud et al. 2015). These findings point to the fact that alpine areas may experience even greater changes since species richness is strongly affected by temperature, precipitation, and soil pH. Acid rain could decrease soil pH

and thus species richness since lower pH decreases species richness in the Alps, Norway (Klanderud et al. 2015; Wohlgemuth 2002)

### *Study limitations and future work*

Our driest site on Guanella Pass was a dry meadow rather than a fell field because, in controlling for elevation, we only selected sites within 90 m of the 3657-meter elevation level. Therefore we were not able to select a representative fell field or ecotone community at Guanella Pass. It was roughly in the middle of the range of species richness across my sites (with 24 species, range 16-33). It would be interesting to find other sites with true fell field vegetation in this precipitation category. This may not be possible as the driest sites are often low connecting ridges in double rain shadows such as Guanella Pass or Hoosier Pass (mountains on both the east and west sides) or low ridges in the rainshadow of larger peaks that most likely support dry meadows.

Through the work at the nine sites we were able to get an idea of what the data looks like across the precipitation gradient in Colorado. In analyzing the data it became apparent that larger sample sizes (ie more sites) would make this a stronger study and help to contribute to a better understanding of drivers in Colorado alpine tundra. Nonetheless strong patterns emerged and precipitation and substrate pH do drive species richness.

Further work in the Southern and Southwestern Mountains of Colorado, especially the Elk Range where additional high precipitation areas comparable to the Park Range with more complete climate data exist closer to the central alpine axis of Colorado. New, more carefully selected sites like this, might serve as more relevant study sites

### *Conclusion*

Precipitation, and substrate pH, are both statistically significant drivers in species richness in nine sites in Central and Northern Colorado's alpine tundra. Together with snow depth, proximity to other alpine areas, both precipitation and substrate pH may offer the best explanation for species richness in Colorado's alpine tundra. Future models for the effects of climate change need to take precipitation into account, given that precipitation type and timing has been proven to change in the Rocky Mountains (Wolfe et al. 2003; Williams et al. 1996). This project explored two important but untested drivers in the alpine tundra of Colorado, greatly adding to our understanding of these fragile environments. Additionally it greatly expanded the scope of study in Colorado's alpine tundra to nine sites across a precipitation gradient, and into areas that had never been studied. A new alpine vegetation community was described, the pseudo-fell field which will help scientists and public land managers better classify and understand alpine vegetation. This project set a baseline for continued studies in Colorado's alpine tundra outside the Front Range areas at Niwot Ridge and Rocky Mountain National Park.

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## CHAPTER 4. ENVIROMENTAL STAKEHOLDER ANALYSIS: TRAMPLING OF ALPINE VEGETATION AT HOOSIER RIDGE

### Introduction

The American West is an emblematic vacation and recreation region. The region is known for its grandeur, vast vistas, pristine forests, and meadows full of wildflowers, attributes which have contributed to a long history of public land use and also a need for conservation. The world's first national parks -- Yellowstone and Yosemite -- were founded in Wyoming in 1872 and California in 1890 respectively, and many more followed. These national parks and other public lands attract massive numbers of visitors each year. In addition to tourism, population growth has contributed to an increase in public land use, which directly corresponds with environmental degradation. This is evidenced in Colorado's delicate alpine areas, which are especially susceptible to human use.

The damage caused by humans to alpine environments in the Colorado Rockies has long been recognized. One human activity that is responsible for damage to this life zone is foot traffic. In fact, a 1960s study by Willard and Marr in Rocky Mountain National Park found that alpine communities such as wet meadows, dry meadows, and fellfields are especially negatively

impacted by foot traffic. This particular study was conducted on a fellfield community near a new parking area that opened on Trail Ridge Road in 1958. Twelve weeks into the study vegetation cover was only eighty-seven percent of what it was prior to the study, and just two years after the parking lot opened the vegetation cover was at thirty-three percent of its former cover. The plants that remained were primarily located in protected areas between or beside rocks. Interestingly, the species that sustained the most damage of all fellfield vegetation included the most compact cushion plants. Eventually the area around the parking lot became a site with a high percentage of sand and gravel after the wind eroded the fine particles that had been held in place by vegetation (1970). In addition to foot traffic, other harmful human activities include collecting rocks, which decreases wind protection; picking wildflowers, which reduces seed set; littering, which shades plants; and driving on the tundra, which tramples and often kills plants (1970).

Thirty-seven years after Willard and Marr's study, the researchers Willard, Cooper and Forebs analyzed data collected between the years of 1959 to 2001 at the same alpine location. The data suggests that once vegetation was protected from human activities it did recover (2007). (These researchers defined recovery as an increase in vegetation cover.) However, Willard, Cooper and Forebs noted that recovery was not the same across all plots and that the degree of winter snowpack and summer drought play an important role in the recovery process (2007). This is because heavy winter snowpack and summer drought shorten the already short alpine growing season, which further slows plant growth and recovery.

Although human impact to the alpine life zone has long been observed, there has been a minimal amount of scientific research done on this topic. This is, in part, because alpine areas are low in biomass and do not yield timber resources. However, the alpine provides important ecosystem services to humans, nonetheless. The researchers Johnson and Brown argue that perhaps the most important service is water retention, and intact vegetation is critical to ensuring an adequate water supply (1979). Indeed, alpine areas are particularly important for watersheds, because they release water later in the season (typically from June through August, but even through September) due to late melting snowfields (Johnson & Brown, 1979; Martinelli, 1975; Carroll, 1976). Vegetation cover plays a pivotal role by slowing the water released by the melting snow and helping it to be absorbed by the soil and preventing erosion (Johnson and Brown 1979). Additional ecosystem services that the alpine provides include mineral extraction,

game hunting, and grazing for livestock later in the summer after lower elevation pastures have dried up.

An area in Colorado that provides valuable ecosystem services is Hoosier Pass, which is located along the Continental Divide between the resort town of Breckenridge and the small town of Fairplay. An important area for several watersheds, the water on the west side of the Divide becomes the headwaters of the Blue River and drains directly into Dillon Reservoir, which Denver Water uses to supply customers in the Denver metropolitan area. The water on the east side, goes directly into the South Platte which flows through Denver and is also a water source for the Denver metropolitan area.

Hoosier Pass is also important because it is botanically rich. The area is noted for a high concentration of alpine flora, which includes both widespread species such as *Geum rossii*, *Minuartia obtusiloba*, and *Phlox condensata* and narrowly endemic species such as *Oxytropis podocarpa*, *Saussurea weberi*, and *Astragalus molybdenus*, the latter of which is endemic to central Colorado. For his masters thesis James Fowler looked at the alpine flora of the Southern Rockies. Fowler notes that 180 species have been documented just on Hoosier Ridge (2014). Furthermore, the north side of the ridge is the only site for *Armeria maritima* in Colorado. Several other rare plants such as *Braya humilis*, *Draba borealis*, *Draba porsildii*, *Phippsia algida*, *Papaver kluanense*, *Saussurea weberi*, *Townsendia rothrockii*, and *Ipomopsis globularis* call this ridge home (Williams, 1992).

This important area receives a considerable amount of vehicle traffic. Hoosier Pass is paved, which allows visitors easy access to elevations above 11,600 feet. Once above treeline, a jeep road allows more adventurous drivers access to an alpine ridge. The old Hoosier Pass, which is now used by OHVs and ATVs, accesses the abandoned North Star Mine with additional smaller roads accessing various points around the mine. One of these social roads traverses a steep slope to the high point between the parking lot of Hoosier Pass and the North Star Mine. These roads have contributed to a considerable amount of trampling to the alpine communities on Hoosier Ridge.

I became aware of the damage to Hoosier Ridge during the summer of 2017 while conducting research on factors that drive species richness in Colorado's alpine vegetation. Hoosier Pass was one of my nine study sites and during the growing season I visited plots on Hoosier Ridge three times: once on June 25<sup>th</sup>, again on June 26<sup>th</sup>, and finally on September 15<sup>th</sup>.

During this time, trampling and damage to the site was substantial: not only was the area trampled by repeated foot traffic, but it had also been driven over and possibly even used as a campsite. In fact, several of my individual plots could not be located because the landscape pins marking them had been removed by hikers or car tires.

Hoosier Pass serves a diverse range of stakeholders from the general public to governmental entities who manage the area for various recreational and economic activities such as hiking, off road vehicle use, hunting, grazing, and urban and rural water resources. The area also provides a long list of ecosystem services that rely on intact and functioning natural plant communities. The values of the individual stakeholders are discussed below.

*National Forest Resource Managers, Wildlife Managers, and Public Water Managers*

These stakeholders are deeply impacted by use in national forests. They must determine what damage is being done, how much damage is occurring, and what resources are being affected, including any rare species that are being impacted. Resource managers and botanists have a legal and professional responsibility to safeguard the resources at hand and protect them not just for future preservation but also for future public use. Their findings and recommendations can set the stage for various management plans, or lack thereof, in these areas. Included in this group are timber managers and other resource managers for the forest service. Animal resources such as hunting and protection of Colorado's native fauna is an important part of what the Colorado Division of Wildlife does. These individuals have an agency goal to protect and manage Colorado's wildlife in a sustainable manner that safeguards the wild species and the resources that support the animals. Wildlife managers partner with hunters to control and thin animal populations.

Water managers for Denver Water and other water suppliers have an interest on how Hoosier Ridge is managed because destruction of vegetation can affect water quality and supplies. With increases in bare soil and erosion, more particulates are carried downstream in the water and runoff will occur more quickly and in higher volumes than on vegetated slopes and ridge lines. Less hiking, off road vehicle use, and grazing will ensure that vegetation remains intact on Hoosier Pass. Employees of Denver Water have an interest in ensuring there is enough clean, usable water for customers. Their livelihood depends on being able to supply water to a growing population. The stakeholders mentioned above have a responsibility to manage the natural resources in a way that allows revenue and resource extraction while at the same time

ensure that the public has minimal impact on these resources. While, the stakeholders below are members of the public or private corporations with interest in what natural areas have to offer.

### *Hunters*

Hunters in turn value the ability to find the animals they are hunting. Reducing hiking, off road vehicle use, and grazing allows more vegetation to support more game animals. Maintaining high concentrations of game open to licensed hunters is what this group values. Limiting hiking and off-road vehicle use will ensure that the wildlife driven to more remote areas. Both wildlife managers and hunters value wildlife for its beauty, importance, and the sporting opportunities that game animals provide.

### *Water Users*

The residents in the metropolitan Denver area receive the vast majority of their drinking, irrigation and household water from the Central mountain of Colorado, which is served by Denver Water. Hoosier Pass sits in the middle of the water supply area. Denver water customers want affordable, unrestricted amounts of safe, clean water for drinking, washing clothes and watering their landscapes.

### *Mining companies*

The Mosquito and Ten Mile ranges are heavy in minerals and have a long mining history and mining companies continue to have an interest in these areas. Mining companies value easy affordable access to minerals, so they can extract them. Employees of these companies need jobs, which are dependent on access to minerals. Mining companies were successful in blocking the implementation of a potential natural research area on Hoosier Pass in the early 1990s. One mining company was afraid that the creation of a natural research area would block access to minerals in the area. Mining on Hoosier Ridge would not only close the area to all users including hikers, ranchers, and hunters, but it also has the potential to pollute water supplies from destruction of vegetation cover and water contamination from the tailings. In the end, mining companies are dependent on access to mineral deposits to make profits.

### *Ranchers*

Because, alpine areas are often used for grazing in the summer season once lower elevation vegetation dries and becomes unfit for grazing. Ranchers and livestock managers will



move their herds and flocks to higher elevations and use grazing permits on public lands. Ranchers and livestock managers need access to these areas at the appropriate times of the year to feed their livestock. Peak hiking season and early hunting seasons overlap with prime alpine grazing times. Livestock owners and managers are ardent supporters of using public resources for the benefit of their livestock.

*The Public (Hikers, Off-road Vehicle Users)*

Hikers and off-road vehicle enthusiasts want easy and plentiful access to trails for recreational use. This group could be at odds with almost all the above groups for access and safety reasons because hunting and hiking on the same trail are not safe. Furthermore, hiking and off-road vehicle use damage vegetation that is valued by ranchers and water managers. This group of stakeholders -- public land users -- can roughly be divided into three groups: Those for unregulated use of public lands, those for sustainable use and those who are unaware of the damage they cause, but with education would change their use to be more sustainable.

*Citizens for unregulated use of public lands.* This group believes that public lands belong to the American public and as such it is their right to have access and to use these areas responsibly. The Forest Service and Bureau of Land management currently close certain roads and trails during seasons when foot, horse or vehicle traffic might damage the trail or road, or when animal species might be using the area for breeding/raising young. There are people who feel that these areas should never be closed. At times these people will enter these areas despite postings and gate closures, by driving around, removing gates, or other means of entry. People who enter these areas illegally are often off-road vehicle enthusiasts; other members of this group will respect postings and closings, but feel they are unconstitutional. This groups values being able to use public lands at their discretion instead of at governmental discretion.

*Citizens for sustainable use of public lands.* There are also citizens who support and want to help protect resources and understand being excluded from areas that are too muddy in the early spring, areas closed for the nesting (e.g. sandhill cranes), or areas that are closed to allow for revegetation to occur. This group of citizens use public lands in a way that protects the landscape and its resources for future generations.

Because Hoosier Pass is so botanically rich, a subgroup of citizens for sustainable use of public lands has emerged: botanists and wildflower enthusiasts. The destruction of native vegetation will affect these stakeholders because as biodiversity decreases, so does aesthetic

quality. Perhaps most importantly to this group, Hoosier Ridge is known for some very rare or sensitive plant populations and an interesting assortment of high elevation plants. These stakeholders value responsible use of the area that safeguards the biodiversity at hand while allowing everyone the opportunity to see masses of wildflowers and rare species not seen elsewhere. Interestingly, a small subset of botanists and wildflower enthusiasts worked in the early 1990s to create the Hoosier Ridge Research Natural Area (Williams 1992), which never came to fruition, due to mining company appeals.

*Citizens who are unaware of the damage they are doing.* While a bit more difficult to define than the above groups, these stakeholders are often visitors or newcomers to the American West. They have often come from areas that have no alpine communities and may be unaware of the damage their driving or walking off defined roads and trails may cause. These individuals are out to enjoy themselves and often with some education, their use would fall into the above group of sustainable use.

The managers mention in the first section of stakeholders must make decisions based on what is best for protecting the resources in question, protecting public safety, while also allowing people access to public areas and to recreational opportunities. Research examining the impacts of public use, and what types of public use are the least and most damaging help policy makers create plans that serve everyone. Policymakers have a legal responsibility to do what is best for resources and the public.

The above groups have different values and reasons for their actions. The recommendation below allows most groups to have some of their values integrated into the plan.

### *Recommendation*

People have the right to access nature and to recreate in nature. Access to nature has been shown to have multiple health and social benefits for people by lowering stress, helping with developing empathy and fostering an appreciation for nature. Furthermore, people who have access to nature are more likely to help preserve natural areas and biodiversity for the future. Thus, a compromise between allowing access to public lands and saving biodiversity and ecosystem services at Hoosier Ridge would be to allow access to some areas, while restricting foot and vehicle traffic to some of the most sensitive areas of Hoosier Pass. Research suggests that closing certain damaged areas permanently to hiking and vehicles allows damage to stop and

recovery to start. For example, Willard and Marr's 1971 study demonstrates that areas that have been lightly trampled for a year or intermittently trampled for years might fully recover within four years. Areas that have experienced heavy foot traffic for twenty-five or more years could also start to recover in as little as 4 years (1971). However, areas that are heavily damaged may not show any signs of recovery in 4 years and instead may take hundreds and possibly a thousand years to recover to a climax ecosystem (1971). Thus, closing sensitive areas to general foot traffic and all off-road vehicle use will allow delicate alpine communities to recover, which fulfills the values of many of the stakeholders listed above.

Studies support that restricting access to certain areas is effective. For example, in Willard and Marr's study, it has been demonstrated that when given a paved or restricted path, less than one percent of visitors will leave the path except near the parking area and at the end in order to get a better view (Willard & Marr, 1971). By creating an area that is specific for foot/vehicle traffic and other areas that are just for foot traffic still allows people access to the tundra and nature. In this scenario, hunters would have access to the area starting October 1st once peak hiking season is over. Hunters will only be allowed access to those areas open to foot or vehicle traffic. Grazing should be discontinued on Hoosier Pass to protect the fragile vegetation and to create a safer environment for hikers. Closing the area to grazing is unfortunate as ranchers could use the forage this alpine area provides. the area however, receives such heavy use that the benefits of closing the area to grazing outweigh the drawbacks. Additionally, placing signs at the parking area educating the public about fragile alpine ecosystems and this botanically rich and irreplaceable area could be helpful. Such signs exist on Shrine Pass near Vail and have helped keep foot traffic on designated trails.

While obtaining funding is a common problem, there are local groups/societies that would likely donate for such a purpose including Colorado Native Plant Society, the Rocky Mountain Chapter of the North American Rock Garden Society (RMC-NARGS), and the Colorado Mountain Club. In fact, one of these societies, RMC-NARGS, helped to fund a board walk across a wet meadow at Shrine Pass in the 1990s. The Colorado Mountain Club also has a long history of public projects involving the improvement of trails and restricting foot traffic to designated trails. Work through these organizations help ensure that people have the beneficial access to nature while preserving it for future generations. Managing these basic interests insures

the American West continues as an emblematic symbol of conservation and human enjoyment working side by side

Damage to vegetation in Colorado's alpine tundra is a sizable problem; it reduces vegetation cover which negatively affects the ecosystem services alpine areas provide: specifically, water management, livestock grazing, game management, aesthetic value of natural communities and endangered rare plant species. Creating specific access trails and road access while closing the area to grazing will allow Public land managers to preserve vegetation cover while balancing the needs of the greatest number of stakeholders. Implementing the above plan will ensure plentiful, healthy game, clean and safe water, while safeguarding rare or unique plants, and a beautiful environment for all to enjoy.

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