

**ALPINE PLANT COMMUNITY DYNAMICS AND CLIMATE IN THE
SENATOR BECK BASIN, COLORADO**

by

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Thesis

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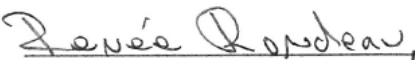
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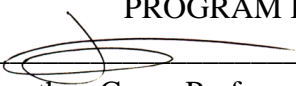
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Alpine Plant Community Dynamics and Climate in the Senator Beck Basin, Colorado

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Abstract

Alpine ecosystems harbor unique and species-rich plant communities that may be particularly vulnerable to a changing climate. Quantifying recent changes, their relationships to climate drivers, and how such changes may be modulated by topographic factors can inform projections of future changes and inform future conservation and management strategies. The San Juan Mountains of southern Colorado contain one of the largest areas of alpine tundra in the USA, yet few studies have examined alpine plant community dynamics in this rapidly warming region. To quantify the direction and rate of change of alpine plant communities and their relationship to climate and topographic variation in this region, 22 vegetation transects spanning an elevation gradient from 3369 to 3992 m were sampled in the Senator Beck Basin, Colorado for the years 2004, 2009, 2014, and 2021. We also sampled key topographic variables associated with moisture and temperature gradients, including slope, Topographic Position Index, and elevation, and employed Moderate Resolution Imaging Spectroradiometer imagery to develop time series of EVI, LST, and NDSI measures. We used randomization tests to assess potential

shifts in the frequencies and elevation means of species, and functional groups over time. We also employed a non-metric multidimensional scaling (NMS) to examine relationships between plant community composition and environmental covariates and vegetation patterns. Over the past two decades, we found a significant increase in both the mean and 90th percentile values of Enhanced Vegetation Index (EVI), and a significant decrease in the mean Normalized Difference Snow Index (NDSI) across the study site, suggesting the lengthening of growing seasons over time. Select species *Festuca brachyphylla*, and *Erigeron peregrinus*, appear to be showing responses to interannual variation when comparing data from 2004 and 2021, but overall we have found little evidence for long-term directional change by any species. Correlations between NMS scores and sampled environmental factors revealed that plant community compositional variation was closely associated with gradients of soil moisture availability and elevation. However, we did not observe concerted compositional shifts among transects or within community types in response to interannual variation, and we found no evidence for directional shifts over the sample period. These findings attest to the relative stasis of these communities, dominated by long-lived perennial plant species, in spite of recent climate variation. While strong plant community responses to climate in this system may not be exhibited yet, ongoing and long-term monitoring will provide valuable tools and information for proactive land management strategies to mitigate the long-term effects of climate change expected across alpine ecosystems and mountain landscapes.

Introduction

Climate change is expected to drive shifts in the structure, composition, and function of plant communities globally (Amagai et al., 2018; Yang et al., 2011). Increasing temperatures and altered moisture availability have the potential to affect the phenology, population vital rates,

and productivity of individual plant species, leading to compositional changes and restructuring the ecosystems they comprise (Dorji et al., 2020; Halloy & Mark, 2003; Hajek & Knapp, 2022). These effects are expected to disproportionately affect mountain ecosystems due to their high sensitivity to temperature changes, the rapid rate of warming in high elevation areas, and the likelihood of reduced snow cover and increased glacier retreat (Huss & Hock, 2018; Inouye, 2020; Nogués-Bravo et al., 2007). Recent studies and predictive models throughout global mountainous regions have recorded changes in plant species' abundances and elevational distributions (Kelly & Goulden, 2008; Lenoir et al., 2008; Vanneste et al., 2017). In particular, warming has the potential to drive major compositional shifts in cold temperature-limited alpine landscapes (Ernakovich et al., 2014). While decreased abundances in cold-adapted plant species have been measured over time across alpine settings (Porro et al., 2019), other plant species have shown increases in cover and productivity in response to warming temperatures (Abeli et al., 2012; Gehrman et al., 2020), highlighting both species-level variability and also that plant community shifts may not be uniformly directional (Gillies et al., 2018). These changes may also vary in intensity depending on the geographic location: while ecosystems in one global region may be enduring rapid, climate-change induced turnover, other regions appear to be relatively unaffected (Bertrand et al., 2011; Sritharan et al., 2021).

Alpine ecosystems in some areas in the United States have exhibited longer growing seasons (Munson & Sher, 2015), increases in woody plant density (Dolanc et al., 2014; Scharnagl et al., 2019), and upward shifts plant species' elevational ranges (Grimm et al., 2013; Smithers et al., 2020). The southern Rocky Mountains support extensive alpine plant communities that have experienced some of the highest levels of recent warming recorded in the conterminous US. Decreased annual snowpack in this region over time has resulted in

measurable changes to some plant species abundance and distribution (Gasarch & Seastedt, 2015; Saavedra et al., 2003). Additionally, shrub expansion has been recorded over time in alpine landscapes, also associated with warming temperatures (Formica et al., 2014). Warming may be compounded by enhanced dust deposits on alpine snow, resulting in earlier annual snowpack melt-out and triggering earlier phenotypic responses in alpine plant species (Fassnacht et al., 2022; Steltzer et al., 2009).

While global primary productivity is generally projected to increase as a result of warming temperatures, these changes can be counteracted by associated shifts in rate-limiting resource availability, particularly water: whereas wetter areas may show an increase in productivity under directional climate change, drier areas may experience productivity declines limited by declining soil moisture availability (Fay et al., 2003; Winkler et al., 2016). Kelsey et al. (2018) found that the extent and direction in which local alpine communities were changing was dependent on the physiography of the landscape, with shifts shaped by topographic influences on snowpack, plant productivity, and soil moisture within alpine ecosystems. Thus, the response of alpine plant communities to environmental change may similarly be modulated by resource availability and limitations, with growing-season or temperature-limited sites expected to experience increased productivity, but moisture-limited sites potentially becoming drier and less productive (Winkler et al., 2016). While field data has traditionally aided in explicating community changes within a geographic area, remote sensing tools have also proven to be effective for monitoring phenological responses to fluctuating environmental covariates (Richardson, 2019). Measures of surface temperature, snow cover, and the productivity and “greenness” levels of alpine plant communities as measured by satellites may be useful to gain insight into how different locations and plant communities may shift in response to climate

change (Eve et al., 1999). In particular, the use of Moderate Resolution Imaging Spectroradiometer (MODIS) imagery, with a record extending back to 1999, allows assessment of trends and their associations with climate data and other environmental covariates (e.g., topographic context) and contrasts with observational field data (Buckley et al., 2017; Tarolli, 2014).

Assessing recent changes in alpine plant community dynamics in response to warming may help facilitate predictions of broader patterns of high elevation plant community change over longer time frames under future climate scenarios. In the Senator Beck Basin (SBB) of southwestern Colorado, a series of alpine plant transects have been sampled at four intervals between 2004 and 2021, yet these data have not been subject to rigorous analysis. This setting thus provides the opportunity for much-needed quantification of the direction and rate of change of alpine plant communities and their relationship to climate variation in this region. The purpose of this study was to characterize patterns of recent alpine plant community change in SBB using field- and satellite-based observations. For this, field- and remotely sensed data were analyzed to facilitate the coupled analysis of shifts in plant communities and key environmental covariates and drivers. Specifically, the objectives of this study were to: 1) characterize plant community compositional changes based on field observations conducted between 2004 and 2021, and 2) assess relationships between compositional, topographic setting, and climate variation. In particular, we examined the data for increases in productivity and plant cover during warmer years and in topographic settings where thermal constraints on productivity and growth may have been reduced, and conversely, declines in productivity and plant cover during drier years and in topographic settings where soil moisture may have been reduced. Accordingly, this research is intended to provide local insight into patterns of plant species and community change

in alpine ecosystems in the San Juan Mountains of the southern Rockies, but also contribute to our general scientific understanding of the varying mechanisms of climate change impacts.

Methods

Study Site

This study was conducted in the Senator Beck Basin (SBB; 37°54'24.8"N, 107°43'34.6"W) of the San Juan Mountains of southern Colorado, USA. The SBB ranges in altitude between 3,371 and 4,118-m, with the two principal vegetation types consisting of subalpine forest and alpine tundra (Fassnacht et al., 2022). The surface geology of SBB is comprised of a mixture of Precambrian crystalline rock and Cenozoic volcanic rock (Drenth et al., 2012). The climate of the area is characterized by moderate summers and cold winters. During the summer, the mean high temperature is 17.7 degrees Celsius, while the mean low is 4.4 degrees Celsius. The yearly rainfall for SBB means 61.5 centimeters, with a yearly snowfall mean of 414.8 centimeters. The landscapes of SBB are public lands managed by the Ouray Ranger District of the Grand Mesa, Uncompahgre, and Gunnison (GMUG) National Forest. While SBB does not contain active roads or established trails, the area supported extensive mining activity during the late 19th century. Under the authority of the U.S. Forest Service (USFS), annual sheep grazing occurs throughout SBB, and on-going snow-study research has taken place since the granting of a special use permit to the Center for Snow and Avalanche Studies (CSAS) in 2003 (Landry et al., 2014). In 2004, an observational field study consisting of research transects spanning an elevational gradient was set up in a collaboration between USFS and CSAS to monitor plant community composition and species abundance over time. This study consisted of 23 transects spanning elevations from 3369 to 3991-m, which were sampled in

2004, 2009, and 2014. In 2014, one transect was removed from the study due to the presence of an archaeological site

Field Sampling

Field measurements of plant cover have been collected four times between 2004 and 2021 in the Senator Beck Basin. Abiotic and plant cover data were collected using Daubenmire plots along 23 established 100-m transects in the years 2004, 2009, 2014, and 2021. Transects were established within three different elevation zones: Transects 31-35 were established at 3369-m, 21-26 were established at 3658-m, and 1-12 were established at 3900-m. Transect 8 was excluded beyond 2009 due to its proximity to an archeological site. Each transect runs south to north, and consists of ten, 20 x 50-cm Daubenmire plots spaced at 10-m intervals, totaling to 230 plots. Within each plot, canopy cover for each plant species and abiotic variables was estimated using the following cover scale: T (trace, 0-0.99%), 1 (1-5%), 2 (6-25%), 3 (26-50%), 4 (51-75%), 5 (76-95%), and 6 (96-100%) (Daubenmire, 1959). This method was changed in 2014, and estimated percentages were documented in lieu of cover class. Field data for all years were digitized and archived by CSAS.

Additional field data was collected during summer 2022. In June, a snow survey was performed to measure the presence or absence of snow at each transect site. Once monthly during July-September, Soil moisture percentages were measured for every plot along established transects with a Campbell Scientific HydroSense 2 Handheld Soil Moisture Sensor. Spatial location and elevation data were recorded at the center of each Daubenmire plot along each transect, using a high-precision (sub-meter) GNSS receiver (Juniper Systems Geode GNS3, 60 cm accuracy).

Topography and Remotely-sensed Predictor Variables

To explore the influences of topography on plant communities, LiDAR data was sourced from the CSAS data archive for the development of a 10-m resolution digital elevation model (DEM) of the study site in ArcGIS Pro (Esri,2022). From this map, we calculated Topographic Position Index (TPI) and slope for each plot through ArcGIS Pro along established transects in the study site via the use of pre-recorded plot-level GPS measurements.

Utilizing the platform Google Earth Engine, spatiotemporal values quantified from MODIS Terra Daily imagery were sourced for the collective study site, as well as individual transects via JavaScript for every year between 2000 and 2021 (Telerik Developer Network, 2015). Time series box plots for the collective study site and individual plant communities were created using the mean and 90th percentile growing-season (June 1st-September 30th) values of Enhanced Vegetation Index (EVI), Land Surface Temperature (LST), and Normalized Difference Snow Index (NDSI) to visualize potential fluctuations in environmental covariates over time, as well as illustrate the change in values for environmental variables over time (Gorelick et al., 2017).

To further analyze fluctuations in climate data for the collective study site, the mean and 90th percentile values for EVI, LST, and NDSI were calculated for each year in the time series. Simple linear regressions were then performed utilizing the Stats package for the annual mean and 90th percentile values of EVI, LST, and NDSI (R Core Team, 2021). For this, each climate variable was run individually as a function of year in order to estimate the relationship between climate values and the predictor variable of year.

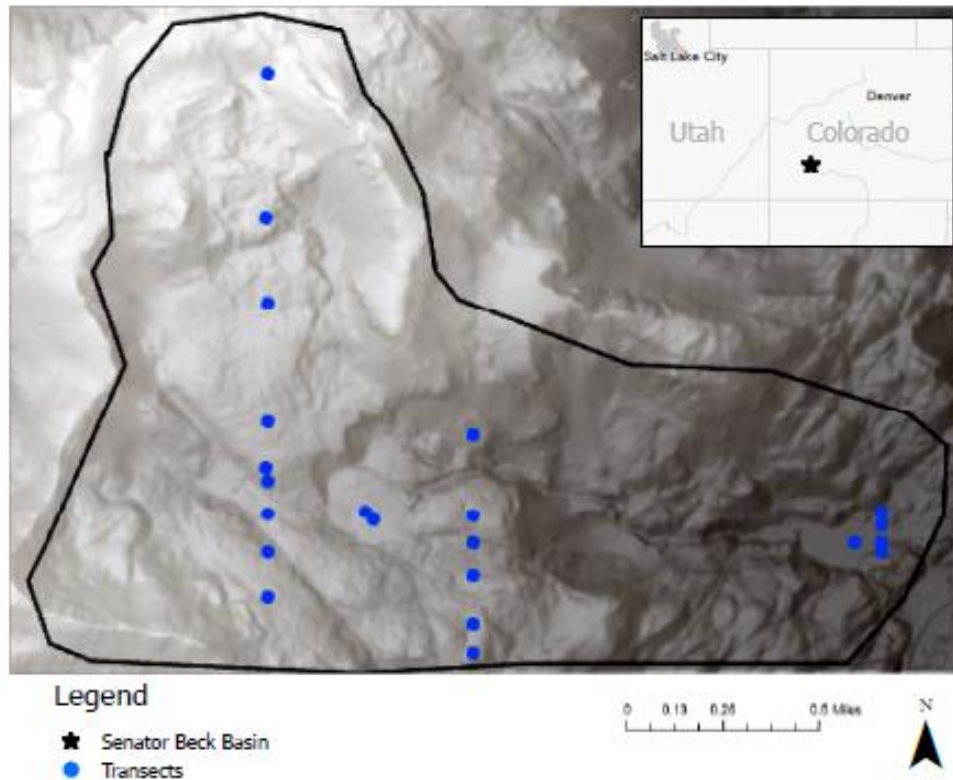


Figure 1. A 10-m resolution digital elevation model (DEM) of the Senator Beck Basin, CO. The boundary of the Basin is represented by a black line, and transect locations are represented by blue pins.

Plant Community Analysis

Analysis for changes in biotic abundance and composition was conducted at three different levels including 1) individual species, 2) functional groups, and 3) community composition. To develop functional groups, species were classified into the following categories: Forb, Graminoid, and Woody. For the forb category, all non-woody, non-graminoid species were included. All species that were labelled as ‘unknown’ were removed from analysis. Non-species

categories (Lichen, Litter, Moss, Soil, Rock, and Water) were not included in any analyses. We also excluded data from the transect (Transect 8) not sampled after 2009. The final dataset included samples of cover from 210 sample plots at 22 transects, over all four sample years (2004, 2009, 2014, 2021). A total of 188 species were recorded across these sites. All analyses were performed utilizing R (R Core Team, 2021).

To calculate the total frequency of each species on each transect during each sample year, we first converted percent cover of each species to presence-absence data (PA) in each sample plot (ten per transect). For the ten most common species, total frequencies of each species across the entire study site were contrasted across each sample year. The weighted mean elevation for each species was designated by multiplying the elevation of each sample plot by the corresponding species frequency, summing the products for all plots within the site, then dividing by the total frequency of that species across the collective site.

To test for directional changes in species frequency, randomization tests were utilized to determine whether any significant relationships between frequency and year were a true effect, or simply due to chance. Randomization tests performing 10,000 iterations were ran using the plot-level frequency and weighted elevation means for all species and functional groups for all year pairings of sampled vegetation data. Significant p-values were then adjusted using the Benjamini and Hochberg step-up procedure (BH) to account for potential false-positive results (Benjamini & Hochberg, 1995).

To explore patterns of community composition in relation to underlying environmental variation, and assess compositional shifts over time, we conducted non-metric multidimensional scaling (NMS). For each sample year, we first calculated the mean percent cover of every

species along each transect. We then constructed a compositional dissimilarity matrix to quantify the pairwise distances between the cover values of 188 species within 22 transects for all years sampled. A Nonmetric Multidimensional Scaling (NMS) ordination plot was generated utilizing the *Vegan* package to illustrate the relationship between rank pairwise dissimilarity and pairwise Euclidean distance within a reduced-dimensional space (Oksanen et al., 2009). NMS ordination scores for sampling years were plotted against abiotic data to illustrate movement in ordination space over time. For topographic variables TPI, and elevation, the *ordisurf* function within the *Vegan* package was employed to overlay variables onto the NMS diagram. Mean soil moisture values were also overlaid onto the NMS diagram using the *ordisurf* function.

To determine the potential relationship between environment and shifts in community function, a correlation test was employed using ordination scores and all abiotic variables to calculate Pearson correlation coefficients and test the null hypothesis of no statistically significant correlation between variables (Kennedy & Keeping, 1962; Edwards, 1976). Arrows were also integrated within the NMS plot to illustrate transect movement in ordination space over sampling years to visualize the direction and extent of these shifts within transects and community types (Fig. 7). The mean change for the collective study site was also calculated and visualized to assess the extent and direction of site changes over time (Fig. 7).

To characterize broader communities within SBB and assess changes in relation to moisture and thermal gradients, transects were categorized into groups based on their location in species space as defined by NMS axis scores. The first and second NMS axes were used to divide sites into four quadrants representing the following community types: dry and high elevation, dry and low elevation, wet and high elevation, and wet and low elevation. Clustered points were then used within the *Plyr* package to compute the complex hulls for each community

and define the specific geometric area that communities occupy within ordination space (Wickham, 2011). Once calculated, these communities were labelled based on their transect makeup and influence to environmental variables. The mean site scores on both NMS 1 and 2, and values for NDSI, EVI, and LST were then calculated for the individual sampling periods of each community and illustrated along with their standard deviations to further analyze individual transect movement within broader community areas over time.

Results

Changes in individual species abundance and elevational distributions over time

Randomization tests were run to evaluate for significant frequency and elevation changes in 188 species over each pair of consecutive sample year, and between the beginning and end years (2004 and 2021) of our study period (4 contrasts total). When comparing 2004 and 2009 data, the following species were found to have significantly changed in their plot-level frequency: *Erigeron peregrinus* ($P=0.02$), *Potentilla pulcherrima* ($P=0.03$), *Vaccinium cespitosum* ($P=0.03$), and *Vaccinium myrtilloides* ($P=0.04$) (Table 1). For the year pairings of both 2009/2014, and 2014/2021, no species were found to be significant. Finally, when comparing 2004 and 2021, *Festuca brachyphylla* ($P=0.01$), and *Erigeron peregrinus* ($P=0.02$) were found to have significantly shifted in their plot-level frequency over time (Table 1). When analyzing elevation data for 2004 and 2009, *Deschampsia cespitosa* ($P=0.002$), *Carex nova* ($P=0.02$), *Potentilla pulcherrima* ($P=0.03$), *Minivartia macrantha* ($P=3.60e-09$), *Viola labradorica* ($P=0.04$), and *Oreoxis alpina* ($P=0.04$) were found to have significantly shifted in their weighted elevation means (Table 2). When comparing years 2009 and 2014, *Trollius albiflorus* ($P=0.03$), and *Noccaea montana* ($P=0.04$) were found to be significant (Table 2). For

the year pairing of 2014 and 2021, *Bocchera drummondii* ($P=0.03$) and *Noccaea montana* ($P=0.04$) were significant (Table 2). However, no species were found to be significant when analyzing the year pairing of 2004 and 2021 (Table 2). When quantifying the yearly average frequencies for significant species, only one species, *Festuca brachyphylla*, demonstrated a consistent, significant decline in frequency from 2004 to 2021 (14%).

During analysis of frequency changes among functional groups, no significant changes in frequency were found. Additionally, no significant shifts were documented for the elevation weighted means of functional groups. When quantifying the yearly average frequencies for the most frequent species for the collective study site, five of ten species exhibited decreases in their average frequencies when comparing 2004 and 2021 data (Table 3). Of these species, *Festuca brachyphylla* (FEBR) showed the largest decrease in frequency, with a frequency decrease of 14%. Of the five species that declined in frequency, *Festuca brachyphylla* (FEBR) and *Podistera eastwoodii* (POEA) were species that demonstrated consistent declines in their average frequencies when comparing values for all sampling years (Table 3). Five of the ten most frequent species exhibited increases in their average frequencies when comparing 2004 and 2021 data (Table 3). *Potentilla diversifolia* (PODI2) showed the largest increase, with a frequency increase of 7% (Table 3).

After calculating the elevation weighted means for the most frequent species for the collective study site, six of ten species exhibited increases in their mean elevations when comparing 2004 and 2021 data (Table 4). Of those species, *Deschampsia cespitosa* (DECE) showed the largest increase, with the mean elevation increasing by 39 m. Of the species that decreased in their mean elevation, *Caltha leptosepela* (CALE4) exhibited the largest decrease, with an elevation decrease of 26 m. Of the species that shifted in their weighted elevational

mean, *Deschampsia cespitosa* (DECE) was the only species demonstrated a consistent directional shift in elevation when comparing data for all sampling years (Table 4).

Table 1. Randomization test values for changes in species frequency over time. P represents adjusted p-values using the Benjamini and Hochberg step-up procedure.

Species Frequency Means 2004-2009			
Species	Code	P	% Change in Frequency
<i>Erigeron peregrinus</i>	ERPE3	0.02	11%
<i>Potentilla pulcherrima</i>	POPU9	0.03	10%
<i>Vaccinium cespitosum</i>	VACE	0.03	10%
<i>Vaccinium myrtilloides</i>	VAMY	0.04	10%
Species Frequency Means 2009-2014			
N/A	-	-	-
Species Frequency Means 2014-2021			
N/A	-	-	-
Species Frequency Means 2004-2021			
<i>Erigeron peregrinus</i>	ERPE3	0.02	11%
<i>Festuca brachyphylla</i>	FEBR	0.01	14%

Table 2. Randomization test values for changes in species weighted elevation mean over time. P represents adjusted p-values using the Benjamini and Hochberg step-up procedure.

Species Elevation Means 2004-2009			
Species	Code	<i>P</i>	Change in elevation (m)
<i>Deschampsia cespitosa</i>	DECE	0.01	63
<i>Carex nova</i>	CANO3	0.03	72
<i>Potentilla pulcherrima</i>	POPU9	0.03	213
<i>Minuartia macrantha</i>	MIMA3	3.6e-09	99
<i>Viola labradorica</i>	VILA10	0.04	161
<i>Oreoxis alpina</i>	ORAL	0.04	240
Species Elevation Means 2009-2014			
<i>Trollius albiflorus</i>	TRAL8	0.03	125
<i>Noccaea montana</i>	NOMO	0.04	184
Species Elevation Means 2014-2021			
<i>Bocchera drummondii</i>	BODR	0.03	238
<i>Noccaea montana</i>	NOMO	0.04	264
Species Elevation Means 2004-2021			
N/A	-	-	-

Table 3. Mean frequency for the ten most abundant vascular plant species in Senator Beck Basin for the years 2004, 2009, 2014, and 2021.

Species	Code	2004	2009	2014	2021
<i>Geum rossii</i>	GERO2	38%	38%	34%	40%
<i>Artemisia scopulorum</i>	ARSC	20%	23%	23%	21%
<i>Polygonum bistortoides</i>	POBI6	27%	28%	19%	22%
<i>Caltha leptosepala</i>	CALE4	21%	22%	22%	20%
<i>Carex nigricans</i>	CANI2	17%	26%	28%	20%
<i>Deschampsia cespitosa</i>	DECE	26%	25%	25%	32%
<i>Festuca brachyphylla</i>	FEBR	22%	14%	14%	8%
<i>Poa alpina</i>	POAL2	28%	24%	26%	20%

<i>Potentilla diversifolia</i>	PODI2	14%	25%	25%	22%
<i>Podistera eastwoodiae</i>	POEA	27%	25%	23%	15%

Table 4. The weighted elevation means for the ten most abundant vascular plant species in Senator Beck Basin for the years 2004, 2009, 2014, and 2021.

Species	Code	2004	2009	2014	2021
<i>Geum rossii</i>	GERO2	3802	3796	3805	3805
<i>Artemisia scopulorum</i>	ARSC	3774	3794	3793	3788
<i>Polygonum bistortoides</i>	POBI6	3757	3783	3777	3773
<i>Caltha leptosepala</i>	CALE4	3674	3659	3653	3648
<i>Carex nigricans</i>	CANI2	3734	3752	3740	3755
<i>Deschampsia cespitosa</i>	DECE	3733	3796	3775	3772
<i>Festuca brachyphylla</i>	FEBR	3794	3785	3762	3785
<i>Poa alpina</i>	POAL2	3797	3801	3768	3795
<i>Potentilla diversifolia</i>	PODI2	3814	3793	3810	3800
<i>Podistera eastwoodiae</i>	POEA	3753	3759	3759	3754

Changes in climate and reflectance measures across the study area over time

Time series plots for the collective study site were developed for the growing season of every year between 2000 and 2021 (Fig. 2). When comparing data from 2004 and 2021, mean EVI values increased from 0.13 to 0.18. Meanwhile, NDSI values decreased from 0.43 to 0.30. LST values also increased from 20 degrees Celsius to 22 degrees Celsius (Fig. 2). When

analyzing 90th percentile values, EVI increased from 0.27 to 0.31, LST increased from 25.73 to 28.55, and NDSI decreased from 0.79 to 0.75. When running simple linear regressions on each of the three climate variables, it was determined that there was a significant linear relationship between both mean and 90th percentile EVI values and year ($P= 0.01$, $P=0.04$) (Fig. 2). There was also a significant linear relationship demonstrated between mean NDSI values and year ($P= 0.01$) (Fig. 2). In contrast, there was not a significant linear relationship found for either mean or 90th percentile LST values and year (Fig. 2).

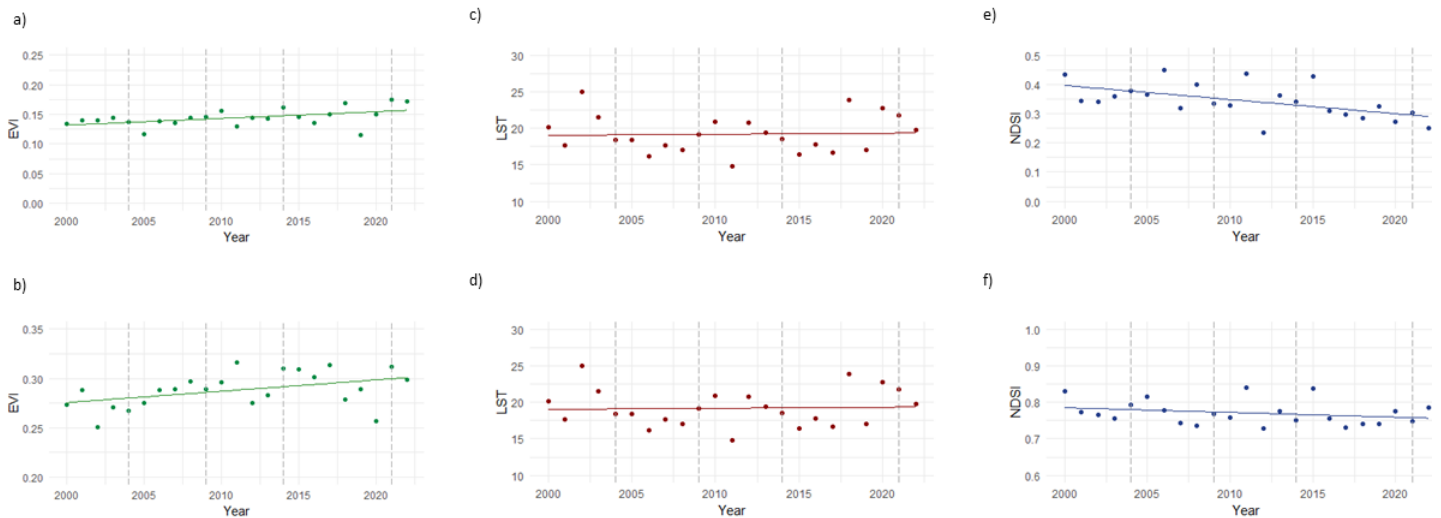


Figure 2. Time-series plots overlaid with horizontal linear regression trend lines that illustrate SBB’s mean and 90th percentile growing season values for environmental variables (a,b) Enhanced Vegetation Index (EVI), (c,d) Land Surface Temperature (LST), and (e,f) Normalized Difference Snow Index (NDSI). Data for the growing season was collected for the period of June 1st-September 30th between the years 2000 and 2021. Colored points represent annual climate values, and vertical, grey lines represent years that vegetation was sampled.

The 3-dimension NMDS ordination plot was produced with stress = 0.13 (Fig. 3a). Axes one and two both demonstrated relationships between shifts in plant community composition and environmental covariates (Fig. 3b; Fig. 4). The first axis, NMS 1, was closely linked to elevation (Pearson's $r = 0.81$, Fig. 4b). NMS 1 was also correlated with NDSI ($r = 0.44$). The second axis, NMS 2, was strongly related to soil moisture ($r = -0.60$, Fig. 4b). NMS 2 was also correlated with LST ($r = 0.53$), NDSI ($r = -0.53$), and weakly correlated with elevation ($r = -0.39$, Fig. 4c), and TPI ($r = -0.39$, Fig. 4a). The third axis, NMS 3, was not closely associated with any measured environmental factors. Environmental covariates also showed relationships between each other. EVI was strongly correlated with snow presence ($r = 0.51$), and also correlated with slope ($r = 0.43$) and soil moisture ($r = -0.4$). LST was strongly correlated with NDSI ($r = -0.99$) and elevation ($r = -0.62$). NDSI was strongly correlated with elevation ($r = 0.70$).

The NMDS ordination plot was split into four quads, representing four different communities and topographic environments within SBB (Fig. 3b). Quad 1, the *Dry Slope* community, contained transects 24, 31, 34, and 35. This community was characterized by low soil moisture, NDSI, and EVI, but high LST and high elevation species. The most dominant species within this community was *Arnica mollis* (ARMO4). Quad 2, the *Shrubby Riparian* community, contained transects 3, 22, 23, 32, and 33. This community was characterized by high soil moisture and EVI, low LST and NDSI, and low elevation species. The most dominant species within this community was *Caltha leptosepala* (CALE4). Quad 3, the *Wet Meadow* community, contained transects 1, 2, 6, 7, 11, 12, and 25. This community was characterized by high soil moisture, EVI, NDSI, and elevation, and low LST. The most dominant species within this community was *Polygonum bistortoides* (POBI6). Quad 4, the *Alpine Steppe* community, contained transects 4, 5, 9, 10, 21, and 26. This community was characterized by low soil

moisture and EVI, as well as high LST, NDSI, and high elevation species. The most dominant species for this community was *Geum rossii* (GERO2) (Fig. 3b).

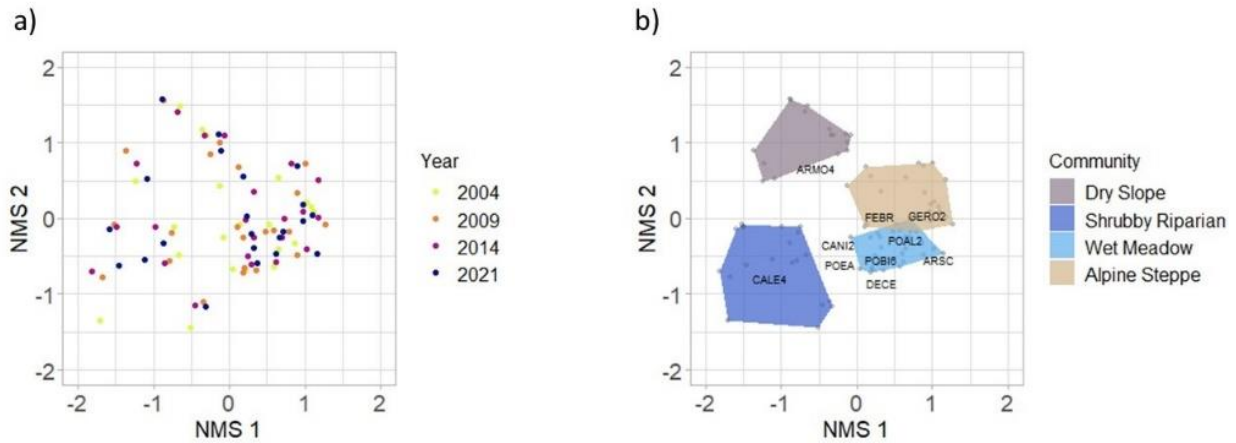


Figure 3. Non-Metric Multidimensional Scaling (NMS) ordination plots illustrating a) locations of the 22 transects in species space during each sample year, and b) four community types based on transect ordination position in species space. Only the first two NMS axes (NMS 1 & 2) are illustrated. Changes in the cover of different transects for the years 2004, 2009, 2014, and 2021 are illustrated by colored dots. Polygons represent community types. Species USDA codes are overlaid on community ordination to represent the dominant plant species within each community.

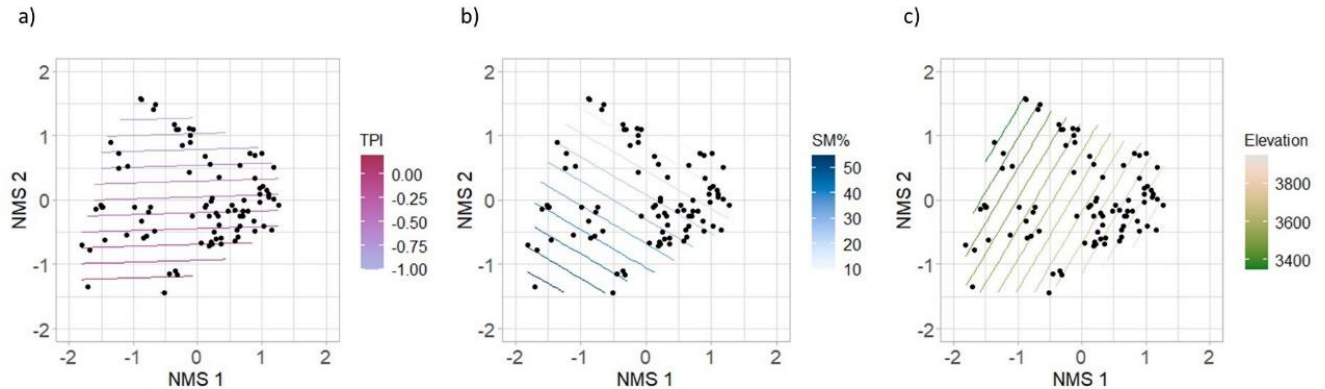


Figure 4. Relationships between NMS ordination axes scores and key environmental variables including (a) Topographic Position Index (TPI), (b) Soil Moisture (SM), and (c) elevation.

To further assess fluctuations in climate for individual community types, time series bar plots were developed for the mean (Fig.5) and 90th percentile value of each sampling year (Fig. 6). Trends were broadly similar across most communities, in particular when comparing 2004 and 2021. In general, each community exhibited increases in both mean percentile values for LST and EVI, while exhibiting decreases in mean values for NDSI when comparing 2004 and 2021 data (Fig. 5). Of all communities, the *Alpine Steppe* community exhibited the largest mean LST difference of 3.6 ° C. For EVI values, the *Alpine Steppe* and *Wet Meadow* communities both demonstrated the largest mean increase of 0.04 units for both communities. The *Dry Slope* and *Shrubby Riparian* communities both showed the largest decrease in mean NDSI levels, with a difference of 0.08 units (Fig. 5). Meanwhile, trends varied across communities when comparing 90th percentile values. All communities exhibited increases in their 90th percentile NDSI values when comparing 2004 and 2021. Communities differed in their LST trends over time, with the *Shrubby Riparian* community having exhibited an increase in LST, while the remaining

communities experienced a decrease in LST. The *Wet Meadow* and *Alpine Steppe* communities both experienced increases in their 90th percentile EVI, while the *Dry Slope* community exhibited a decrease over time. EVI values remained the same for the *Shrubby Riparian* community. Both the *Wet Meadow* and *Alpine Steppe* communities exhibited the largest increase in 90th percentile EVI of 0.04 units, while the *Dry Slope* community showed a decrease of 0.01 units. While the *Alpine Steppe* community exhibited the largest decrease in 90th percentile LST of 3.85 degrees Celsius, the *Shrubby Riparian* community demonstrated an increase of 0.04 degrees Celsius. Both the *Alpine Steppe* and *Dry Slope* communities exhibited the largest decrease in 90th percentile NDSI of 0.05 units.

Finally, to assess the relationship between environmental variation and transect position in ordination space, arrows were positioned at each transect point within the NMS plot (Fig. 7). We found no evidence of unidirectional movements among transects for years sampled, nor did we find evidence when measuring the mean change across the collective sample. When assessing movement within ordination quadrants, no evidence of directional and communal compositional change was observed within any of the established community types. Furthermore, analysis of small-scale systematic shifts occurring in response to interannual climate variation were also generally not present.

Alpine Community Dynamics in SBB

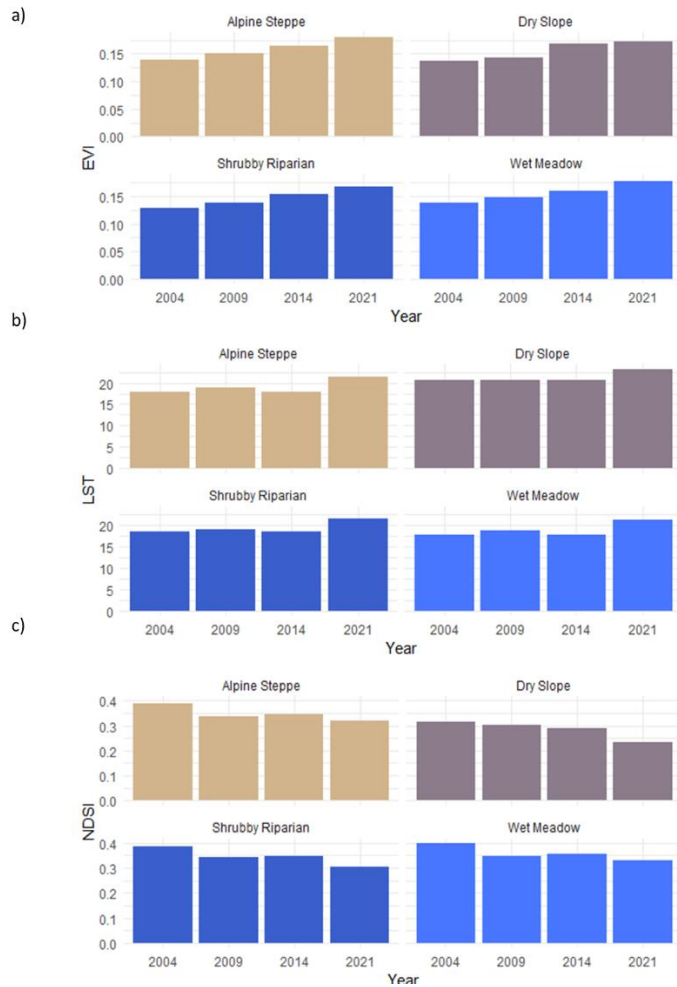


Figure 5. Bar plots illustrating community mean growing season values for environmental variables (a) Enhanced Vegetation Index (EVI), (b) Land Surface Temperature (LST), and (c) Normalized Difference Snow Index (NDSI) for the years 2004, 2009, 2014, and 2021. Data for the growing season was collected for the period of June 1st-September 30th of each year.

Alpine Community Dynamics in SBB

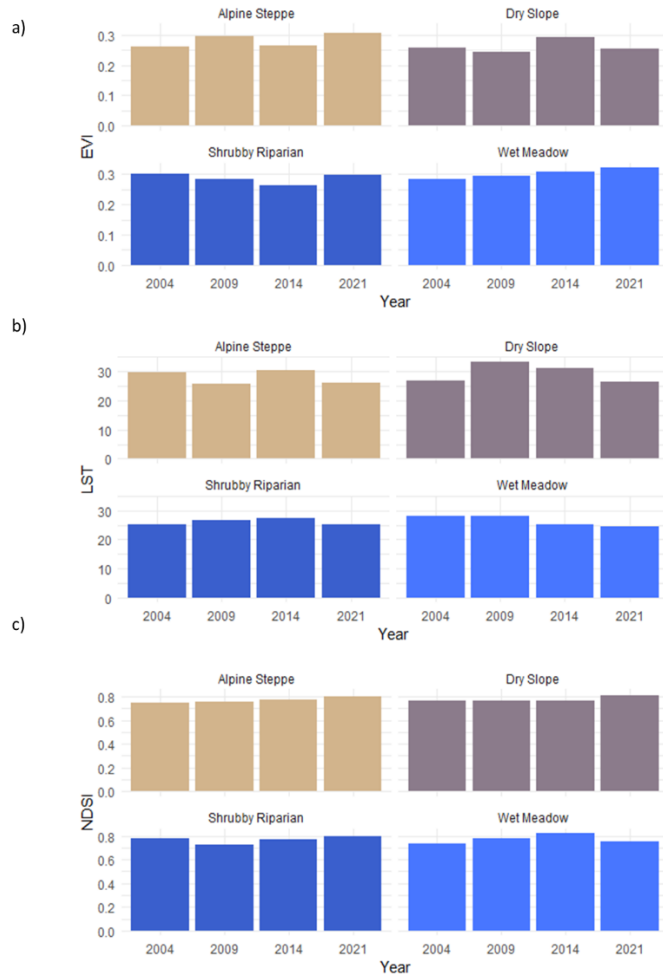


Figure 6. Bar plots illustrating community 90th percentile growing season values for environmental variables (a) Enhanced Vegetation Index (EVI), (b) Land Surface Temperature (LST), and (c) Normalized Difference Snow Index (NDSI) for the years 2004, 2009, 2014, and 2021. Data for the growing season was collected for the period of June 1st-September 30th of each year.

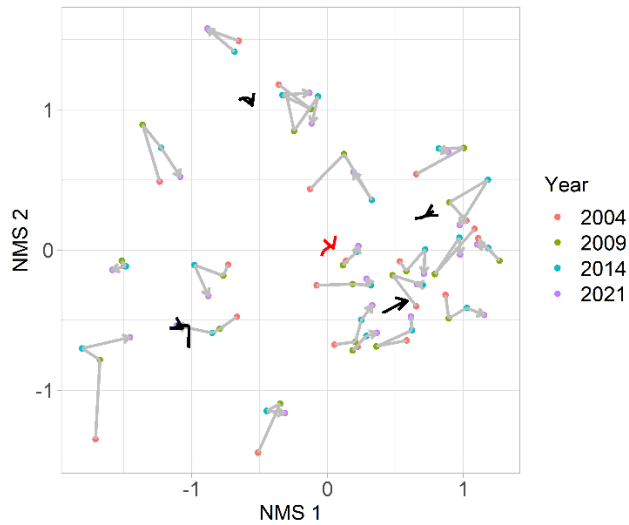


Figure 7. NMS ordination plot with arrows indicating the movement of each transect in ordination space over time. Dots indicate transects, and arrows indicate the direction and length of position movement over sampling years 2004, 2009, 2014, and 2021. Grey arrows indicate individual transect movement, while the red arrow indicates the mean change for the collective study site.

Discussion

Findings from the statistical analyses of vegetation and climate data within the Senator Beck Basin suggest that the plant communities and individual plant species in this geographic area have shown only little change over the past 18 years, despite substantial year-to-year variation in climate and a trend of lengthening growing seasons and decreasing snowpack duration. These findings are in contrast with others showing predictable changes in alpine plant communities in response to climate, and suggest that communities in the SBB may be changing at a non-uniform and slower rate than those in other global mountainous regions (Klanderud &

Birks, 2003; Lenoir et al., 2008). While we expected to document shifts in species distribution over time, findings from the randomization tests indicated that few species have exhibited significant directional shifts in species' frequency or weighted mean elevation, and only select species have demonstrated significant changes in their frequency and weighted mean elevation when comparing 2004 and 2021 data. Similarly, transect composition did not show directional or concerted changes in species space, as assessed by tracking site scores over time in NMS ordination plots.

Time series data for plant communities revealed that every community experienced an increase in their mean LST and EVI values when comparing 2004 and 2021 data, while also experiencing a decrease in their mean NDSI levels. This was also observed when examining time series data for the collective study site. However, community trends were not uniform when analyzing their 90th percentile climate values, revealing unique differences in environmental covariates among community types.

The findings from the simple linear regression models strengthened these observations, and exposed the significant changes in both the mean and 90th percentile values for EVI, and the mean values for NDSI. Linear regression also revealed a higher significance in the mean values for EVI and NDSI than the 90th percentile values, suggesting that the annual growing season has increased over time, while the annual snow season has decreased. Interestingly, LST did not experience a significant increase over time for either set of values, which differs from significant LST trends exhibited within other mountainous regions (Zou et al., 2020). These results demonstrate that although the sensitivity of this alpine ecosystem may be comparatively low to other alpine regions (Pauli et al., 1996), the growing season of alpine plants in SBB has increased over time, suggesting an earlier green-up of plant species over time.

The negative correlation observed between EVI and soil moisture levels in SBB implies that a consistent decrease in soil moisture over time could potentially lead to an increase in vegetation density and productivity within traditionally wet regions as they become drier over time. Studies suggest that moderate declines in soil moisture may stimulate short-term plant growth in alpine communities that have historically been documented as wetter, while drier communities may experience a more negative response (Cowels et al., 2018; Li et al., 2018). Consequently, the *Shrubby Riparian* and *Wet Meadow* communities of SBB are more likely to experience higher productivity levels as conditions become drier and hotter over time, while the moisture limited communities of *Dry Slope* and *Alpine Steppe* are more likely to see declines in productivity and plant density. This is supported through the negative correlation that exists between EVI and soil moisture, suggesting that plant productivity increases as soil moisture decreases. While increases in the *Wet Meadow* mean EVI over time supports this hypothesis, identical mean increases in the *Alpine Steppe* community does not. These findings suggest that though the *Alpine Steppe* and *Wet Meadow* communities may have discernable disparities in soil moisture, these variations are not likely substantial enough to give rise to contrasting levels of plant productivity. Further, the convergence of NMS polygons for these communities suggests that they may possess shared attributes that contribute to similar productivity outcomes, such as elevation and species composition. It is probable that there is an overlap in species composition among communities located along a comparable elevation gradient, which could result in similar responses to climate fluctuations, notwithstanding variations in abiotic factors such as soil moisture.

Overall, these findings highlight the variability of alpine community response to climate change, and reveal the complex interplay that exists between environmental factors and species

resiliency within alpine systems (Du et al., 2021; Junker & Larue-Kontić, 2018; Måsviken et al., 2020). There are many circumstances that can drive the rate and direction of change within alpine ecosystems over time (Dullinger et al., 2012). For example, alpine ecosystems with long-lived perennial species demonstrate a higher likelihood of resilience to climate change over time due to their inherent capacity to endure harsh environments (Jabis, 2018; Kobiv, 2017). The long lifespan of these species likely provides them with opportunities to experience and adapt to various environmental stressors, which allows them to develop physiological mechanisms that enhance their stress tolerance. Thus, areas such as SBB that are characterized by these species are less likely to exhibit significant shifts in their frequency or elevational distribution over time (Miller, 2012). The growing-season productivity and biomass accumulation of alpine plant communities are also typically lower than other systems (Atkin et al., 1996; Bliss, 1971), inferring that these species have limited energy and resources available for growth and reproduction. The gradual nature of alpine ecological dynamics likely allows for a more tapered response to changing conditions that may not be measurable within a timeframe of two decades (Clarke et al., 2019).

While these hypotheses individually highlight possible reasons why alpine ecosystems may exhibit unique responses to changes in climate, it is likely a combination of these factors are influencing the response of plant communities within SBB (Brooker et al., 2007; Jonas et al., 2008). The relative stability of individual plant species within SBB provides an excellent opportunity for the execution of preemptive conservation initiatives and strategies that emphasize habitat conservation for specialist alpine species. For the duration of this study, climate measures should consistently be recorded for the collective study site to continue monitoring environmental trends occurring in SBB. Documenting growing season values such as

EVI, NDSI, and LST will aid in predicting future climate trends and community responses within SBB, particularly when coupled with additional years of sampled vegetation data (Jiang et al., 2023; Schwager & Berg, 2021). To elucidate the mechanisms underlying the relationship between disturbance and species composition, grazing exclusion plots should be established throughout the study area, which would quantify the effects of grazing disturbance on species abundance and diversity. Establishing additional research plots such as grazing exclosures within SBB will not only further our understanding of what factors influence alpine plant communities the most, but will also provide the opportunity for informing policy changes and outlining management strategies that benefit these unique systems. The continuation of ecological monitoring and data collection within alpine landscapes like SBB is integral to maintaining the resiliency of alpine plant species and broader communities throughout the San Juan Mountains as well as other global mountainous regions.

Conclusions

Shifts in the climate of alpine ecosystems are expected to drastically shape the diversity, abundance, and productivity of the plant species that comprise them (He et al., 2019; Inouye, 2020). This study highlights the interplay that exists between climate and vegetation in the Senator Beck Basin, and elucidates that alpine ecosystem response to climate change in southwestern Colorado may be more complex and multi-faceted than previously expected. Here, we expose the significant changes in select species frequency and elevation over time, while also highlighting changes in functional group frequency. Additionally, we quantify the linear relationship that exists between two key climate variables (NDSI, and EVI), and year through the use of MODIS imagery and simple linear regression, while also revealing the higher significance existing between mean EVI and NDSI values then 90th percentile values. We describe four

unique communities in SBB that are characterized by unique abiotic variables such as soil moisture and elevation. We also reveal the negative relationship that exists between EVI and soil moisture, suggesting that soil moisture plays an important role in regulating vegetation growth in SBB, and predicting that wetter communities are likely to experience increased plant growth as they become drier. These findings underscore the need for continued monitoring and research to better understand the impacts of climate change on local alpine systems and inform management decisions to ensure their long-term sustainability (Burns et al., 2014). Quantifying growing season snowpack, plant growth, and soil moisture in SBB will continue to be important for recognizing potential patterns in climate that develop during future sampling years, and their influence on species distribution. Additionally, establishing grazing exclusion plots will assist in measuring the effects of grazing disturbance on plant species abundance and diversity.

Conserving the unique environmental variability, biodiversity, and habitat that exists within unique landscapes such as the Senator Beck Basin are essential to maintaining the resiliency of alpine plant species and broader communities throughout the San Juan Mountains and global mountainous regions.

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