# 30 Years of Change: Visualizing Hotter Drought at Upper Treeline Along the Colorado Trail

A Thesis presented to The Faculty of the Graduate School at the University of Missouri - Columbia

In Partial Fulfillment of the Requirements for the Degree Master of Arts

By

COREY J. ALDRED Dr. Grant P. Elliott, Thesis Supervisor May 2023

#### APPROVAL

The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

30 YEARS OF CHANGE: VISUALIZING HOTTER DROUGHT

## AT UPPER TREELINE ALONG THE COLORADO TRAIL

presented by Corey Aldred,

a candidate for the degree of Master of Arts,

and hereby certify that, in their opinion, it is worthy of acceptance.

Dr. Grant Elliott

Dr. Clayton Blodgett

Dr. Michael Stambaugh

#### ACKNOWLEDGEMENTS

My thanks to the Department of Geography for bringing this lost mountain man not only into this program, but into this wonderful community of good folks. I would like to extend my gratitude to John Fielder, who has spent a lifetime capturing the beauty of Colorado and compiling important photographic artifacts of landscapes that have undergone substantial change. I thank him for being supportive of my work and helping me to relocate his original photographs from 30 years ago. My heartfelt thanks to my advisor, Dr. Grant Elliott, who provided me with the opportunity to conduct academic research in the mountains and forests that I had recreated in for many years. My special thanks to my committee members; Dr. Clayton Blodgett, who went out of his way and spent many hours assisting me with complicated geospatial tools, and Dr. Michael Stambaugh, who helped edit early drafts and provided important perspective on forest disturbances. I thank the Biogeography Specialty Group and the Graduate Professional Council for helping to fund the fieldwork portion of this research in Colorado. Last, but certainly not least, I would be remised if I did not thank my thoughtful and supportive partner, Becca Elder. She brought me to Missouri, encouraged me to apply for graduate school, took care of our dogs and house while I was away all summer working and conducting research, dealt with my stress that grad school entails, and critiqued and edited my work throughout.

## TABLE OF CONTENTS

| ACKNOWLEDGEMENTS                      | ii |
|---------------------------------------|----|
| LIST OF ILLUSTRATIONS                 | iv |
| ABSTRACT                              | vi |
| 1. INTRODUCTION                       | 1  |
| 2. STUDY AREA                         | 6  |
| 2.1 TOPOGRAPHY                        | 6  |
| 2.2 CLIMATE                           | 7  |
| 2.3 VEGETATION                        |    |
| 3. METHODS                            | 9  |
| 3.1 REPEAT PHOTOGRAPHY                | 9  |
| 3.2 CLIMATE DATA                      |    |
| 4. RESULTS                            |    |
| 4.1 TREELINE DYNAMICS                 |    |
| 4.2 SPRUCE BEETLE                     |    |
| 4.3 WILLOW EXPANSION                  |    |
| 4.4 CLIMATE PATTERNS                  |    |
| 5. DISCUSSION                         |    |
| 5.1 TREELINE ADVANCE                  |    |
| 5.2 SPRUCE BEETLE-INDUCED MORTALITY   | 15 |
| 5.3 VEGETATION COMPOSITION SHIFT      |    |
| 5.4 TEMPERATURE-MOISTURE INTERACTIONS |    |
| 6. CONCLUSION                         |    |
| 7. REFERENCES                         |    |
| 8. TABLES, FIGURES, AND PHOTOS        |    |
| 8.1 TABLES                            |    |
| 8.2 FIGURES                           |    |
| 8.3 REPEAT PHOTOS                     |    |

## LIST OF ILLUSTRATIONS

| Table 1. Repeat photo site information                   | .37  |
|----------------------------------------------------------|------|
| Table 2. Observed results from repeat photo pairs.       | .37  |
| Table 3. Annual precipitation, 1895-2022 Tukey HSD Test. | .38  |
| Table 4. Annual precipitation data summary, 1895-2022    | .38  |
| Table 5. Annual precipitation data summary, 1992-2022    | . 39 |
| Table 6. Warm Season VPD Min Tukey HSD Test.             | . 39 |
| Table 7. Warm Season VPD Max Tukey HSD Test              | .40  |

| Fig. 1. Study area along the Colorado Trail                                              | 41 |
|------------------------------------------------------------------------------------------|----|
| Fig. 2. Spruce beetle mortality Google Earth screenshot                                  | 42 |
| Fig. 3. Spruce beetle mortality Google Earth screenshot                                  | 42 |
| Fig. 4. Defoliated spruce at upper treeline in the west San Juan Mountain Range          | 43 |
| Fig. 5. Upper treeline forest near San Luis Peak in the La Garita Wilderness             | 44 |
| Fig. 6. Precipitation pie chart, 1895-2022                                               | 44 |
| Fig. 7. Annual deviations from the 20th Century mean of precipitation, 1895-2022.        | 45 |
| Fig. 8. Annual deviations from the 20th Century mean of warm season VPD Min, 1895-2022.  | 45 |
| Fig. 9. Annual deviations from the 20th Century mean of warm season VPD Max, 1895-2022   | 46 |
| Fig. 10. Annual deviations from the 20th Century mean of cool season VPD Min, 1895-2022. | 46 |
| Fig. 11. Annual deviations from the 20th Century mean of cool season VPD Max, 1895-2022. | 47 |
| Fig. 12. Summer (June-Aug) temperature graphs                                            | 48 |
| Fig. 13. Upper treeline forest near San Luis Peak in the La Garita Wilderness            | 49 |
| Fig. 14. Spruce living amongst willow.                                                   | 49 |
| Fig. 15. Standing bristlecone pine                                                       | 50 |

| Photo Site 1. ITR 1            | 51 |
|--------------------------------|----|
| Photo Site 2. ITR 2            |    |
| Photo Site 3. San Luis Peak    |    |
| Photo Site 4. Sunflower.       |    |
| Photo Site 5. Southern Sawatch |    |
| Photo Site 6. Antora Peak.     |    |
| Photo Site 7. Fooses           |    |
| Photo Site 8. Searle Pass      |    |

| Photo Site 9. Breckenridge. | 59 |
|-----------------------------|----|
| Photo Site 10. GP Pond 1    | 60 |
| Photo Site 11. GP Pond 2    | 61 |
| Photo Site 12. GP Snow      |    |

#### ABSTRACT

Over the last 30 years, the Southern Rocky Mountains (SRM) have experienced an unprecedented period of warming and aridity. The consequences of this hotter and drier climate are becoming increasingly evident across Rocky Mountain forests, where megadisturbances are resulting in state shifts from forested to non-forested ecosystems. This research, which revisits twelve photographs taken along the Colorado Trail in 1992, has revealed alarming new findings. It shows that some of the highest treeline ecotones along the spine of the Rockies have been devastated by spruce beetle-induced mortality and that spruce seed production will be increasingly constrained by threshold high temperatures. The repeat photos also reveal that a dramatic vegetation composition shift is occurring in the SRM with the accelerated proliferation of willow into alpine tundra, thriving under warmer conditions amid spruce beetle devastation. Furthermore, this study highlights that projected declines in forest cover in western North America must now take into account the loss of Engelmann spruce from upper treeline ecotones and that the trend of expansion of the mountain forest belt via treeline advance appears to be particularly unlikely and is instead likely to be one of forest contraction. Ultimately, the results of this regional-scale repeat photography study point to a future of spruce at treeline that is not promising because of (1) beetle-induced mortality, (2) rising temperature stressing seed production, (3) the need for moisture, (4) challenges to natural seed dispersal, and (5) willow encroachment throughout the alpine tundra.

## 1. INTRODUCTION

The combined disturbances of climate change and hotter drought on regional vegetation and landscape demography threaten the resilience of high-elevation mountain forests and the scenic beauty of popular trails like the Colorado Trail (CT). Rates of warming at high altitudes are more than twice as high than for the rest of the world (Pepin et al. 2015). As the climate continues to warm and alter disturbance regimes, increases in disturbance extent, frequency, and interactions will result in the continuation of widespread tree mortality (Allen et al. 2015, Abatzoglou & Williams 2016, Hammond et al. 2022) and a reduction of climatic suitability for high elevation species (Bell et al. 2014) where a lack of water availability increasingly threatens survivorship (Gill et al. 2015, Hammond et al. 2019). Critically, intensifying drought stress (Breshears et al. 2005, Allen et al. 2015, Hammond et al. 2022) is eroding forest resilience and resulting in state shifts to non-forested ecosystems (Millar & Stephenson 2015, Harvey et al. 2016, Kemp et al. 2016, Stevens-Rumann et al. 2018, Rodman et al. 2020, Schapira et al. 2021) and novel successional trajectories (Zhang et al. 2023). Vegetation projections in western North America (NA), for example, suggest a reduction of about half of the needleleaf evergreen tree coverage and just a 14% increase in grasses and shrubs by the end of the 21<sup>st</sup> century (Jiang et al. 2013). The resulting effects on carbon storage (Bonan 2008, McDowell et al. 2020) due to extensive tree reduction create the potential to convert the forests of western NA from a net carbon sink to a net carbon source (Jiang et al. 2013). Climate change is already materializing across mountain forests (Davis et al. 2019, McDowell et al. 2020, Hammond et al. 2022) by lengthening the growing season and

increasing evaporative demand (Kueppers et al. 2017), which is augmenting the geographic distributions of plant species (Andrus et al. 2021). This poses substantial management challenges in sustainable forest conservation.

The position of upper treeline throughout a large portion of the U.S. Rocky Mountains is at the highest extent in at least the past 350 years (Elliott 2012a) primarily from pulses of tree establishment since 1950, which in central Colorado, matched the highest recorded elevation of treeline for the past 1200 years (Carrara & McGeehin 2015). Sustained warming in mountain environments has been temporally aligned with this abrupt upslope advance of many upper treeline ecotones since 1950 (Camarero & Gutiérrez 2004, Walther et al. 2005, Beckage et al. 2008, Lenoir et al. 2008, Elliott & Kipfmueller 2011, Case & Duncan 2014, Liang et al. 2016, Huang et al. 2017, Du et al. 2018, Elliott & Petruccelli 2018) and forest density increases (Szeicz & MacDonald 1995, Klasner & Fagre 2002, Lloyd & Fastie 2003, Camarero & Gutiérrez 2004, Danby & Hik 2007, Batllori & Gutiérrez 2008, Liang et al. 2011, Millar et al. 2015, Camarero et al. 2017). It is noteworthy, however, that varied spatial and temporal patterns of tree establishment (Elliott & Kipfmueller 2010) from ecologically important local scale processes (Elliott 2011, Loranger et al. 2016, Lyu et al. 2016, Bader et al. 2021) suggest that soil moisture conditions are increasingly influencing seedling establishment in upper treeline ecotones (Daniels & Veblen 2004, Elliott 2012a, Liang et al. 2014, Sigdel et al. 2018, Elliott et al. 2021, Wang et al. 2021). Across portions of the Southern Rocky Mountains (SRM), for instance, pulses of tree recruitment over the past 30 years have been increasingly confined to wetter north-facing slopes (Elliott et al. 2021). Perhaps most striking, there has been a complete lack of recruitment over the past decade within

upper treeline ecotones along the Sangre de Cristo Mountain Range within the SRM (Bailey et al. 2021). Consequently, temperature-moisture interactions at upper treeline and across the mountain forest belt are frequently associated with the crossing of a bioclimatic threshold where it is now too hot and too dry for successful recruitment of conifer tree species in recent decades (Elliott 2012b, Elliott & Cowell 2015, Moyes et al. 2015, Zhang et al. 2015, Kueppers et al. 2017, Andrus et al. 2018, Babst et al. 2019, Jiang et al. 2019, Lu et al. 2019, Shestakova et al. 2019, Zhang et al. 2020, Elliott et al. 2021, Bailey et al. 2021, Lu et al. 2021).

In the western United States, the two major disturbance agents that kill trees are wildfire and bark beetle outbreaks, both of which are made more frequent and severe from hotter drought stress. Spruce-fir forests across high elevations of the Rocky Mountains have recently experienced epidemic proportions of spruce beetle (Dendroctonus rufipennis Kirby) outbreak that have resulted in >95% mortality of overstory Engelmann spruce (Pettit et al. 2019). Between 2011 and 2015, spruce beetle activity in and around the San Juan and Rio Grande National Forests, both of which the CT passes through, left very little of the region unaffected by spruce beetle attack (Woodward et al. 2018). The spruce beetle has remained the most damaging forest pest in the state of Colorado for ten consecutive years, as of 2022 aerial surveys data (US Forest Service 2022). In 2021, spruce beetle affected roughly 53,400 acres (21,400 hectares) of high-elevation Engelmann spruce forests in Colorado, with the most intense infestations in south-central Colorado where much of the CT is located (US Forest Service 2022). Bark beetle epidemics have also expanded into persistent infestations in habitats that previously had only rarely been affected (Raffa et al. 2008). Because bark beetles cause

mortality to both the trees and the seed source, soil moisture deficits from persistent drought will reduce the likelihood of future germination of the seeds that are left and thus challenge the retention of spruce forests.

In addition to tree recruitment across treeline ecotones, shrub cover has expanded at an exponential rate since the 1950's (Formica et al. 2014) and there have been consistent and increasing rates of recruitment of alpine willows (*Salix planifolia*; planeleaf willow) (Myers-Smith & Hik 2018). Additionally, variations of aspect, elevation and species identity do not explain variation in recruitment patterns, suggesting a regional factor, such as climate, as the driver of observed shrubline advance (Myers-Smith & Hik 2018). Indeed, observed increases in woody plant species in arctic tundra ecosystems over decadal time scales are frequently linked to concurrent periods of climate warming (Chapin et al. 2005, Weintraub & Schimel 2005, Formica et al. 2014). Warming temperatures are facilitating willow growth and are advancing encroachment into many arctic and alpine tundra herbaceous-dominated communities (Sturm et al. 2001, Stow et al. 2004, Tape et al. 2006, Cannone et al. 2007, Hallinger et al. 2010, Myers-Smith et al. 2011, Rundqvist et al. 2011). Yet what this means for upper treeline dynamics remains less clear.

The expansion of shrub cover in recent years is the result of multiple interacting factors, including climate warming, changes in nutrient cycling, altered disturbance patterns, and local variability in topography and hydrology (Mekonnen et al. 2018). Under warmer conditions, tall deciduous shrubs can be more competitive than other plant types in tundra ecosystems because of their taller maximum canopy heights and often dense canopy structure (Mekonnen et al. 2018). An increase of shrub cover in alpine

tundra is expected to cause a net decrease in both summer and winter albedo, increasing summer and winter soil temperature (Formica et al. 2014). Although shrubs are capable of trapping snow, studies suggest that they typically have similar melt-out dates as tundra vegetation, since shrub areas start melting earlier (Sturm et al. 2005a, 2005b). Overall, lower albedo along with both increased N (Mack et al. 2004, Sturm et al. 2005b, Weintraub & Schimel 2005) and C cycling (Shaver et al. 1998) suggests that increased soil temperatures may generate positive feedbacks, further accelerating willow encroachment (Sturm et al. 2001, 2005b).

To assess how the aforementioned vegetation dynamics are manifesting across upper treeline environments across the SRM under the influence of unprecedented and catastrophic hotter drought conditions (Williams et al. 2022), this research uses groundbased repeat photography along the CT to examine how thirty years of sharp rises in temperature have affected upper treeline ecotones. The notoriety, extensiveness, and abundance of treeline terrain along the CT make for the ideal medium to extract how the differences in continental-scale climate patterns, biogeography, and latitudinal gradients influence upper treeline response to the emergence of a global acceleration of lethal climate conditions (Hammond et al. 2022). Given the rapidity of threshold-induced regime shifts seen in recent years in ecological systems (Wolkovich et al. 2014, Cooper et al. 2020, Turner et al. 2020), thirty years of photographic evidence (i.e. Munro et al. 2008) provides an appropriate temporal scale to answer the following research questions regarding high-elevation treeline environments along the Colorado Trail:

- 1. Is there evidence of upper treeline advance?
- 2. Is there evidence of spruce beetle-induced mortality at upper treeline?

3. Is there evidence of willow encroachment into alpine tundra?

## 2. STUDY AREA

## 2.1 TOPOGRAPHY

The CT is a 782 km (486 mi) popular recreational trail that spans from Denver to Durango, entirely south of 40° N latitude (Fig. 1). The trail cuts through six National Forests, six Wilderness areas, and crosses five major river systems, while passing over eight of Colorado's mountain ranges (Jacobs & Fielder 1994). At an average elevation of 3,140 m (10,300 ft), it spans across the Continental Divide (CD) through the heart of the SRM. Much of the CT is over 2,740 m (9,000 ft) in elevation and occasionally exceeds 3,960 m (13,000 ft) in the San Juan Mountain Range, placing it in direct contact with and often in plain view of upper treeline, which averages 3,350 m (11,000 ft) – 3,660 m (12,000 ft) in the region (Peet 200). All the photos for this study were taken from sites that lie between 3,530 m and 3,950 m.

The La Plata Mountain Range outside of Durango is situated in a semi-arid environment and offer a unique ecosystem due to their position on the eastern edge of the Colorado Plateau and their proximity to the CD. The San Juan Mountains (SJM) are an east–west-oriented range formed from Miocene to Quaternary volcanic deposits (Baker 2009). Soil properties including moisture and total N and P are highest on the lee side of existing vegetation at treeline (Bourgeron et al. 2015). The Sawatch Range is a prominent mountain range of the CT located to the northeast of the SJM. It occupies a pivotal position between the drier north-south oriented ranges to the east and the moister eastwest oriented ranges to the west. The range extends over 130 km (81 mi) in a north-south direction, with much of the 8450 sq. km (5250 sq. mi) area above timberline (Hartman & Rottman, 1988).

## 2.2 CLIMATE

The timing and duration of the growing season have been shifting, with earlier snowmelt leading to earlier spring growth, and longer growing seasons leading to changes in the composition and structure of vegetation at treeline (Kueppers et al. 2017). The SRM of southern Colorado warmed at one of the highest rates in the contiguous US in the early 21st century, accompanied by drying trends and modifications of climate type at higher elevations (Blair & Bracksieck 2011). Annual soil water deficits are low in this region and gradually increase moving north (Elliott & Cowell 2015) as moist air masses move inland from the Pacific Ocean and Gulf of Mexico and strike the Western San Juans first in the SRM region (Blair & Bracksieck 2011). Synoptic-scale Pacific climate patterns resulting from the El Nino Southern Oscillation (ENSO) are relatively uniform across the SRM south of 40° N, with infrequent intrusions of Pacific air masses during the winter and an influx of monsoonal moisture from July through September (Blair & Bracksieck 2011, Elliott et al. 2021). Regional climate models project 2°C or higher increases in minimum temperature (Tmin) and maximum temperature (Tmax) for all seasons (Rangwala et al. 2012). However, there are much greater ( $>3^{\circ}$ C) increases in Tmax during summer at higher elevations and in Tmin during winter at lower elevations (Rangwala et al. 2012). Critically, Tmax increases during summer are associated with drying conditions (Rangwala et al. 2012), contributing to hotter drought. Extremely low temperatures are rarely observed west of the CD, as bitter arctic air is generally confined to the east (Barry 2008).

## 2.3 VEGETATION

The SRM comprise the highest treeline ecotones along the spine of the Rocky Mountains and include the broadest expanse of climatically sensitive boundaries where subalpine forest borders alpine tundra capable of supporting treeline advance upslope (Butler et al. 2007, Elliott & Petruccelli 2018). Forests cover 55% of the SRM and subalpine forests lie at the highest forested elevations c. 2700–3600 m, making up 51% of the total forest area (40,000 km<sup>2</sup>) (Rodman et al. 2021). Notably, the Sawatch Range contains the southern range limit of lodgepole pine forests in the Rocky Mountains (Peet 2000). Forest cover at upper treeline is dominated by Englemann spruce (Picea engelmannii) and subalpine fir (Abies lasiocarpa), with Colorado bristlecone pine (Pinus aristata) on south-facing slopes east of the CD (Elliott et al. 2021). Most spruce-fir stands at or near treeline, however, are composed purely of Engelmann spruce (Blair & Bracksieck 2011) in a more open canopy or patch-like structure than at lower elevations. For this study, the focus is on Engelmann spruce, which is a later successional species tolerant of shade and adapted to higher moisture substrates (Jabis et al. 2020). These trees are well-adapted to the region's high elevation and cold, snowy winters, and are able to survive in a variety of soil types and moisture conditions. The shrub vegetation in the alpine zone of the SRM are typically dominated by willows (Salix planifolia) (Blair & Bracksieck 2011).

## 3. METHODS

### **3.1 REPEAT PHOTOGRAPHY**

Repeat photography involves locating the exact photo point to take a photograph that is identical to the original, usually taken several decades earlier (Zier & Baker 2006). Most examples of repeat photography compare present-day scenes with historical photographs taken over a century ago (e.g., Veblen & Lorenz 1991, Fielder 1999, Elliott & Baker 2004, Zier & Baker 2006), yet this study seeks to capture rapid threshold changes that climate is capable of triggering across high-elevation mountain landscapes since sharp rises in temperature began in the early 1990s (see Elliott et al. 2021).

For this research, I re-took original ground-based photographs published in two books: *Along the Colorado Trail* (Fielder & Fayhee 1992) and *The Colorado Trail: The Official Guidebook* (Jacobs & Fielder 1994). The original photos in the study came with minimal location data. The descriptions in the books the photos were pulled from only provided general mountain range information, as well as which CT Segment they were within, but no coordinate information. Inherently, finding the exact photo points thirty years later involved a little guess work, a lot of hiking, and extensive location scouting. Given that I was not thru-hiking the CT to find all the photos, it was important to make a plan in advance of which roads were navigable, where to camp, and where the best CT access trails were to each of the general photo locations. Once along the CT, in order to know that I was in the right location to repeat the photographs, I had the original photos with me in the field and took great care to identically lineup landscape features in the foreground, such as boulders or ridges, with mountain peaks in the background. Once in the right location, I set up a tripod and used a Nikon D3400 DSLR camera to take multiple photos with slightly different angles in an iterative process before obtaining the correct match to the original. It was often the case that I had to wait for cloud cover to dissipate or change my position on the ground just slightly to accurately replicate the photo. I then geo-referenced each photo location with lat/long/elevation data so that future visits to these sites would be more straightforward and repeatable (Table 1; Hammond et al. 2020). Along the CT, I photographed relevant examples of more widespread changes observed in the repeat photo pairs to help illustrate the ongoing changes within these landscapes. Once back from the field, all photos were visually observed on a projector screen to classify more accurately which of the result types, according to the research questions, occurred in each 30-year photo pair (Table 2).

## **3.2 CLIMATE DATA**

Climate data for this study were downloaded from PRISM (PRISM Group, Oregon State University, http:// www.prismclimate.org) for five repeat photo locations for the entire climate record available, 1895-2022. These data are extracted from 4km grid cells that accurately represent precipitation and temperature values across remote mountain regions that are heavily influenced by varied elevation and complex topography (Daly et al. 2008). The following climate variables were analyzed and graphed using Microsoft Office's Power BI software: (1) Total Annual Precipitation, (2) Annual Deviation from the 20<sup>th</sup> Century Mean of Precipitation (3) Annual Warm Season Vapor Pressure Deficit Maximum, (4) Annual Warm Season Vapor Pressure Deficit Minimum, (5) Annual Cool Season Vapor Pressure Deficit Maximum, (6) Annual Cool Season Vapor Pressure Deficit Minimum. Statistical computations of precipitation data were conducted utilizing the open-source, web-based platform Vassar Stats ANOVA (http://vassarstats.net/).

## 4. RESULTS

## **4.1 TREELINE DYNAMICS**

For this study, I successfully repeated 12 photographs of upper treeline environments along the CT (Table 1). The primary landscape changes evident over the past thirty years of warming include treeline advance and densification, spruce beetleinduced mortality, and the expansion of willow into alpine tundra (Table 2). A clear increase in either treeline advance, densification, or seedling establishment is visually observed in all twelve (100%) repeat photography scenes (Table 2). Treeline advance and increased tree recruitment were particularly notable in the photo from the Tenmile Range above the town of Breckenridge (Photo Site 9).

#### **4.2 SPRUCE BEETLE**

Spruce beetle-induced mortality at treeline was observed in five (42%) photo pairs (Table 2). The foreground forests in both images from the Eastern San Juans (ESJ) in the La Garita Wilderness near San Luis Peak (Photo Site 3 & 4) reveal near-total spruce beetle-induced mortality, contracting the forest belt hundreds of meters downslope from treeline (Fig. 2 & 3). The three replicated photographs in the southern end of the Sawatch Range (Photo Site 5, 6, & 7) all reveal an outbreak of spruce beetles at upper treeline, but not at the density or spatial extent seen in the ESJ. Additionally, I photographed the defoliation of an Engelmann spruce actively under beetle attack west of the CD in the western San Juan mountains where spruce-beetle mortality is not otherwise evident (Fig. 4). Interestingly, I found no evidence of spruce beetle at any of the repeat photo sites, or at upper treeline in general, north of 39° latitude within the study area.

#### **4.3 WILLOW EXPANSION**

Willow expansion was observed in ten of the 12 (83%) replicated photographs, as well as an overall increase in vegetation density in all mountain ranges photographed except for the southern Sawatch. Willow expansion was particularly notable in the ESJ in repeat photography scenes and from extensive field observations (Fig. 5) where spruce beetle-induced mortality was also the most widespread. Additionally, the three photos of a single location in the Front Range (Photo Site 10, 11, & 12) revealed substantial proliferation of willow in a snow melt-driven, persistently wet alpine environment.

## **4.4 CLIMATE PATTERNS**

Synoptic climate patterns produce significantly different (P < 0.01) precipitation regimes across the five mountain ranges, with the La Plata range west of the Continental Divide receiving the most precipitation (Table 4). The mean precipitation for all five ranges combined fell from 850 mm in the1895-2022 record (Table 4) to 831 mm during the 1992-2022 repeat photo study period (Table 5). Notably, however, the La Plata, ESJ, and southern Sawtach ranges experienced a reduction in annual precipitation from 1992-2022 compared to the entire climate record, while the Mosquito and Front ranges received more average precipitation during the 1992-2022 period compared to the entire record (See Table 4 & 5). Interestingly, while the La Plata Mountain Range receives considerably more precipitation than the other mountain ranges, accounting for nearly 30% of the total precipitation of all five mountain ranges from 1895-2022 (Fig. 6), this range also experienced the sharpest dips from the 20<sup>th</sup> Century mean in the early 21<sup>st</sup> Century with multiple years approaching a deficit of as much as 650 mm below the mean (Fig. 7).

The deviations from the 20th century mean of warm season vapor pressure deficit (VPD) revealed a notable increase in minimum VPD values across all mountain ranges (Fig. 8) compared to maximum VPD values (Fig. 9). However, both have steadily risen early in the 21<sup>st</sup> Century, reaching their peak in 2020 before dropping the two following warm seasons. Deviations from the 20<sup>th</sup> Century mean of cool season VPD remained mostly steady for the period of record for both min and max (Fig. 10 & 11). However, the cool season VPD min data reveal a considerable trend upwards beginning in the mid 1990's and continuing to the present day (Fig. 10). Notably, warm season minimum VPD values for the La Plata Mountain Range were significantly higher (P < 0.01) than all other ranges (Table 6). On the other hand, warm season maximum VPD values for the southern Sawatch were significantly higher (P < 0.01) (Table 7). Furthermore, in congruence with rising warm season VPD values, mean summer (June-Aug) temperatures are quickly rising across all five mountain ranges analyzed when compared to the 1970-2000 mean, particularly on Searle Pass in the Mosquito Range (Fig. 12).

## 5. DISCUSSION

#### **5.1 TREELINE ADVANCE**

At upper treeline, with trees positioned at or near their physiological range limit, there is an increased probability of even subtle variations in climate parameters exceeding critical thresholds that initiate rapid changes in the pace and pattern of tree establishment (Danby & Hik 2007, Bailey et al. 2021, Elliott et al. 2021). Moreover, treelines are sensitive to temperature increases associated with anthropogenic climate change, and they can provide early indications of the responses to be expected elsewhere in forest ecosystems (Greenwood and Jump 2014). Warmer growing season temperature in conjunction with sufficient moisture seem to benefit seedling emergence and growth at alpine treelines (Kueppers et al. 2017). One of the key benefits of warming may be that early and late in the growing season, it has been shown to alleviate seasonally low temperature stress (Kueppers et al. 2017).

However, warming throughout the growing season, which is increasingly common (Fig. 12) appears to counteract this benefit by enhancing moisture stress (Moyes et al. 2015). For example, scenes from both the ESJ and southern Sawatch are indicative of the passing of a threshold at some point in the 30-year span, whereby a warming climate released these forests from previous temperature limitations allowing for range expansion. More recently, however, spruce beetle infestations overwhelmed these forests either because of the depleted soil-moisture conditions triggered by hotter drought (i.e. Hart et al. 2014) or due to a sharp rise in temperature alone (Fig. 12; Pettit et al. 2020). Without a simultaneous increase in precipitation, warmer temperatures are likely increasing the evaporative demand of the soil to the point of a bioclimatic threshold where intensifying drought stress is also limiting seedling establishment (Elliott et al. 2021). Moreover, rather than on the enhanced growth of established trees (Holtmeier & Broll, 2007), the ascent of alpine treeline depends on the successful recruitment and establishment of young trees, which is increasingly difficult without a nearby or local

seed source (Jabis et al. 2020). Consequently, treeline shifts in temperate areas, such as the SRM, may slow down or even reverse as the climate becomes warmer and drier (Lu et al. 2020). While all the sites photographed exhibited evidence of treeline advance, this research cannot quantify whether any new establishment has occurred within the past decade (c.f. Bailey et al. 2021). Yet it remains clear that upper treeline advance has occurred over the past 30 years along the CT. This continues the trend that began during the 1950s along the spine of the Rocky Mountains (Elliott 2012b, Elliott & Petruccelli 2018) and underlies the importance of studying the pace and pattern of vegetation change at upper treeline at relatively fine temporal scales under the influence of 21<sup>st</sup>-century warming.

## 5.2 SPRUCE BEETLE-INDUCED MORTALITY

The subalpine zone of the SRM has been greatly impacted by bark beetle outbreaks, resulting in extensive tree mortality since the late 1990s (Rodman et al. 2021). In the San Juan Range specifically, a severe outbreak event occurred between 2011 and 2015 (Woodward et al. 2018), and repeat photography evidence from Elliott et al. (2021) confirms spruce beetle-induced mortality at upper treeline in the region. However, this study expands upon this work at a broader regional scale along the CT and provides important context to these findings.

The two scenes photographed in the ESJ (Photo Site 3 & 4), along with other photos shot in the region (Fig. 13), reveal the most striking results of mortality in this study. The near complete loss of overstory Engelmann spruce from spruce beetle infestation at upper treeline shows that hotter drought conditions have pushed these

forests beyond their bioclimatic optimum for survival (e.g. Elliott et al. 2021). Importantly, these two photos show spruce beetle devastation across both north- and south-facing slopes, suggesting that even the mediating role of slope aspect on moisture availability cannot offset intensifying drought stress in this region.

Because high-severity spruce beetle outbreaks result in limited regeneration, especially from years 2016-2018 in the San Juan Mountains when a severe warm fallwinter drought occurred (Carlson et al. 2020), a return to a dominant spruce stand in this location seems unlikely. Furthermore, increases in seed output of any remaining spruce will likely be constrained by threshold high temperatures (ca. 20% above 1970-2000 mean summer temperature; Buechling et al. 2016) in the seed maturation year, which are increasingly common at all sites (Fig. 12). The extensive canopy disturbance photographed in the ESJ contains the most convincing evidence yet that upper treeline ecotones of the SRM should be considered for long-term predictions of forest decline with climate change and that an abrupt transition in foundation tree species is possible.

The spatial pattern of spruce beetle-induced mortality at the Fooses Creek site (Photo Site 7) suggests that there are different biogeographical factors mediating its spread compared to the pure spruce stands to the south in the ESJ. Because spruce is less abundant here and increasingly shares space with lodgepole pine, the spatial extent was reduced, but not necessarily the vulnerability to attack (de Groot et al. 2023). Indeed, spruce beetle mortality appeared high for the percentage of spruce present and as such the existence of lodgepole pine did not hamper the outbreak severity, only the spatial extent and/or density of mortality. Because this was not a homogenous stand like those in the ESJ, the spatial pattern is more varied, and more live trees of other species still stand. The fact that no observations were made of spruce beetle-induced mortality north of the Sawatch range, I assumed could be due to the increased presence of lodgepole pine in these areas. It appeared that lodgepole pine were acting as a buffer against spruce beetle expansion in these upper treeline communities. A recent publication by De Groot et al. (2023), however, suggests that tree species diversity does not prevent bark beetle outbreaks in forests, but it does influence the severity of potential outbreaks. While the outbreak itself is not limited by tree species diversity and can still cause mortality to the majority of the population under attack, the presence of live trees allows for some of the forest structure to persist, and thus the resilience of treeline forests. Importantly, De Groot et al. (2023) also found that largescale factors such as temperature or drought have a larger effect on the onset of an outbreak event than stand level variables such as tree species richness. While temperatures have risen rapidly (Fig. 12) even at sites with no visual evidence of spruce beetle infestation, an increase in precipitation has also occurred in the Mosquito and Front Range mountains (Table 4 & 5), which could be supplying enough moisture to inhibit the onset of hotter drought conditions, and thus the onset of spruce beetle outbreaks, at those sites.

#### 5.3 VEGETATION COMPOSITION SHIFT

With spruce beetle continuing to be the most damaging forest pest in Colorado and Engelmann spruce not being well-adapted to warming climate conditions (Jabis et al. 2020), shifts in forest composition, particularly towards subalpine fir, are likely to endure for decades (Rodman et al. 2022). While recent outbreaks of native bark beetles have been widespread, causing tree mortality across millions of hectares throughout western North America (Raffa et al. 2008), these outbreaks are not catastrophic disturbances

driving forest loss (Rocca & Romme 2009). The upper treeline ecotone, however, is not accounted for in these previous studies because mortality events as catastrophic as the one photographed in the ESJ have never been reported throughout upper treeline ecotones. Engelmann spruce demonstrates low potential for range expansion where moisture availability is limited (Jabis et al. 2020), which will be increasingly constrained with projected warming temperatures. Reductions in the current range of Engelmann spruce under warming climate conditions (Dobrowski et al. 2015, Kueppers et al. 2017) are likely to occur on both dry south-facing slopes where recruitment has been nonexistent over the last decade (Bailey et al. 2021) and on wetter and cooler northfacing slopes with better habitat suitability for bark beetle where they can proliferate in dense, homogenous stands of spruce (Hart et al. 2015). Additionally, the upper treeline forests of the ESJ are composed purely of Engelmann spruce (Blair & Bracksieck 2011). Consequently, the shift to subalpine fir, a species that relies heavily on seed dispersal from live trees (Rodman et al. 2022), at upper treeline is improbable and will result in a large contraction of treeline forests, driving forest loss in these high-mountain ecosystems. Because rising temperatures are increasingly approaching the 20% threshold above the mean at each photo site and wind dispersal can only spread seed rain up to a few hundred meters (Holtmeier & Broll 2010), it is unlikely that if a bark beetle infestation were to occur at these sites, that Engelmann spruce would be able to successfully regenerate. Since the successful establishment of seedlings is limited by the requirement of a suitable microenvironment following successful dispersal, current trends of warming across the CT heighten the susceptibility to mortality of newly established seedlings by introducing heat-induced moisture stress and by limiting both the temporal

and spatial range of habitat suitability at treeline (Elliott 2017). Thus, the trend of expansion of the mountain forest belt via treeline advance appears to be particularly unlikely and is instead likely to be one of forest contraction as evidenced by the mortality downslope from treeline in the ESJ exceeding the seed dispersal range (Fig. 2 & 3).

The shift in vegetation composition, particularly the expansion of willows, in response to rapid climate warming in these high-altitude ecosystems is a crucial observation. During my extensive hiking along various sections of the CT, I witnessed and captured photographs of rapid willow expansion that is narrowing the trails, replacing spruce in disturbed forests, and establishing at higher elevations. This trend is consistent with a broad range of evidence indicating that woody plants, especially tall deciduous shrubs, are experiencing accelerated growth, abundance, and expansion upslope into alpine tundra (Formica et al. 2014, Kambo & Danby 2018) and northward into Arctic tundra (Myers-Smith & Hik 2018, Mekonnen et al. 2021). The thermal limitations of woody plants at the limits of their latitudinal ranges are similar to those at high altitudes (Randin et al. 2013). Therefore, the demographic and range dynamics of both latitudinal and alpine shrublines should be comparable (Wang et al. 2021). My field research suggests that a *shrubification* of the upper treeline ecotone has been taking place in the SRM. It appears that hotter drought, a severe climate-mediated disturbance, has exceeded the threshold of forest resilience in this ecosystem, triggering a transition from a forest-dominant to a shrubland-dominant landscape amidst standing dead spruce (sensu Millar & Stephenson 2015). However, without data at a finer temporal resolution, it cannot be determined whether the trend of willow densification and advance are ongoing. Indeed, alpine ecosystems may have already passed their climatic optima, as evidenced

by the slowed rate of shrub recruitment and shrubline advance under climatic warming post-2010 on the Tibetan Plateau, driven by moisture limitation, which has acted as an important environmental modulator of changes to alpine vegetation (Wang et al. 2021).

Due to its preference for high soil moisture and shade, the retention of Engelmann spruce across upper treeline ecotones may be strongly influenced by the ideal microclimate (Jabis et al. 2020) created by the proliferation of willow (Myers-smith & Hik 2013) in alpine communities following bark beetle mortality (See Fig. 14). However, diverging patterns of spruce seedling establishment from the presence of shrub cover can occur, on the one hand, from increased snow depth that can provide overwinter protection and minimize seedling damage (Renard et al. 2016). An overabundance of shrubs, however, can hinder seedling occurrence by competing for soil nutrients (Kambo & Danby 2018). There appears to be a seedling preference for areas of intermediate shrub cover and density (between 9% and 72%; see Kambo & Danby 2018), which suggests that if shrub cover becomes too dense it will set into motion positive feedbacks that will hasten the transition of the upper treeline ecotone to one that is no longer dominated by Engelmann spruce in the SRM. However, due to their ability to tolerate low moisture conditions, their deep roots, and their ability to survive without protection from neighboring species (Jabis et al. 2020), 5-needle pine species (bristlecone pine and limber pine) (Kueppers et al. 2017) and even lodgepole pine (Elliott 2012b) appear to be wellsuited to replace Engelmann spruce in upper treeline ecotones.

#### 5.4 TEMPERATURE-MOISTURE INTERACTIONS

The increase in atmospheric water demand and decreased relative humidity caused by the upward trend of both minimum and maximum VPD values can have significant ecological implications. With a rise in VPD, the amount of water vapor in the air is reduced, which can lead to a decline in plant growth and survival (McDowell et al. 2020, Hammond et al. 2022). As trees rely on atmospheric moisture to meet their water needs, a decrease in relative humidity may result in a higher risk of tree water stress and reduced productivity, which has been observed in the past decade (McDowell et al. 2020). Rising temperatures which force an exponential rise in VPD ultimately help drive the type of species composition shifts (McDowell et al. 2020) that this study photographed along the CT. Adult trees experiencing prolonged drought conditions are also at greater risk of mortality from pests or pathogens due to stomatal closure in response to high VPD and low soil moisture (Brodersen et al. 2019).

Given that most plants cannot reduce their size, which would be advantageous to transport water in arid conditions, forests respond through increased mortality of large plants, which are replaced by smaller ones (McDowell et al. 2020), such as willow (Fig. 5). Hydraulic theory suggests that under rising VPD, functional traits of high conductance, low stature, and low leaf area should best enable survival, all of which are characteristics of pioneer, shrub, and weed species (McDowell et al. 2020). Due to rising VPD values along the CT, Engelmann spruce, which are later-successional tree species, are being outcompeted by willow in high-mountain environments. Because mountain ecosystems contain forests that are particularly vulnerable to the influences of a rapidly changing climate, it appears likely that the unprecedented warming of the 21st century,

along with projected intensifying drought stress, will foster dramatic changes in vegetation community dynamics across upper treeline in the SRM.

Over the course of the 30-year photo period, the trend of decreasing precipitation across the mountain ranges was evident, but surprisingly not as much as assumed, with the mean only dropping 19 mm across all five ranges combined compared to the entire record. Notably, the La Plata Mountain Range experiences precipitation patterns that are solely independent of the other four ranges studied. The data reveal that not only does a significantly more amount of precipitation accumulate there (Table 3), but this site also experiences more extremes with multiple recent years approaching or surpassing 600 mm below the 20<sup>th</sup> Century mean (Fig. 7). The annual mean from 1895-2022 in the La Plata Range was more than twice that in the Front Range (Table 4), yet both study sites appeared visually healthy and thriving during the summer of 2022 field work. This could be due to the fact that during the repeat photo period, the Front Range mean actually increased compared to the 1895-2022 mean (Table 5), while the La Plata Range experienced a decline, but still received a significant amount more than the Front Range.

The fact that the average summer temperatures were roughly equivalent to the 1970-2000 mean before steadily rising beginning in the 1990's indicates a clear departure from historical norms. This also suggests that because precipitation values have remained steady in recent decades that the rapid rise in temperature is likely to be the main cause for the dramatic shifts seen in the repeat photo sites (sensu Pettit et al. 2020). Indeed, rapidly rising temperatures in high-elevation mountain forests with water-limited growing seasons, such as in the SRM, are likely to trigger recruitment declines as the climate continues to warm, growing seasons lengthen, and evaporative demand increases

(Kueppers et al. 2017). Warmer temperatures could also be leading to a reduction in soil moisture driven by increased evapotranspiration at alpine treeline ecotones (Sigdel et al. 2018), thus weakening the health and defense mechanisms of trees in upper elevation forests (McDowell et al. 2020).

## 6. CONCLUSION

The findings from this regional-scale repeat photography study suggest that the ongoing hotter drought affecting upper treeline ecotones could potentially lead to substantial contractions in the ranges of Engelmann spruce in certain mountain ranges, ultimately bringing about significant changes to these high mountain ecosystems. Given that spruce beetle-induced mortality extends across all size classes (Fig. 5) and willow expansion (Fig. 14) is prominent across the SRM, it appears that bioclimatic conditions in this region are favoring a vegetation composition shift to willow and pine species at the expense of spruce. The lack of evidence of spruce regeneration in the dead forests is concerning considering that rising temperatures will increasingly constrain spruce seed production. Nevertheless, the standing bristlecone pine captured in the ESJ (Fig. 15) suggests that the future of the upper treeline forest belt in that area may involve an increase in pine and as evidenced, willow, while the surrounding ranges maintain their traditional coverage of spruce, fir and occasionally lodgepole pine, at least until a mountain pine beetle (*Dendroctonus ponderosae*) outbreak occurs. The new pockets of willow expansion filling in alpine ecotones, densification of spruce-fir forests in some ranges, and forests that have been affected by spruce beetle in others are giving rise to novel landscapes. These changes will have significant implications for the biodiversity and functioning of the SRM, as well as its overall resilience in the face of climate change.

This research provides important insights into how upper treeline conifer forests are responding to regional hotter drought in the SRM. The vegetation conditions captured in the 30-year repeat photos reflect many of the patterns observed in previous literature on forest response to a warming climate, such as increased densification, upslope advance, significant vertical growth, contraction of Engelmann spruce, and willow regeneration. However, the uniqueness of this study lies in the fact that it has revealed near-total spruce beetle-induced mortality of upper treeline forests at some of the highest treeline ecotones in the Rocky Mountains along the CT. This study shows that temperature and moisture thresholds have been crossed in the ESJ and Southern Sawatch ranges, but it remains unclear if the other mountain ranges in this study will experience similar results. Rapidly rising temperatures on Searle Pass in the Mosquito Range suggest that if a bark beetle outbreak does occur there, it is extremely likely that this upper treeline ecotone will undergo a vegetation composition shift to one that no is no longer dominated by Engelmann spruce. Overall, the results of this repeat photography study point to a future of spruce at treeline that is not promising because of (1) beetle-induced mortality, (2) rising temperature stressing seed production, (3) the need for moisture, (4)challenges to natural seed dispersal, and (5) willow encroachment throughout the alpine tundra.

## 7. REFERENCES

Abatzoglou, J. T., & Williams, A. P. (2016). Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences*, 113(42), 11770–11775. <u>https://doi.org/10.1073/pnas.1607171113</u>

Aerial survey: Spruce beetle remains most deadly forest pest. (2022). US Forest Service.

- Allen, C. D., Breshears, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6(8), art129. <u>https://doi.org/10.1890/ES15-00203.1</u>
- Andrus, R. A., Hart, S. J., Tutland, N., & Veblen, T. T. (2021). Future dominance by quaking aspen expected following short-interval, compounded disturbance interaction. *Ecosphere*, 12(1). <u>https://doi.org/10.1002/ecs2.3345</u>
- Andrus, R. A., Harvey, B. J., Rodman, K. C., Hart, S. J., & Veblen, T. T. (2018). Moisture availability limits subalpine tree establishment. *Ecology*, 99(3), 567– 575. <u>https://doi.org/10.1002/ecy.2134</u>
- Babst, F., Bouriaud, O., Poulter, B., Trouet, V., Girardin, M. P., & Frank, D. C. (2019). Twentieth century redistribution in climatic drivers of global tree growth. *Science Advances*, 5(1), eaat4313. <u>https://doi.org/10.1126/sciadv.aat4313</u>
- Bader, M. Y., Llambí, L. D., Case, B. S., Buckley, H. L., Toivonen, J. M., Camarero, J. J., Cairns, D. M., Brown, C. D., Wiegand, T., & Resler, L. M. (2021). A global framework for linking alpine-treeline ecotone patterns to underlying processes. *Ecography*, 44(2), 265–292. <u>https://doi.org/10.1111/ecog.05285</u>
- Bailey, S. N., Elliott, G. P., & Schliep, E. M. (2021). Seasonal temperature–moisture interactions limit seedling establishment at upper treeline in the Southern Rockies. *Ecosphere*, 12(6). <u>https://doi.org/10.1002/ecs2.3568</u>
- Baker, W. L. (2009). Fire ecology in Rocky Mountain landscapes. Island Press.
- Barry, R. G. (2008). *Mountain weather and climate* (2nd ed.). Cambridge University Press.
- Batllori, E., & Gutiérrez, E. (2008). Regional tree line dynamics in response to global change in the Pyrenees. *Journal of Ecology*, 96(6), 1275–1288. https://doi.org/10.1111/j.1365-2745.2008.01429.x
- Beckage, B., Osborne, B., Gavin, D. G., Pucko, C., Siccama, T., & Perkins, T. (2008). A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proceedings of the National Academy of Sciences*, 105(11), 4197–4202. <u>https://doi.org/10.1073/pnas.0708921105</u>

- Bell, D. M., Bradford, J. B., & Lauenroth, W. K. (2014). Mountain landscapes offer few opportunities for high-elevation tree species migration. *Global Change Biology*, 20(5), 1441–1451. <u>https://doi.org/10.1111/gcb.12504</u>
- Blair, R., & Bracksieck, G. (Eds.). (2011). The eastern San Juan Mountains: Their geology, ecology, and human history. University Press of Colorado; Mountain Studies Institute/San Juan Collaboratory.
- Bonan, G. B. (2008). Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, 320(5882), 1444–1449. <u>https://doi.org/10.1126/science.1155121</u>
- Bourgeron, P. S., Humphries, H. C., Liptzin, D., & Seastedt, T. R. (2015). The forest– alpine ecotone: A multi-scale approach to spatial and temporal dynamics of treeline change at Niwot Ridge. Plant Ecology & Diversity, 8(5–6), 763–779. https://doi.org/10.1080/17550874.2015.1126368
- Breshears, D. D., Cobb, N. S., Rich, P. M., Price, K. P., Allen, C. D., Balice, R. G., Romme, W. H., Kastens, J. H., Floyd, M. L., Belnap, J., Anderson, J. J., Myers, O. B., & Meyer, C. W. (2005). Regional vegetation die-off in response to globalchange-type drought. *Proceedings of the National Academy of Sciences*, *102*(42), 15144–15148. <u>https://doi.org/10.1073/pnas.0505734102</u>
- Brodersen, C. R., Germino, M. J., Johnson, D. M., Reinhardt, K., Smith, W. K., Resler, L. M., Bader, M. Y., Sala, A., Kueppers, L. M., Broll, G., Cairns, D. M., Holtmeier, F.-K., & Wieser, G. (2019). Seedling survival at timberline is critical to conifer mountain forest elevation and extent. *Frontiers in Forests and Global Change*, 2, 9. https://doi.org/10.3389/ffgc.2019.00009
- Buechling, A., Martin, P. H., Canham, C. D., Shepperd, W. D., & Battaglia, M. A. (2016). Climate drivers of seed production in *Picea engelmannii* and response to warming temperatures in the southern Rocky Mountains. *Journal of Ecology*, 104(4), 1051–1062. <u>https://doi.org/10.1111/1365-2745.12572</u>
- Butler, D. R., Malanson, G. P., Walsh, S. J., & Fagre, D. B. (2007). Influences of geomorphology and geology on alpine treeline in the american west—More important than climatic influences? *Physical Geography*, 28(5), 434–450. https://doi.org/10.2747/0272-3646.28.5.434
- Camarero, J. J., & Gutiérrez, E. (2004). Pace and pattern of recent treeline dynamics: Response of ecotones to climatic variability in the spanish pyrenees. *Climatic Change*, 63(1/2), 181–200. <u>https://doi.org/10.1023/B:CLIM.0000018507.71343.46</u>
- Camarero, J. J., Linares, J. C., García-Cervigón, A. I., Batllori, E., Martínez, I., & Gutiérrez, E. (2017). Back to the future: The responses of alpine treelines to

climate warming are constrained by the current ecotone structure. *Ecosystems*, 20(4), 683–700. <u>https://doi.org/10.1007/s10021-016-0046-3</u>

- Cannone, N., Sgorbati, S., & Guglielmin, M. (2007). Unexpected impacts of climate change on alpine vegetation. *Frontiers in Ecology and the Environment*, 5(7), 360–364. <u>https://doi.org/10.1890/1540-9295(2007)5[360:UIOCCO]2.0.CO;2</u>
- Carlson, A. R., Sibold, J. S., & Negrón, J. F. (2020). Canopy structure and below-canopy temperatures interact to shape seedling response to disturbance in a Rocky Mountain subalpine forest. *Forest Ecology and Management*, 472, 118234. <u>https://doi.org/10.1016/j.foreco.2020.118234</u>
- Carrara, P. E., & McGeehin, J. P. (2015). Evidence of a higher late-Holocene treeline along the Continental Divide in central Colorado. *The Holocene*, 25(11), 1829– 1837. <u>https://doi.org/10.1177/0959683615591353</u>
- Case, B. S., & Duncan, R. P. (2014). A novel framework for disentangling the scaledependent influences of abiotic factors on alpine treeline position. *Ecography*, 37(9), 838–851. <u>https://doi.org/10.1111/ecog.00280</u>
- Chapin, F. S., Sturm, M., Serreze, M. C., McFadden, J. P., Key, J. R., Lloyd, A. H., McGuire, A. D., Rupp, T. S., Lynch, A. H., Schimel, J. P., Beringer, J., Chapman, W. L., Epstein, H. E., Euskirchen, E. S., Hinzman, L. D., Jia, G., Ping, C.-L., Tape, K. D., Thompson, C. D. C., ... Welker, J. M. (2005). Role of land-surface changes in arctic summer warming. *Science*, 310(5748), 657–660. https://doi.org/10.1126/science.1117368
- Cooper, G. S., Willcock, S., & Dearing, J. A. (2020). Regime shifts occur disproportionately faster in larger ecosystems. *Nature Communications*, 11(1), 1175. https://doi.org/10.1038/s41467-020-15029-x
- Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J., & Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, 28(15), 2031–2064. <u>https://doi.org/10.1002/joc.1688</u>
- Danby, R. K., & Hik, D. S. (2007). Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. *Journal of Ecology*, 95(2), 352–363. https://doi.org/10.1111/j.1365-2745.2006.01200.x
- Daniels, L. D., & Veblen, T. T. (2004). Spatiotemporal influences of climate on altitudinal treeline in northern patagonia. *Ecology*, 85(5), 1284–1296. <u>https://doi.org/10.1890/03-0092</u>
- Davis, K. T., Dobrowski, S. Z., Higuera, P. E., Holden, Z. A., Veblen, T. T., Rother, M. T., Parks, S. A., Sala, A., & Maneta, M. P. (2019). Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration.

*Proceedings of the National Academy of Sciences*, *116*(13), 6193–6198. https://doi.org/10.1073/pnas.1815107116

- De Groot, M., Ogris, N., Diaci, J., & Castagneyrol, B. (2023). When tree diversity does not work: The interacting effects of tree diversity, altitude and amount of spruce on European spruce bark beetle outbreaks. *Forest Ecology and Management*, 537, 120952. https://doi.org/10.1016/j.foreco.2023.120952
- Dobrowski, S. Z., Swanson, A. K., Abatzoglou, J. T., Holden, Z. A., Safford, H. D., Schwartz, M. K., & Gavin, D. G. (2015). Forest structure and species traits mediate projected recruitment declines in Western US tree species. Global Ecology and Biogeography, 24(8), 917–927. <u>https://doi.org/10.1111/geb.12302</u>
- Du, H., Liu, J., Li, M., Büntgen, U., Yang, Y., Wang, L., Wu, Z., & He, H. S. (2018). Warming-induced upward migration of the alpine treeline in the Changbai Mountains, northeast China. *Global Change Biology*, 24(3), 1256–1266. <u>https://doi.org/10.1111/gcb.13963</u>
- Elliott, G. P. (2011). Influences of 20th-century warming at the upper tree line contingent on local-scale interactions: Evidence from a latitudinal gradient in the Rocky Mountains, USA: Climate-pattern interactions at the tree line. *Global Ecology and Biogeography*, 20(1), 46–57. <u>https://doi.org/10.1111/j.1466-8238.2010.00588.x</u>
- Elliott, G. P. (2012a). The role of thresholds and fine-scale processes in driving upper treeline dynamics in the bighorn mountains, wyoming. *Physical Geography*, 33(2), 129–145. <u>https://doi.org/10.2747/0272-3646.33.2.129</u>
- Elliott, G. P. (2012b). Extrinsic regime shifts drive abrupt changes in regeneration dynamics at upper treeline in the Rocky Mountains, USA. *Ecology*, 93(7), 1614–1625. https://doi.org/10.1890/11-1220.1
- Elliott, G. P. 2017. Treeline ecotones. In International encyclopedia of geography, ed. N. Castree, M. F. Goodchild, A. Kobayashi, W. Liu, and R. A. Marston, 1–10. Chichester, U.K.: Wiley.
  <u>https://onlinelibrary.wiley.com/doi/abs/10.1002/9781118786352.wbieg0539</u>
- Elliott, G. P., Bailey, S. N., & Cardinal, S. J. (2020). Hotter drought as a disturbance at upper treeline in the southern rocky mountains. *Annals of the American Association of Geographers*, 111(3), 756–770. <u>https://doi.org/10.1080/24694452.2020.1805292</u>
- Elliott, G. P., & Baker, W. L. (2004). Quaking aspen (Populus tremuloides Michx.) at treeline: A century of change in the San Juan Mountains, Colorado, USA: Quaking aspen at treeline. *Journal of Biogeography*, *31*(5), 733–745. https://doi.org/10.1111/j.1365-2699.2004.01064.x
- Elliott, G. P., & Cowell, C. M. (2015). Slope aspect mediates fine-scale tree establishment patterns at upper treeline during wet and dry periods of the 20th

century. *Arctic, Antarctic, and Alpine Research*, 47(4), 681–692. https://doi.org/10.1657/AAAR0014-025

- Elliott, G. P., & Kipfmueller, K. F. (2011). Multiscale influences of climate on upper treeline dynamics in the southern rocky mountains, usa: Evidence of intraregional variability and bioclimatic thresholds in response to twentieth-century warming. *Annals of the Association of American Geographers*, 101(6), 1181–1203. https://doi.org/10.1080/00045608.2011.584288
- Elliott, G. P., & Petruccelli, C. A. (2018). Tree recruitment at the treeline across the Continental Divide in the Northern Rocky Mountains, USA: The role of spring snow and autumn climate. *Plant Ecology & Diversity*, *11*(3), 319–333. https://doi.org/10.1080/17550874.2018.1487475
- Fielder, J. (1999). Colorado 1870-2000. Westcliffe Publishers, Inc., Englewood, CO.
- Fielder, J., & Fayhee, M. J. (1992). *Along the Colorado trail*. Westcliffe Publishers, Inc., Englewood, CO.
- Formica, A., Farrer, E. C., Ashton, I. W., & Suding, K. N. (2014). Shrub expansion over the past 62 years in rocky mountain alpine tundra: Possible causes and consequences. *Arctic, Antarctic, and Alpine Research*, 46(3), 616–631. <u>https://doi.org/10.1657/1938-4246-46.3.616</u>
- Gill, R. A., Campbell, C. S., & Karlinsey, S. M. (2015). Soil moisture controls Engelmann spruce (*picea engelmannii*) seedling carbon balance and survivorship at timberline in Utah, USA. *Canadian Journal of Forest Research*, 45(12), 1845– 1852. <u>https://doi.org/10.1139/cjfr-2015-0239</u>
- Greenwood, S., & Jump, A. S. (2014). Consequences of treeline shifts for the diversity and function of high altitude ecosystems. *Arctic, Antarctic, and Alpine Research*, 46(4), 829–840. <u>https://doi.org/10.1657/1938-4246-46.4.829</u>
- Hallinger, M., Manthey, M., & Wilmking, M. (2010). Establishing a missing link: Warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. New Phytologist, 186(4), 890–899. https://doi.org/10.1111/j.1469-8137.2010.03223.x
- Hammond, W. M., Stone, M. E. B., & Stone, P. A. (2020). Picture worth a thousand words: Updating repeat photography for 21st century ecologists. *Ecology and Evolution*, 10(24), 14113–14121. <u>https://doi.org/10.1002/ece3.7001</u>
- Hammond, W. M., Williams, A. P., Abatzoglou, J. T., Adams, H. D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D. D., & Allen, C. D. (2022). Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nature Communications*, *13*(1), 1761. https://doi.org/10.1038/s41467-022-29289-2

- Hammond, W. M., Yu, K., Wilson, L. A., Will, R. E., Anderegg, W. R. L., & Adams, H. D. (2019). Dead or dying? Quantifying the point of no return from hydraulic failure in drought-induced tree mortality. *New Phytologist*, 223(4), 1834–1843. <u>https://doi.org/10.1111/nph.15922</u>
- Hart, S. J., Veblen, T. T., Eisenhart, K. S., Jarvis, D., & Kulakowski, D. (2014). Drought induces spruce beetle (dendroctonus rufipennis) outbreaks across northwestern Colorado. Ecology, 95(4), 930–939. <u>https://doi.org/10.1890/13-0230.1</u>
- Hart, S. J., Veblen, T. T., Mietkiewicz, N., & Kulakowski, D. (2015). Negative feedbacks on bark beetle outbreaks: Widespread and severe spruce beetle infestation restricts subsequent infestation. *PLOS ONE*, *10*(5), e0127975. https://doi.org/10.1371/journal.pone.0127975
- Hartman, E. L., & Rottman, M. L. (1988). THE VEGETATION AND ALPINE VASCULAR FLORA OF THE SAWATCH RANGE, COLORADO. *California Botanical Society*.
- Harvey, B. J., Donato, D. C., & Turner, M. G. (2016). High and dry: Post-fire tree seedling establishment in subalpine forests decreases with post-fire drought and large stand-replacing burn patches: Drought and post-fire tree seedlings. *Global Ecology and Biogeography*, 25(6), 655–669. <u>https://doi.org/10.1111/geb.12443</u>
- Holtmeier, F. K., & Broll, G. E. (2007). Treeline advance—Driving processes and adverse factors. Landscape Online, 1, 1–33. <u>https://doi.org/10.3097/LO.200701</u>
- Holtmeier, F.-K., & Broll, G. (2010). Wind as an ecological agent at treelines in north america, the alps, and the european subarctic. Physical Geography, 31(3), 203–233. <u>https://doi.org/10.2747/0272-3646.31.3.203</u>
- Huang, M., Piao, S., Janssens, I. A., Zhu, Z., Wang, T., Wu, D., Ciais, P., Myneni, R. B., Peaucelle, M., Peng, S., Yang, H., & Peñuelas, J. (2017). Velocity of change in vegetation productivity over northern high latitudes. *Nature Ecology & Evolution*, *1*(11), 1649–1654. <u>https://doi.org/10.1038/s41559-017-0328-y</u>
- Jabis, M. D., Germino, M. J., & Kueppers, L. M. (2020). Colonisation of the alpine tundra by trees: Alpine neighbours assist late-seral but not early-seral conifer seedlings. Plant Ecology & Diversity, 13(3–4), 209–224. https://doi.org/10.1080/17550874.2020.1762134
- Jacobs, R., & Fielder, J. (1994). The colorado trail: The official guidebook. Westcliffe .
- Jiang, P., Liu, H., Piao, S., Ciais, P., Wu, X., Yin, Y., & Wang, H. (2019). Enhanced growth after extreme wetness compensates for post-drought carbon loss in dry forests. *Nature Communications*, 10(1), 195. <u>https://doi.org/10.1038/s41467-018-08229-z</u>

- Jiang, X., Rauscher, S. A., Ringler, T. D., Lawrence, D. M., Williams, A. P., Allen, C. D., Steiner, A. L., Cai, D. M., & McDowell, N. G. (2013). Projected future changes in vegetation in western north america in the twenty-first century. *Journal of Climate*, 26(11), 3671–3687. <u>https://doi.org/10.1175/JCLI-D-12-00430.1</u>
- Kambo, D., & Danby, R. K. (2018). Factors influencing the establishment and growth of tree seedlings at Subarctic alpine treelines. *Ecosphere*, 9(4). https://doi.org/10.1002/ecs2.2176
- Kemp, K. B., Higuera, P. E., & Morgan, P. (2016). Fire legacies impact conifer regeneration across environmental gradients in the U.S. northern Rockies. *Landscape Ecology*, 31(3), 619–636. <u>https://doi.org/10.1007/s10980-015-0268-3</u>
- Klasner, F. L., & Fagre, D. B. (2002). A half century of change in alpine treeline patterns at glacier national park, montana, u. S. A. *Arctic, Antarctic, and Alpine Research*, *34*(1), 49–56. <u>https://doi.org/10.1080/15230430.2002.12003468</u>
- Kueppers, L. M., Conlisk, E., Castanha, C., Moyes, A. B., Germino, M. J., Valpine, P., Torn, M. S., & Mitton, J. B. (2017). Warming and provenance limit tree recruitment across and beyond the elevation range of subalpine forest. *Global Change Biology*, 23(6), 2383–2395. <u>https://doi.org/10.1111/gcb.13561</u>
- Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884), 1768–1771. <u>https://doi.org/10.1126/science.1156831</u>
- Liang, E., Dawadi, B., Pederson, N., & Eckstein, D. (2014). Is the growth of birch at the upper timberline in the Himalayas limited by moisture or by temperature? *Ecology*, 95(9), 2453–2465. <u>https://doi.org/10.1890/13-1904.1</u>
- Liang, E., Wang, Y., Piao, S., Lu, X., Camarero, J. J., Zhu, H., Zhu, L., Ellison, A. M., Ciais, P., & Peñuelas, J. (2016). Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau. *Proceedings of the National Academy of Sciences*, 113(16), 4380–4385. https://doi.org/10.1073/pnas.1520582113
- Lloyd, A. H., & Fastie, C. L. (2003). Recent changes in treeline forest distribution and structure in interior Alaska. *Écoscience*, 10(2), 176–185. <u>https://doi.org/10.1080/11956860.2003.11682765</u>
- Loranger, H., Zotz, G., & Bader, M. Y. (2016). Early establishment of trees at the alpine treeline: Idiosyncratic species responses to temperature-moisture interactions. *AoB Plants*, 8, plw053. <u>https://doi.org/10.1093/aobpla/plw053</u>
- Lu, X., Liang, E., Wang, Y., Babst, F., & Camarero, J. J. (2021). Mountain treelines climb slowly despite rapid climate warming. *Global Ecology and Biogeography*, 30(1), 305–315. <u>https://doi.org/10.1111/geb.13214</u>

- Lu, X., Liang, E., Wang, Y., Babst, F., Leavitt, S. W., & Julio Camarero, J. (2019). Past the climate optimum: Recruitment is declining at the world's highest juniper shrublines on the Tibetan Plateau. *Ecology*, 100(2), e02557. <u>https://doi.org/10.1002/ecy.2557</u>
- Lyu, L., Zhang, Q.-B., Deng, X., & Mäkinen, H. (2016). Fine-scale distribution of treeline trees and the nurse plant facilitation on the eastern Tibetan Plateau. *Ecological Indicators*, 66, 251–258. <u>https://doi.org/10.1016/j.ecolind.2016.01.041</u>
- Mack, M. C., Schuur, E. A. G., Bret-Harte, M. S., Shaver, G. R., & Chapin, F. S. (2004). Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature*, 431(7007), 440–443. <u>https://doi.org/10.1038/nature02887</u>
- McDowell, N. G., Allen, C. D., Anderson-Teixeira, K., Aukema, B. H., Bond-Lamberty, B., Chini, L., Clark, J. S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G. C., Jackson, R. B., Johnson, D. J., Kueppers, L., Lichstein, J. W., Ogle, K., Poulter, B., Pugh, T. A. M., Seidl, R., ... Xu, C. (2020). Pervasive shifts in forest dynamics in a changing world. *Science*, *368*(6494), eaaz9463. https://doi.org/10.1126/science.aaz9463
- Mekonnen, Z. A., Riley, W. J., Berner, L. T., Bouskill, N. J., Torn, M. S., Iwahana, G., Breen, A. L., Myers-Smith, I. H., Criado, M. G., Liu, Y., Euskirchen, E. S., Goetz, S. J., Mack, M. C., & Grant, R. F. (2021). Arctic tundra shrubification: A review of mechanisms and impacts on ecosystem carbon balance. *Environmental Research Letters*, 16(5), 053001. https://doi.org/10.1088/1748-9326/abf28b
- Millar, C. I., & Stephenson, N. L. (2015). Temperate forest health in an era of emerging megadisturbance. *Science*, 349(6250), 823–826. <u>https://doi.org/10.1126/science.aaa9933</u>
- Millar, C. I., Westfall, R. D., Delany, D. L., Flint, A. L., & Flint, L. E. (2015). Recruitment patterns and growth of high-elevation pines in response to climatic variability (1883–2013), in the western Great Basin, USA. *Canadian Journal of Forest Research*, 45(10), 1299–1312. <u>https://doi.org/10.1139/cjfr-2015-0025</u>
- Moyes, A. B., Germino, M. J., & Kueppers, L. M. (2015). Moisture rivals temperature in limiting photosynthesis by trees establishing beyond their cold-edge range limit under ambient and warmed conditions. *New Phytologist*, 207(4), 1005–1014. <u>https://doi.org/10.1111/nph.13422</u>
- Munro, R. N., Deckers, J., Haile, M., Grove, A. T., Poesen, J., & Nyssen, J. (2008). Soil landscapes, land cover change and erosion features of the Central Plateau region of Tigrai, Ethiopia: Photo-monitoring with an interval of 30 years. *CATENA*, 75(1), 55–64. <u>https://doi.org/10.1016/j.catena.2008.04.009</u>

- Myers-Smith, I. H., Hik, D. S., Kennedy, C., Cooley, D., Johnstone, J. F., Kenney, A. J., & Krebs, C. J. (2011). Expansion of canopy-forming willows over the twentieth century on Herschel Island, Yukon Territory, Canada. *Ambio*, 40(6): 610–623.
- Myers-smith, I. H., & Hik, D.S. (2013). Shrub canopies influence soil temperatures but not nutrient dynamics: an experimental test of tundra snow–shrub interactions. *Ecology and Evolution* 3:3683–3700.
- Myers-Smith, I. H., & Hik, D. S. (2018). Climate warming as a driver of tundra shrubline advance. *Journal of Ecology*, 106(2), 547–560. <u>https://doi.org/10.1111/1365-2745.12817</u>
- Peet, R.K. (2000). Forests and meadows of the Rocky Mountains. *North American terrestrial vegetation, 2nd edition*. Cambridge University Press, Cambridge, pp 75–122
- Pepin, N., R. S. Bradley, H. F. Diaz, and M. Baraer. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5(5), 424– 430. <u>https://doi.org/10.1038/nclimate2563</u>
- Pettit, J. M., Burton, J. I., DeRose, R. J., Long, J. N., & Voelker, S. L. (2019). Epidemic spruce beetle outbreak changes drivers of Engelmann spruce regeneration. *Ecosphere*, 10(11). <u>https://doi.org/10.1002/ecs2.2912</u>
- Pettit, J. M., Voelker, S. L., DeRose, R. J., & Burton, J. I. (2020). Spruce beetle outbreak was not driven by drought stress: Evidence from a tree-ring iso-demographic approach indicates temperatures were more important. Global Change Biology, 26(10), 5829–5843. https://doi.org/10.1111/gcb.15274
- Raffa, K. F., Aukema, B. H., Bentz, B. J., Carroll, A. L., Hicke, J. A., Turner, M. G., & Romme, W. H. (2008). Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. *BioScience*, 58(6), 501–517. <u>https://doi.org/10.1641/B580607</u>
- Randin, C. F., Vuissoz, G., Liston, G. E., Vittoz, P., & Guisan, A. (2009). Introduction of snow and geomorphic disturbance variables into predictive models of alpine plant distribution in the western swiss alps. *Arctic, Antarctic, and Alpine Research*, 41(3), 347–361. https://doi.org/10.1657/1938-4246-41.3.347
- Rangwala, I., Barsugli, J., Cozzetto, K., Neff, J., & Prairie, J. (2012). Mid-21st century projections in temperature extremes in the southern Colorado Rocky Mountains from regional climate models. *Climate Dynamics*, 39(7–8), 1823–1840. <u>https://doi.org/10.1007/s00382-011-1282-z</u>
- Renard, S. M., McIntire, E. J. B., & Fajardo, A. (2016). Winter conditions—Not summer temperature—Influence establishment of seedlings at white spruce alpine treeline in Eastern Quebec. *Journal of Vegetation Science*, 27(1), 29–39. <u>https://doi.org/10.1111/jvs.12347</u>

- Rocca, M. E., & Romme, W. H. (2009). Beetle-infested forests are not "destroyed." Frontiers in Ecology and the Environment, 7(2), 71–72. https://doi.org/10.1890/09.WB.003
- Rodman, K. C., Andrus, R. A., Butkiewicz, C. L., Chapman, T. B., Gill, N. S., Harvey, B. J., Kulakowski, D., Tutland, N. J., Veblen, T. T., & Hart, S. J. (2021). Effects of bark beetle outbreaks on forest landscape pattern in the southern rocky mountains, u. S. A. *Remote Sensing*, *13*(6), 1089. <u>https://doi.org/10.3390/rs13061089</u>
- Rodman, K. C., Veblen, T. T., Battaglia, M. A., Chambers, M. E., Fornwalt, P. J., Holden, Z. A., Kolb, T. E., Ouzts, J. R., & Rother, M. T. (2020). A changing climate is snuffing out post-fire recovery in montane forests. *Global Ecology and Biogeography*, 29(11), 2039–2051. <u>https://doi.org/10.1111/geb.13174</u>
- Rundqvist, S., Hedenås, H., Sandström, A., Emanuelsson, U., Eriksson, H., Jonasson, C., & Callaghan, T. V. (2011). Tree and shrub expansion over the past 34 years at the tree-line near abisko, sweden. AMBIO, 40(6), 683–692. https://doi.org/10.1007/s13280-011-0174-0
- Schapira, Z. H., Stevens-Rumann, C. S., & Shorrock, D. (2021). Subalpine tree seedlings: Assessing aging methodology and drivers of establishment. *Forest Ecology and Management*, 497, 119516. <u>https://doi.org/10.1016/j.foreco.2021.119516</u>
- Shaver, G. R., Johnson, L. C., Cades, D. H., Murray, G., Laundre, J. A., Rastetter, E. B., Nadelhoffer, K. J., & Giblin, A. E. (1998). Biomass and co 2 flux in wet sedge tundras: Responses to nutrients, temperature, and light. Ecological Monographs, 68(1), 75. https://doi.org/10.2307/2657144 Shestakova, T. A., Voltas, J., Saurer, M., Berninger, F., Esper, J., Andreu-Hayles, L., Daux, V., Helle, G., Leuenberger, M., Loader, N. J., Masson-Delmotte, V., Saracino, A., Waterhouse, J. S., Schleser, G. H., Bednarz, Z., Boettger, T., Dorado-Liñán, I., Filot, M., Frank, D., ... Gutiérrez, E. (2019). Spatio-temporal patterns of tree growth as related to carbon isotope fractionation in European forests under changing climate. *Global Ecology and Biogeography*, 28(9), 1295–1309. https://doi.org/10.1111/geb.12933
- Sigdel, S. R., Wang, Y., Camarero, J. J., Zhu, H., Liang, E., & Peñuelas, J. (2018). Moisture-mediated responsiveness of treeline shifts to global warming in the Himalayas. *Global Change Biology*, 24(11), 5549–5559. <u>https://doi.org/10.1111/gcb.14428</u>
- Stevens-Rumann, C. S., Kemp, K. B., Higuera, P. E., Harvey, B. J., Rother, M. T., Donato, D. C., Morgan, P., & Veblen, T. T. (2018). Evidence for declining forest resilience to wildfires under climate change. *Ecology Letters*, 21(2), 243–252. <u>https://doi.org/10.1111/ele.12889</u>
- Stow, D. A., Hope, A., McGuire, D., Verbyla, D., Gamon, J., Huemmrich, F., Houston, S., Racine, C., Sturm, M., Tape, K., Hinzman, L., Yoshikawa, K., Tweedie, C., Noyle, B., Silapaswan, C., Douglas, D., Griffith, B., Jia, G., Epstein, H., ...

Myneni, R. (2004). Remote sensing of vegetation and land-cover change in Arctic Tundra Ecosystems. *Remote Sensing of Environment*, 89(3), 281–308. https://doi.org/10.1016/j.rse.2003.10.018

- Sturm, M., Holmgren, J., McFadden, J. P., Liston, G. E., Chapin, F. S., & Racine, C. H. (2001). Snow–shrub interactions in arctic tundra: A hypothesis with climatic implications. *Journal of Climate*, 14(3), 336–344. <u>https://doi.org/10.1175/1520-0442(2001)014<0336:SSIIAT>2.0.CO;2</u>
- Sturm, M. (2005). Changing snow and shrub conditions affect albedo with global implications. *Journal of Geophysical Research*, 110(G1), G01004. <u>https://doi.org/10.1029/2005JG000013</u>
- Sturm, M., Schimel, J., Michaelson, G., Welker, J. M., Oberbauer, S. F., Liston, G. E., Fahnestock, J., & Romanovsky, V. E. (2005). Winter biological processes could help convert arctic tundra to shrubland. *BioScience*, 55(1), 17. <u>https://doi.org/10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2</u>
- Szeicz, J. M., & Macdonald, G. M. (1995). Recent white spruce dynamics at the subarctic alpine treeline of north-western canada. *The Journal of Ecology*, 83(5), 873. <u>https://doi.org/10.2307/2261424</u>
- Tape, K., Sturm, M., & Racine, C. (2006). The evidence for shrub expansion in northern alaska and the pan-arctic: Shrub expansion in northern alaska and pan-arctic. *Global Change Biology*, 12(4), 686–702. <u>https://doi.org/10.1111/j.1365-</u> 2486.2006.01128.x
- Turner, M. G., Calder, W. J., Cumming, G. S., Hughes, T. P., Jentsch, A., LaDeau, S. L., Lenton, T. M., Shuman, B. N., Turetsky, M. R., Ratajczak, Z., Williams, J. W., Williams, A. P., & Carpenter, S. R. (2020). Climate change, ecosystems and abrupt change: Science priorities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1794), 20190105. https://doi.org/10.1098/rstb.2019.0105
- Veblen, T. T., & Lorenz, D. C. (1991). *The Colorado Front Range: A century of ecological change*. University of Utah Press, Salt Lake City, UT.
- Walther, G., Beißner, S., & Burga, C. A. (2005). Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, 16(5), 541–548. <u>https://doi.org/10.1111/j.1654-1103.2005.tb02394.x</u>
- Wang, Y., Liang, E., Lu, X., Camarero, J. J., Babst, F., Shen, M., & Peñuelas, J. (2021). Warming-induced shrubline advance stalled by moisture limitation on the Tibetan Plateau. *Ecography*, 44(11), 1631–1641. <u>https://doi.org/10.1111/ecog.05845</u>
- Weintraub, M. N., & Schimel, J. P. (2005). Nitrogen cycling and the spread of shrubs control changes in the carbon balance of arctic tundra ecosystems. *BioScience*,

55(5), 408. <u>https://doi.org/10.1641/0006-</u> 3568(2005)055[0408:NCATSO]2.0.CO;2

- Williams, A. P., Cook, B. I., & Smerdon, J. E. (2022). Rapid intensification of the emerging southwestern North American megadrought in 2020–2021. *Nature Climate Change*, 12(3), 232–234. <u>https://doi.org/10.1038/s41558-022-01290-z</u>
- Wolkovich, E. M., Cook, B. I., McLauchlan, K. K., & Davies, T. J. (2014). Temporal ecology in the Anthropocene. *Ecology Letters*, 17(11), 1365–1379. <u>https://doi.org/10.1111/ele.12353</u>
- Woodward, B., Evangelista, P., & Vorster, A. (2018). Mapping progression and severity of a southern colorado spruce beetle outbreak using calibrated image composites. *Forests*, 9(6), 336. <u>https://doi.org/10.3390/f9060336</u>
- Zhang, P., Jeong, J.-H., Yoon, J.-H., Kim, H., Wang, S.-Y. S., Linderholm, H. W., Fang, K., Wu, X., & Chen, D. (2020). Abrupt shift to hotter and drier climate over inner East Asia beyond the tipping point. *Science*, 370(6520), 1095–1099. <u>https://doi.org/10.1126/science.abb3368</u>
- Zhang, Q.-B., Evans, M. N., & Lyu, L. (2015). Moisture dipole over the Tibetan Plateau during the past five and a half centuries. *Nature Communications*, *6*(1), 8062. <u>https://doi.org/10.1038/ncomms9062</u>
- Zhang, L., Xiao-Ming Lu, Hua-Zhong Zhu, Shan Gao, Jian Sun, Hai-Feng Zhu, Jiang-Ping Fang, J. Julio Camarero, Er-Yuan Liang (2023). A rapid transition from spruce-fir to pine-broadleaf forests in response to disturbances and climate warming on the southeastern Qinghai-Tibet Plateau. *Plant Diversity*, ISSN 2468-2659, https://doi.org/10.1016/j.pld.2023.03.002.

# 8. TABLES, FIGURES, AND PHOTOS

## 8.1 TABLES

| Photo Site | Site Name        | Latitude  | Longitude  | Elevation (m) | Camera Bearing | CT Segment # | Mountain Range   | Side of CD (E/W) |
|------------|------------------|-----------|------------|---------------|----------------|--------------|------------------|------------------|
| 1          | ITR 1            | 37.461111 | 108.034444 | 3727          | 50° NE         | 27           | La Platas        | W                |
| 2          | ITR 2            | 37.460319 | 108.034781 | 3720          | 220° SW        | 27           | La Platas        | W                |
| 3          | Sunflower        | 37.970556 | 106.991944 | 3852          | 235° SW        | 20           | East San Juans   | W                |
| 4          | San Luis         | 37.972222 | 106.988056 | 3922          | 65° NE         | 20           | East San Juans   | W                |
| 5          | Antora           | 38.351667 | 106.264722 | 3634          | 120° SE        | 16           | Southern Sawatch | E                |
| 6          | Southern Sawatch | 38.351667 | 106.264722 | 3634          | 0° N           | 16           | Southern Sawatch | E/W              |
| 7          | Fooses Creek     | 38.454722 | 106.274167 | 3630          | 0° N           | 14           | Southern Sawatch | E                |
| 8          | Searle Pass      | 39.454167 | 106.235278 | 3745          | 120° E         | 8            | Mosquito Range   | W                |
| 9          | Breckenridge     | 39.521111 | 106.109444 | 3581          | 162° SSE       | 7            | Tenmile Range    | W                |
| 10         | GP Pond 1        | 39.456603 | 105.90134  | 3535          | 70° E          | 6            | Front Range      | E                |
| 11         | GP Pond 2        | 39.456603 | 105.90134  | 3535          | 7° N           | 6            | Front Range      | E                |
| 12         | GP Snow          | 39.458445 | 105.90033  | 3550          | 237° SW        | 6            | Front Range      | E                |

**Table 1.** Repeat photo site information. Color-coded by mountain range. Side of CD (E/W) indicates whether the photo site was East or West of the Continental Divide.

| Photo Name - Mountain Range  | Treeline Advance | Spruce Beetle Mortality | Willow Expansion |
|------------------------------|------------------|-------------------------|------------------|
| ITR 1 - La Platas            | Х                |                         | Х                |
| ITR 2 - La Platas            | Х                |                         | Х                |
| Sunflower - ESJ              | Х                | Х                       | Х                |
| San Luis - ESJ               | Х                | Х                       | Х                |
| Antora - SS                  | Х                | Х                       |                  |
| Southern Sawatch - SS        | Х                | Х                       |                  |
| Fooses Creek - SS            | Х                | Х                       | Х                |
| Searle Pass - Mosquito Range | Х                |                         | Х                |
| Breckenridge - Tenmile Range | Х                |                         | Х                |
| GP Pond 1 - Front Range      | Х                |                         | Х                |
| GP Pond 2- Front Range       | Х                |                         | Х                |
| GP Snow - Front Range        | Х                |                         | Х                |
| % of Repeat Photos           | 100% (n=12)      | 42% (n=5)               | 83% (n=10)       |

**Table 2.** Observed results from repeat photo pairs, color-coded by mountain range. "X" denotes that the result type was observed in the 30-year repeat photo span.

| M1 vs M2 | P <.01 |
|----------|--------|
| M1 vs M3 | P <.01 |
| M1 vs M4 | P <.01 |
| M1 vs M5 | P <.01 |
| M2 vs M3 | P <.01 |
| M2 vs M4 | P <.01 |
| M2 vs M5 | P <.01 |
| M3 vs M4 | P <.01 |
| M3 vs M5 | P <.01 |
| M4 vs M5 | P <.01 |

**Table 3.** Annual precipitation, 1895-2022 Tukey HSD Test. Results gathered from Vassar Stats One-Way ANOVA. M1 = La Platas. M2 = ESJ. M3 = Southern Sawatch. M4 = Searle Pass. M5 = Front Range.

| Data Summary |             |            |            |             |             |           |
|--------------|-------------|------------|------------|-------------|-------------|-----------|
|              | Samples     |            |            |             |             |           |
|              | 1           | 2          | 3          | 4           | 5           | Total     |
| Ν            | 128         | 128        | 128        | 128         | 128         | 640       |
| ΣX           | 161519      | 114945.6   | 89501.7    | 98437.2     | 79759.9     | 544163.4  |
| Mean         | 1261.8672   | 898.0125   | 699.232    | 769.0406    | 623.1242    | 850.2553  |
| $\Sigma X^2$ | 212734175.: | 106931304  | 64890353.8 | 77971264.68 | 51021362.6: | 513548460 |
| Variance     | 70225.5814  | 29202.5069 | 18172.4282 | 17866.6053  | 10401.868   | 79609.763 |
| Std.Dev.     | 265.0011    | 170.8874   | 134.8051   | 133.666     | 101.9895    | 282.152   |
| Std.Err.     | 23.423      | 15.1045    | 11.9152    | 11.8145     | 9.0147      | 11.153    |

**Table 4.** Annual precipitation data summary for the entire period of record, 1895-2022. Results gathered from Vassar Stats One-Way ANOVA. 1 = La Platas. 2 = ESJ. 3 = Southern Sawatch. 4 = Searle Pass. 5 = Front Range.

|              | Samples     |             |             |             |             |            |
|--------------|-------------|-------------|-------------|-------------|-------------|------------|
|              | 1           | 2           | 3           | 4           | 5           | Total      |
| Ν            | 31          | 31          | 31          | 31          | 31          | 155        |
| ΣX           | 35132.5     | 26107.9     | 21438.7     | 25534.1     | 20641.6     | 128854.8   |
| Mean         | 1133.3065   | 842.1903    | 691.571     | 823.6806    | 665.8581    | 831.3213   |
| $\Sigma X^2$ | 41173968.9: | 22649159.43 | 15243279.6: | 21509746.9! | 14008208.64 | 114584363  |
| Variance     | 45269.3333  | 22044.6236  | 13896.5701  | 15926.7663  | 8794.4272   | 48471.5905 |
| Std.Dev.     | 212.7659    | 148.4743    | 117.8837    | 126.2013    | 93.7786     | 220.1626   |
| Std.Err.     | 38.2139     | 26.6668     | 21.1725     | 22.6664     | 16.8431     | 17.6839    |

**Table 5.** Annual precipitation data summary for the repeat photo period, 1992-2022. Results gathered from Vassar Stats One-Way ANOVA. 1 = La Platas. 2 = ESJ. 3 = Southern Sawatch. 4 = Searle Pass. 5 = Front Range.

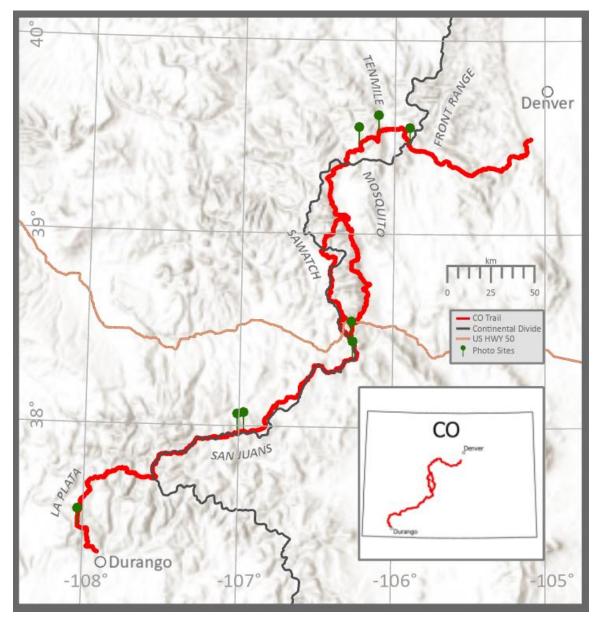
| M1 vs M2                                     | P <.01                                                       |
|----------------------------------------------|--------------------------------------------------------------|
| M1 vs M3                                     | P <.01                                                       |
| M1 vs M4                                     | P <.01                                                       |
| M1 vs M5                                     | P <.01                                                       |
| M2 vs M3                                     | nonsignificant                                               |
| M2 vs M4                                     | P <.05                                                       |
| M2 vs M5                                     | nonsignificant                                               |
| M3 vs M4                                     | nonsignificant                                               |
| M3 vs M5                                     | nonsignificant                                               |
| M4 vs M5                                     | nonsignificant                                               |
| M2 vs M4<br>M2 vs M5<br>M3 vs M4<br>M3 vs M5 | P <.05<br>nonsignificant<br>nonsignificant<br>nonsignificant |

**Table 6.** Warm Season VPD Min Tukey HSD Test. Results gathered from Vassar Stats ANOVA. M1 = La Platas. M2 = ESJ. M3 = Southern Sawatch. M4 = Searle Pass. M5 = Front Range.

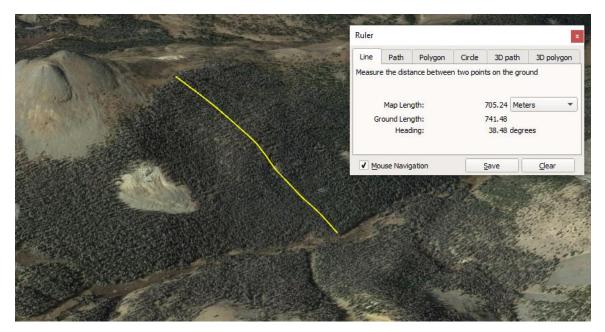
| M1 vs M2 | P <.01         |
|----------|----------------|
| M1 vs M3 | P <.01         |
| M1 vs M4 | nonsignificant |
| M1 vs M5 | nonsignificant |
| M2 vs M3 | P <.01         |
| M2 vs M4 | nonsignificant |
| M2 vs M5 | P <.05         |
| M3 vs M4 | P <.01         |
| M3 vs M5 | P <.01         |
| M4 vs M5 | nonsignificant |
|          |                |

**Table 7.** Warm Season VPD Max Tukey HSD Test. Results gathered from Vassar Stats ANOVA. M1 = La Platas. M2 = ESJ. M3 = Southern Sawatch. M4 = Searle Pass. M5 = Front Range.

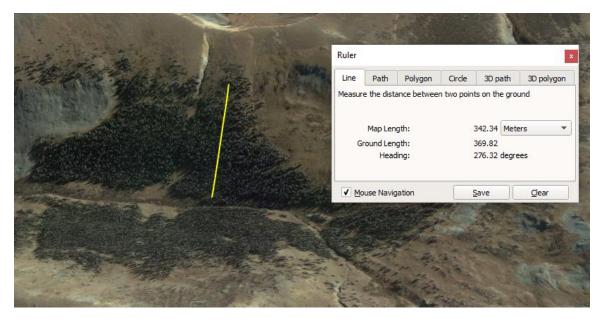
#### **8.2 FIGURES**



**Fig. 1.** Study area along the Colorado Trail. US HWY 50 is shown as an important dividing line where sites to the south have extensive spruce beetle mortality (except for La Platas) while sites to the north do not.



**Fig. 2.** A Google Earth screenshot measuring the distance of spruce beetle mortality downslope from the highest climatic treeline on Photo Site 3, measuring 742 m.



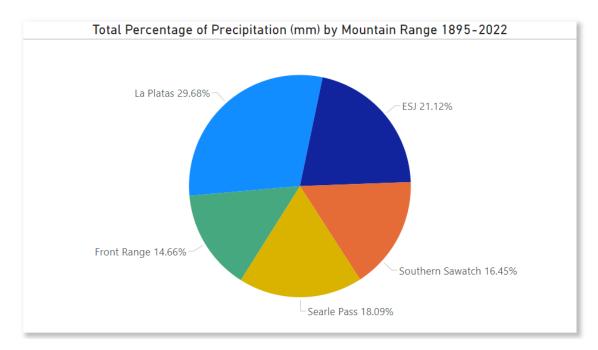
**Fig. 3.** A Google Earth screenshot measuring the distance of spruce beetle mortality downslope from the highest climatic treeline on Photo Site 4, measuring 370 m.



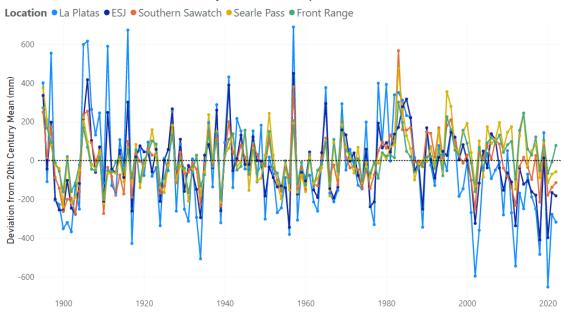
Fig. 4. Defoliated spruce from spruce beetle at upper treeline in the west San Juan Mountain Range.



**Fig. 5.** A close-up shot of a representative upper treeline zone near San Luis Peak in the La Garita Wilderness. This is not a repeat photo and provides clear evidence of spruce beetle-induced mortality across multiple size classes of trees along with willow proliferation.

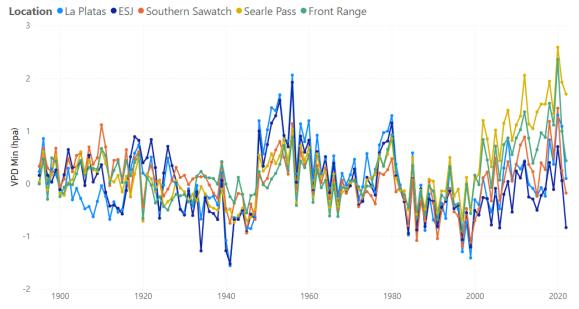


**Fig. 6.** Pie chart representing the total precipitation accumulated across all five repeat photo sites by percentage from 1895-2022.



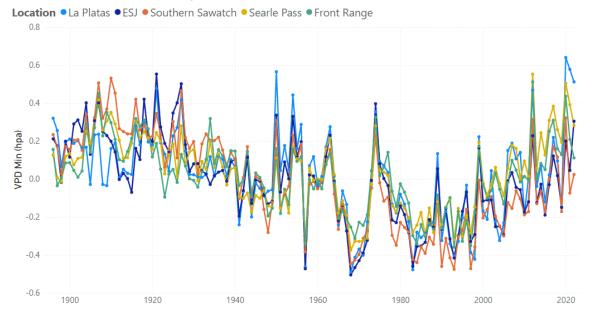
#### Annual Deviation from 20th Century Mean of Precipitation

**Fig. 7.** Annual deviations from the 20th Century mean of precipitation, 1895-2022 across five of the six repeat photo site locations. Notice the sharp dips in the early 21<sup>st</sup> Century, especially in the La Plata Mountain Range. There are also no notable years above the mean in the early 21st Century.

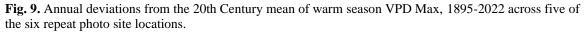


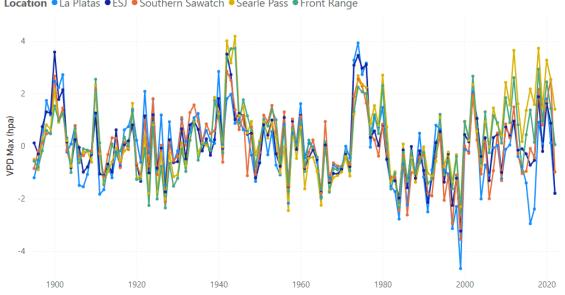
Deviation from the 20th Century Mean of Warm Season VPD Min

**Fig. 8.** Annual deviations from the 20th Century mean of warm season VPD Min, 1895-2022 across five of the six repeat photo site locations. Notice the upwards trend for much of the early 21<sup>st</sup> Century, before falling in the two most recent years.



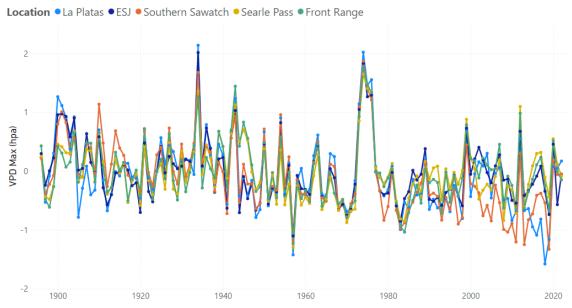
Deviations from 20th Century Mean of Cool Season VPD Min





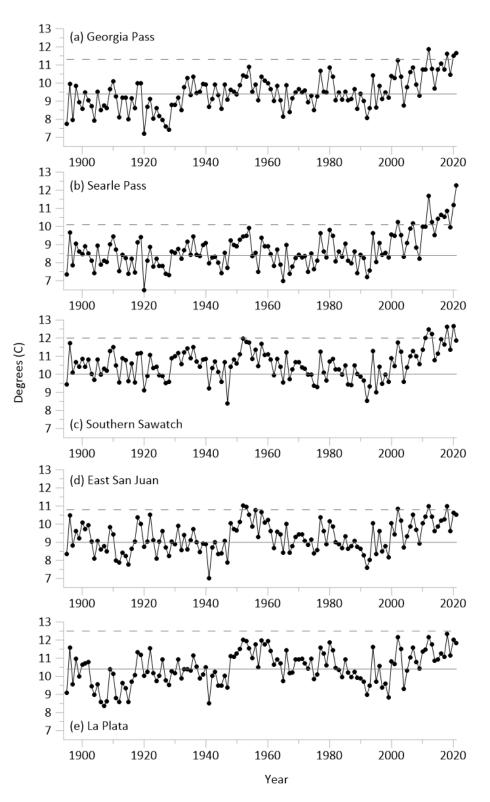
Deviation from 20th Century Mean of Warm Season VPD Max Location • La Platas • ESJ • Southern Sawatch • Searle Pass • Front Range

**Fig. 10.** Annual deviations from the 20th Century mean of cool season VPD Min, 1895-2022 across five of the six repeat photo site locations. Notice the upwards trend in the most recent decade.



Deviations from 20th Century Mean of Cool Season VPD Max

**Fig. 11.** Annual deviations from the 20th Century mean of cool season VPD Max, 1895-2022 across five of the six repeat photo site locations.



**Fig. 12.** Summer (June-Aug) temperature graphs. 1970-2000 mean represented by solid line. 20% increase from mean to show threshold temperature which constrains spruce seed production (cf. Buechling et al. 2016) represented by the dashed line.



**Fig. 13.** Upper treeline forest near San Luis Peak in the La Garita Wilderness. This is not a repeat photo, but it does provide clear evidence of spruce beetle-induced mortality.



Fig. 14. Spruce living amongst willow while the dense stands have been killed by spruce beetle.



**Fig. 15.** Standing Rocky Mountain bristlecone pine (*Pinus aristata*) with interspersed young Engelmann spruce on a south-facing slope opposite Photo Site 3 in the ESJ. Heterogeneity and more open-canopy stands on south-facing slopes may offer resilience against severe spruce beetle outbreaks in the face of hotter drought at upper treeline.

### **8.3 REPEAT PHOTOS**



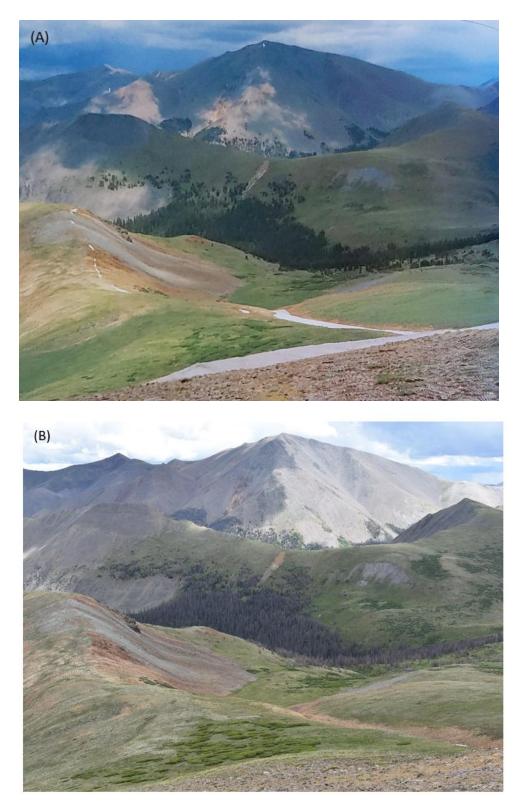
**Photo Site 1.** View is looking northeast from Indian Trail Ridge at an elevation of 3,727 m along Segment 27 of the CT. It showcases a vast expanse of undisturbed forested landscape unaffected by recent fire or bark beetle outbreak in San Juan National Forest, in the La Plata Mountains. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: *Along the Colorado Trail*, 1992.



**Photo Site 2.** View is looking southwest from Indian Trail Ridge in the La Plata Mountains at an elevation of 3,720 m along Segment 27 of the CT depicting a patch of healthy upper treeline forest with no visible signs of disturbance. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: *Along the Colorado Trail*, 1992.



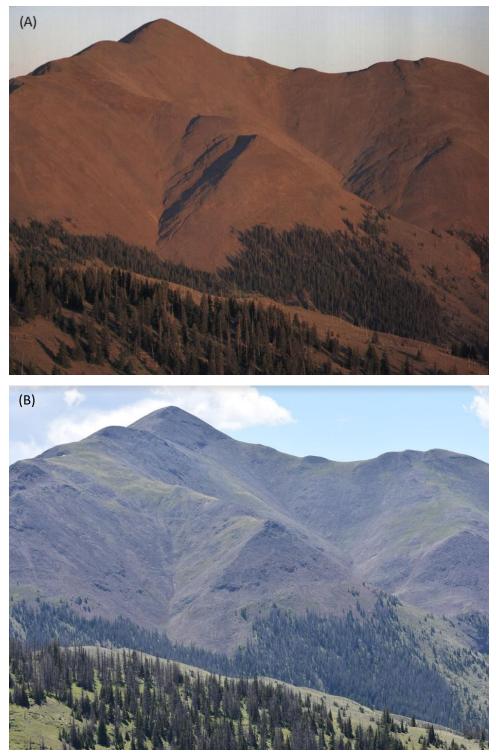
**Photo Site 3.** View is looking southwest from an elevation of 3,852 m below San Luis Peak, in the La Garita Wilderness. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: Along the Colorado Trail, 1992.



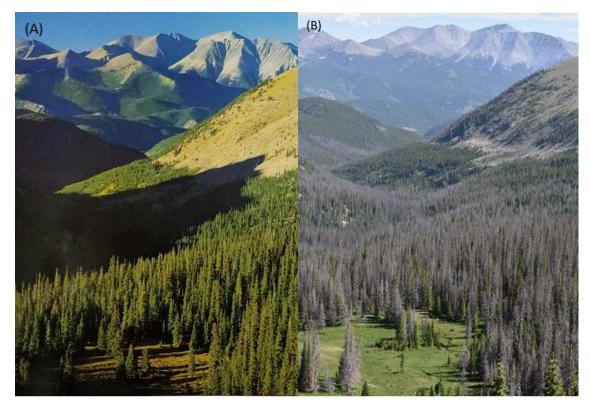
**Photo Site 4.** Northeast looking view of 14,014 feet San Luis Peak captured from an elevation of 3,922 m, in the La Garita Wilderness. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: Along the Colorado Trail, 1992.



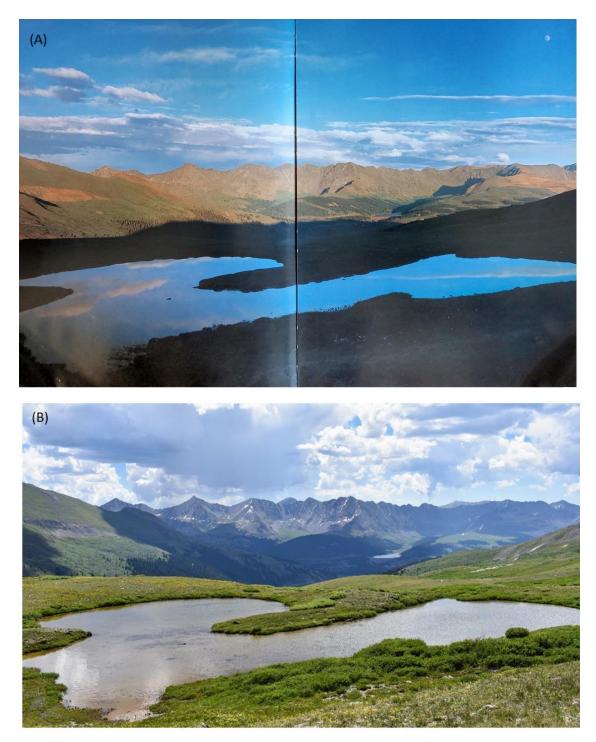
**Photo Site 5.** View is north, looking at the southern Sawatch Range from the top of Windy Peak at 3,634 m along the Continental Divide. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: *Along the Colorado Trail*, 1992.



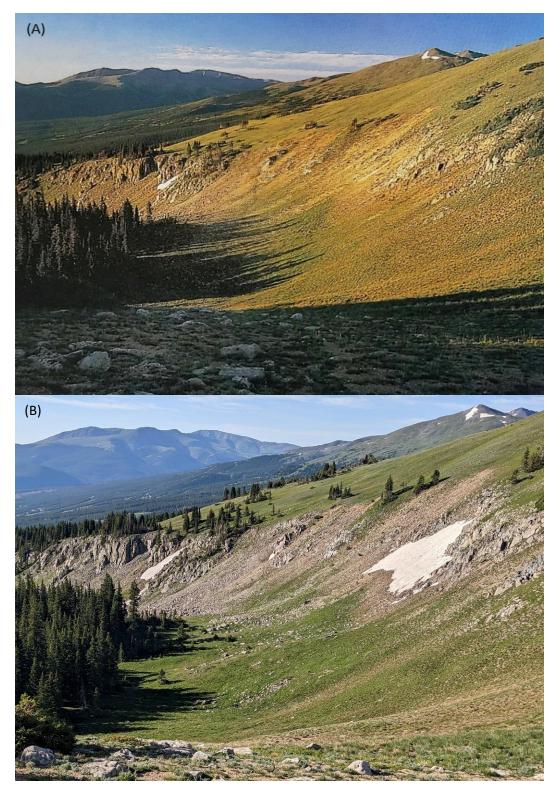
**Photo Site 6.** View is southeast, looking at of 13,269-foot Antora Peak from the top of Windy Peak at 3,634 m along the Continental Divide. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: *Along the Colorado Trail*, 1992.



**Photo Site 7.** Northward looking view of 14,155-foot Tabeguache and 14,225-foot Shavano peaks from the head of Fooses Creek from an elevation of 3,630 m in San Isabel National Forest. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: Along the Colorado Trail, 1992.



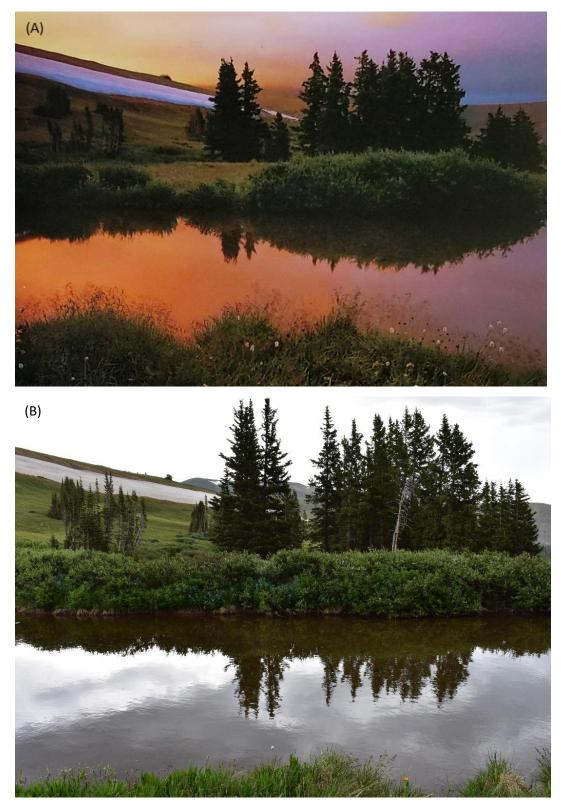
**Photo Site 8.** View is east, from Searle Pass at 3,745 m, in the Mosquito Range. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: *Along the Colorado Trail*, 1992.



**Photo Site 9.** View is south above the town of Breckenridge at 3,581 m in the Tenmile Range. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: *The Colorado Trail Official Field Guide*, 1994.



**Photo Site 10.** View is south along the Jefferson Creek Loop Trail near Georgia Pass at about 3, 535 m in the Front Range. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: *The Colorado Trail Official Field Guide*, 1994.



**Photo Site 11.** View is east along the Jefferson Creek Loop Trail near Georgia Pass at about 3,535 m in the Front Range. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: *The Colorado Trail Official Field Guide*, 1994.



**Photo Site 12.** View is southwest along the Jefferson Creek Loop Trail near Georgia Pass at about 3,550 m in the Front Range. The original photo (A) was taken by John Fielder in 1992, (B) was taken in July of 2022. Source: *Along the Colorado Trail*, 1992.