The Compounding Consequences of Climate Change and Wildfire for a High Elevation Wildflower (Saxifraga austromontana)

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The Compounding Consequences of Climate Change and Wildfire for a High Elevation Wildflower (Saxifraga austromontana)

By

Trevor David Snow Bloom

Accepted in Partial Completion
Of the Requirements for the Degree
Master of Science

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MASTER’S THESIS

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Trevor David Snow Bloom
Fall, 2016
The Compounding Consequences of Climate Change and Wildfire for a High Elevation Wildflower (*Saxifraga austromontana*)

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Completion
Of the Requirements for the Degree
Master of Science

By
Trevor David Snow Bloom
Fall, 2016
Abstract:

Climate change disproportionately impacts alpine ecosystems. Many species unique to high elevation habitats are at great risk of population and species level extinctions due to changes in the climate, partially forced by anthropogenic emissions of greenhouse gases. The direct effects of climate change, such as increases in temperature and altered precipitation patterns, also induce indirect effects, defined as changes in ecological interactions and disturbances. One of the most eminent and tangible indirect effects of climate change in western North America is a startling (6x) increase in rare, large wildfire events since 1970; a number projected to increase over the century. Wildfires have moved up in elevation into the alpine, regions where fire was once extremely rare or absent, due to elevated temperatures, early snowmelt, and ultimately drier fuels. My thesis aims to quantify and qualify the compounding impacts of climate change and wildfire on high elevation ecosystems, using the wildflower species Saxifraga austromontana Wiegand (Saxifragaceae) as a study system. First, I modeled the direct impacts of climate change on S. austromontana using Species Distribution Models (SDMs) to precisely estimate the present and future climate envelope of the species, projecting the average conditions for 2041-2070 under a moderate and realistic emission scenario. In doing so, I discovered that many of the historic records I used, archived in herbaria (plant museums), did not contain accurate geographic coordinates. Thus, I developed a novel standardized method to prepare historic occurrence records (museum and herbarium collections) for use in spatial analyses. I present this new method, the Spatial Analysis Georeferencing Accuracy (SAGA) protocol, and test its rigor against other previous methods in Chapter 2: Why Georeferencing Matters: Introducing a Practical Protocol to Prepare Species Occurrence Records for Spatial Analysis. Utilizing this new method, combined with an arduous five-month field experiment, high resolution SDMs, and fire predictive models, I completed the first documented study on the compounding impacts of climate change and wildfire on a high elevation species. Chapter 3: The Compounding Consequences of Climate Change and Wildfire for a High Elevation Wildflower is the culmination of my efforts at Western Washington University and in the field traversing the latitudinal range of the Rocky Mountains collecting data. I worked closely with my exceptional adviser, Dr. Eric DeChaine, and collaborated with my brilliant committee members to prepare two manuscripts for submission to scientific journals. This body of work has the potential to advance the utility of invaluable historic records for spatial analyses, and reveals a novel understanding of the compounding impacts of climate change and wildfire on North American alpine ecosystems.
Acknowledgments:

I would like to earnestly thank my thesis adviser, committee chair, and mentor Dr. Eric G. DeChaine for his leadership and encouragement throughout this project. He consistently went above and beyond to advance me as both a scientist and as a well-rounded individual. I am forever grateful for his guidance. My committee members, extended between the Biology Department and the Department of Environmental Studies, provided incredible insight into my project, and overall personal development during my stay at Western. Aquila Flower, David Hooper, and Michael Medler eagerly devoted their time and bestowed unparalleled feedback.

The community at Western Washington University was truly empowering. I would like to especially thank my fellow graduate students Samual Wershow and Donal O’Leary who both significantly contributed throughout all phases of my study design, analysis, and editing. I extend gratitude to my undergraduate research assistants Matthew Kneipp, who spent more than four months with me traversing the Rocky Mountains collecting specimens for analysis, and Caroline Baber, who prepared the specimens for preservation in the Pacific Northwest Herbarium (WWB) and analyzed wildfire charcoal. The faculty and staff of the Biology Department were unwavering in their devotion to me, my project, and my fellow graduate students. It is with deep appreciation that I radiate love and gratitude towards my entire community of family and friends for their wholehearted admiration, support, and inspiration.

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Chapter 1: Project Summary

Climate change will decrease the amount of available alpine habitat in the mountains of North America, thus increasing the risk of extinction for many high elevation plant species that exist nowhere else. Effectively, cold adapted species have two options to cope with warming temperatures: move up in elevation or north in latitude. Yet, alpine species already at the limit of their elevational range risk local extinction as they become forced upwards and eventually squeezed off the summit and northward expansion is limited by the dispersal ability of the organism and interspecific competition. In addition to the direct effects of climate-driven habitat loss, such as increased temperatures and changes in precipitation, species must also respond to altered ecological interactions and disturbances, or “indirect effects.” One of the most powerful indirect effects already in action is the overall proliferation of wildfire, resulting in amplified fire frequency and intensity. Future wildfire activity is expected to increase rapidly across most of the globe, with the most pronounced upsurge in the mid to high latitudes.

My interest in fire and climate was first sparked during my youth, raised in Jackson, Wyoming in the shadow of the Tetons and the burn scars of Yellowstone. I came to Western Washington University (WWU) with a background in ecology and the desire to develop a project that could directly guide conservation efforts related to climate change in the alpine. Dr. Eric G. DeChaine, curator of the Pacific Northwest Herbarium and director of the Alpine-Arctic Research lab at WWU, was the ideal adviser. With the help of Dr. DeChaine, and my exceptional committee members, who span the Department of Biology and the Department of Environmental Studies, I developed my broad research question: what are the combined impacts of climate change and wildfire on alpine ecosystems? To date, no one has published on this subject.
We chose *Saxifraga austromontana* Wiegand (Saxifragaceae), the Spotted Saxifrage, as a study system due to its well-defined range, Dr. DeChaine’s previous work on the species, and its extensive historical collections (herbarium records). The Spotted Saxifrage is an ornate wildflower with tiny cream-colored petals mottled in brilliant shades of red, orange, and yellow. Found exclusively in the mountains of western North America, it exhibits the characteristic growth form of high elevation, cold adapted wildflowers. The response of this species may elucidate the fate of many similar species under changing climate and wildfire conditions.

To address my question effectively required extensive background research, a rigorous field study, and the development of novel computer modeling techniques. The core of my analysis uses Species Distribution Models (SDMs), the most widely used tools to predict current and future distributions of organisms under climate change projections. Essentially SDMs are trained with a number of species occurrence records and a suite of response variables, often climatic conditions such as mean annual temperature, to model the climate envelope in which the species is known to exist. This envelope can be projected into geographic space in the form of a map highlighting climatically suitable habitat. Most SDMs do not consider wildfire as a response variable, potentially underestimating future species range reductions. We deemed it imperative to couple direct climate variables with wildfire when considering the future persistence of alpine vegetation, and my thesis is the first study of its kind to do so.

During the development of my initial SDMs, it became grossly apparent that most historic records of *S. austromontana* did not contain accurate geographic coordinates. The more I dug into this, the more I realized that the pair of coordinates on the specimen label often conflicted
with the written site description. For example, a collection that was made at the summit of a mountain included a coordinate taken at the latrine near the trailhead over ten kilometers away and at an entirely different elevation. The most important variables for creating reliable SDMs are the number and accuracy of species occurrence records used to train the model. It became very apparent that to create an accurate SDM every record would need to be “georeferenced,” the process of interpreting the written description of site localities and verifying the associated geographic coordinates or assigning new coordinates. I also realized that most of the scientific articles I read which utilized SDMs did not explicitly state how or if the samples they used to train their models were georeferenced. Thus, Dr. DeChaine, Dr. Flower, and I developed a rigorous and standardized protocol of georeferencing to classify the spatial resolution of museum records specifically for building more useful SDMs. We statistically tested the new method against others in the literature and built a suite of SDMs. This project, an offshoot of my original question, manifested itself into a lofty research endeavor, a new standardized method - the Spatial Analysis Georeferencing Accuracy (SAGA) protocol, the second chapter of my thesis, and a manuscript that was submitted for publication to a high-impact scientific journal on November 11, 2016. Dr. DeChaine contributed extensive intellectual merit to the paper, and added 89 field collections of *S. austromontana*. Dr. Flower provided invaluable guidance in the development and implementation of my modeling methods.

The third chapter of my thesis, *The Compounding Impact of Climate Change and Increased Fire for an Alpine Wildflower*, uses the SDM methods outlined in Chapter 2 and is the culmination of my research efforts at WWU. I combined an extensive field study with computer modeling to test the hypothesis that wildfire compounded with direct climatic changes will
further reduce the future suitable habitat of *S. austromontana*, compared to predictions based on climate alone. To quantify the impact of fire on this species, I ran an analysis using herbarium records and historic wildfire perimeters to locate every known population that had been burned by a large (>400 ha) fire since 1984. In order to isolate the effect of fire, I paired “burned” sites with “unburned” sites of similar environmental conditions, visited each site in the field, and took measurements on the abundance of *S. austromontana*, among many other environmental observations.

In the summer of 2015, my field assistant Matt Kneipp, and I traversed the entire Rocky Mountain range from the Gila Wilderness of New Mexico north to central British Columbia. Matt was presently a student in the Environmental Science Department of Huxley College, and received 300 internship hours for his work on this project. I could not have completed the field work without his loyal partnership. In just over four months we sampled 76 alpine sites in 6 states and 2 Canadian provinces, and had our fair share of adventure. We averaged approximately 18 miles of hiking per day, and successfully visited every potential burn site except for two, which were inaccessible due to current fire activity. The field study revealed that historic populations of *S. austromontana* were completely extirpated (locally extinct) 43% of the time in burn sites, compared to only 7% in unburned sites. Further, in sites that did not experience complete extirpation, the abundance was significantly reduced. I used the results of the field study to further inform SDMs, and made the first model to integrate future climate and wildfire predictions on a high elevation forb (Chapter 3, Figure 4). We found that fire may in fact compound the impacts of climate, especially in the Middle Rockies which includes the coveted Greater Yellowstone Ecosystem. Thus, we deem it wise to include wildfire as a response variable
when projecting future range contractions under climate change scenarios, and hope to build on
the resolution of these models in the future. I coauthored a scientific manuscript with my
committee members Dr. DeChaine, Dr. Medler, and Dr. Flower to be submitted this winter.

In addition to my scientific investigations and publications, I maintained an extensive
public outreach campaign to raise awareness about the impacts of climate change and wildfire in
the mountains. Science outreach is a strong passion of mine, and it is my goal to always include a
component of education in my research. Increased wildfire activity is a tangible result of climate
change experienced by millions of Americans, providing an opportunity for engagement in
climate literacy issues. For example, 2015 was the largest wildfire year on record for the state of
Washington. During the entirety of my graduate student career, I maintained a website for the
public to view the progress of my fieldwork and research, under the campaign name “Climb-it
Change.” I gave three public outreach presentations hosted by the Washington Native Plants
Society (Koma Kulshan Chapter), the Jackson Hole Conservation Alliance, and the North
Cascades Audubon Society. In spring 2015, I visited the White Pass Middle School in Randle,
WA and presented my research to grades 6-8. I also presented at four academic conferences
across the nation. Chiefly, I utilized video equipment to record a short documentary throughout
our journey traversing the Rocky Mountains. The documentary, both an adventure and
educational film, includes interviews with professors, National Park staff, scientists, and fire
fighters on the topic of climate and fire in the mountains of western North America. We have
been working closely with HandCrank Films in Bellingham to produce a documentary to be
freely shared at film festivals and schools across the world. This research and outreach aims to
increase public involvement in science, thereby increasing partnerships between academia, industry, and outdoor recreationalists to better appreciate and conserve the alpine environment.

Mountains are teachers

Flowers bloom occult petals

Bliss in the alpine

Trevor David Snow Bloom

Fall, 2016

www.ClimbItChange.com
Chapter 2

Why Georeferencing Matters: Introducing a Practical Protocol to Prepare Species Occurrence Records for Spatial Analysis

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Abstract

Aim Species Distribution Models (SDMs) are widely used to forecast species range shifts in response to climatic changes. The quality of input data determines the model’s accuracy. While museum records are great sources of presence data for many species, they do not always include accurate geographic coordinates. Therefore, actual locations must be verified through the process of georeferencing. We aim to answer the question: what are the consequences of using occurrence data of varying level of spatial accuracy in SDMs? We introduce a standardized georeferencing protocol, and highlight the current shortcomings of species occurrence records.

Location Mountain ranges of Western North America including the Rockies, Tetons, Beartooths, North Cascades, and British Columbia Coast Range.
Methods We present a practical manual georeferencing method (the SAGA protocol) to classify the spatial resolution of museum records specifically for building improved SDMs. The high-elevation plant *Saxifraga austromontana* Wiegand (Saxifragaceae), was used as a test subject. In MAXENT, we generated and compared SDMs using a comprehensive occurrence dataset that had undergone three different levels of georeferencing: 1) trained using all publicly available herbarium records of the species, minus outliers 2) trained using herbarium records claimed to be previously georeferenced, and 3) trained using herbarium records that have been georeferenced to a ≤1 km resolution using the SAGA protocol.

Results Model predictions of suitable habitat for *S. austromontana* differed greatly depending on georeferencing level. The SDMs fitted with presence locations georeferenced using SAGA outperformed all others. Differences among models were exacerbated for future distribution predictions.

Main Conclusions Under rapid climate change, accurately forecasting the response of species becomes increasingly important. Failure to georeference location data and cull inaccurate samples leads to erroneous model output, limiting the utility of spatial analyses. We present a simple, standardized georeferencing method to be adopted by curators, ecologists, and modelers to improve the geographic accuracy of museum records and SDM predictions.
Introduction

Climate change is projected to result in massive species range shifts and population level extinctions (Thomas et al., 2004; Thuiller et al., 2005; Hijmans & Graham, 2006). Observing, describing, and forecasting patterns of biodiversity under changing climate conditions are critical goals in the fields of biogeography, conservation, and ecology (Bucklin et al., 2015). Species Distribution Models (SDMs), also referred to as Ecological Niche Models or Bioclimatic Envelope Models, are the most widely used approach for predicting past, present, and future suitable habitats for common and rare species (Hijmans & Graham, 2006; Phillips & Dudík, 2008; Wiens et al., 2009; Elith et al., 2010). These models are used to predict climate change impacts (Keith et al., 2008; Wiens et al., 2009; Serra-Diaz et al., 2014), construct phylogeographic patterns (Forester et al., 2013), and guide efforts to locate new populations of rare species (Williams et al., 2009). Reliable SDMs can inform land managers where to concentrate conservation resources to best preserve areas of ecological importance. Because SDMs rely on species occurrence coordinates, climate data, and other environmental variables to define a species' bioclimatic niche and forecast future ranges (Flower et al., 2013; Bucklin et al., 2015), the accuracy of those variables defines the credibility of the model's predictions. In this paper, we analyze the effects of using species presence records of varying accuracy, demonstrating the importance of rigorous georeferencing to obtain optimal SDM results.

Although there are a variety of modeling methods and algorithms for generating SDMs, correlative models constructed using only species occurrence records and climate data are commonly used tools (Flower et al., 2013; Bucklin et al., 2015; Guillera-Arroita et al., 2015; Oke & Thompson, 2015). These models do not include true absence data, nor do they explicitly
account for additional variables such as interspecies interactions or species’ dispersal abilities (Pearson & Dawson, 2003; Flower et al., 2013). Correlative models predict the realized niche of the species, not the fundamental niche, due to their reliance on observed presence records (Wiens et al., 2009). There are several notable sources of uncertainty in the process of SDM development (Wiens et al., 2009). First, any ecological or climatic model is constrained by the selection of environmental variables. While there is no consensus as to which environmental or climate variables are to be included in standard SDMs, many agree that the selection of variables can potentially introduce bias (Bucklin et al., 2015). Second, the model is constrained by the resolution and quality of the climate data (Real et al., 2010). Climate data is usually represented as continuous grids interpolated from quality-controlled climate station data sets (Daly et al., 2008). The quality of these climate data, and the methods of interpolating from point records to a continuous surface and correcting for factors such as elevation and aspect can be sources of error in SDMs (Real et al., 2010). Third, there can be issues regarding the taxonomic identification of the specimen (Lozier et al., 2009). Species can be misidentified, or the systematics and taxonomy may have evolved over the years to include different species classifications. Sampling bias and imperfect detection are also noted limitations of the current available data for species distributions (Boakes et al., 2010; Newbold, 2010; Fourcade et al., 2014; Guillera-Arroita et al., 2015). Among all these variables, the most important variable for creating reliable SDMs is the accuracy of the species occurrence localities (Newbold, 2010). Without accurately georeferenced presence points, it is impossible to create an accurate SDM.

Museum and herbarium records provide invaluable information on the distribution of extinct and extant species (Newbold, 2010; Anderson, 2012; Davis et al., 2015). Millions of occurrence records can be accessed directly from the museum or in reputable online databases,
many publicly available (Newbold, 2010). Most include a written site description and often geographic coordinates (see Figure S1 in Supporting Information). The quality of location data generally declines with specimen age. Herbarium records’ site descriptions and associated geographic coordinates are frequently used to build high resolution SDMs (Lozier et al., 2009; Flower et al., 2013; Forester et al., 2013; Alvarado-Serrano & Knowles, 2014). Site coordinates must have as good or better resolution than the climate data, often ≤1km², in order to produce useful SDMs (Wiens et al., 2009) and failure to assess spatial error in these coordinates can have significant impacts on apparent species distributions (Rowe, 2005). Several studies address the effect of sampling bias on SDM output (Phillips et al., 2009; Boakes et al., 2010; Fourcade et al., 2014), but less attention has been paid to the standardization of georeferencing to improve model performance.

Most herbarium and museum records were not documented by collectors with the intention of use in geographic modeling, resulting in many potential sources of spatial error (Bowe & Haq, 2010). Recently, there have been increasing inventories of so-called “georeferenced” natural history collections available to scientists (Randin et al., 2009). Georeferencing is the process of interpreting the written description of site localities and verifying the associated geographic coordinates or assigning new coordinates (Rowe, 2005). Though no standard georeferencing process currently exists, many projects have developed individual guidelines (Chapman et al., 2006). Examples of georeferencing practices and programs include the Mammal Networked Information System- MANIS guidelines (Wieczorek & Wieczorek 2015; Wieczorek et al. 2004), MapSteDI (Murphey et al., 2004), BioGeomancer (Chapman et al., 2006), and GEOLocate (http://www.museum.tulane.edu/geolocate/). The two main branches of georeferencing methods are manual georeferencing and “Georeference Calculators”.
Manual georeferencing requires the meticulous human interpretation of site descriptions and assigning coordinates using detailed topographic maps. This can take several minutes per sample, and is increasingly taxing with large datasets. Georeference Calculators are computer algorithms designed to automate the tedious process of interpreting written site descriptions to estimate geographic coordinates and a degree of confidence (Wieczorek & Wieczorek, 2015). Many publications present SDM results, at varying spatial resolution, without explicitly stating how or if the data were georeferenced (Table 1).

In this paper, we set out to answer the following question: **what are the consequences of using occurrence data of varying levels of spatial accuracy in SDMs?** To address this question, first we outline a standardized method of georeferencing occurrence records specifically for building more useful SDMs, the Spatial Analysis Georeferencing Accuracy (SAGA) protocol, Table 2. Next, to demonstrate the importance of a standardized process, we built current and future SDMs for the high elevation wildflower *Saxifraga austromontana* Wiegand (Saxifragaceae), using three sets of herbarium records, each georeferenced to a different level of spatial accuracy. Although we focus on a plant species, the methods could be extended to any taxon with historical museum or herbarium occurrence records.

**Methods**

*Study system: Saxifraga austromontana*

*Saxifraga austromontana*, the Prickly Saxifrage, is an ideal case-study species for investigating how various georeferencing methods affect SDM results because of its geographically large, but topographically limited, range and extensive herbarium records. First, this plant is endemic to, but widely distributed across, mountainous regions of western North
America from 30-55 degrees’ latitude (Figure 1), where it inhabits a topographically complex region near tree-line. Second, it has an extensive history of collections spanning over 200 years resulting in over 3000 herbarium records available in online databases. The extensive collections of this species, and others in the genus with overlapping and extended ranges, limit the effect of sampling bias.

**Historical Herbarium Record Data**

We compiled a complete "Original" (O) dataset of herbarium records for *S. austromontana*. In May 2015, we downloaded all search records for “*Saxifraga austromontana*” and its taxonomic synonym “*Saxifraga bronchialis*” from the Consortium of the Pacific Northwest Herbarium, Consortium of Intermountain Herbarium, Consortium of Rocky Mountain Herbarium, SEINet, and Canadensys. We included additional records from the Pacific Northwest Herbarium (WWB), University of Washington Herbarium (WTU), University of Oregon Herbarium (ORE), Mount Rainer National Park Herbarium (MORA), Royal BC Museum (V), University of British Columbia Herbarium (UBC) and the B.A. Bennett Herbarium (BABY).

The O dataset was edited to omit duplicate records and extreme outliers. Duplicate records across herbaria were found using accession numbers, GUID numbers, collector numbers and site descriptions. Outliers were defined as occurrence records obviously outside of the known species range, such as records in the oceans, in the Great Plains, outside of North America, north of 55 degrees’ latitude (no confirmed records exist north of this latitude), and records in the state of Oregon outside of the Wallowa mountain range (the range of *S. vespertina*). Omission of outliers is common practice for building SDMs, yet not everyone goes beyond this step (Table 1). The O dataset includes 1363 unique herbarium records (Figure 1).
The “Previously Georeferenced” (PG) dataset includes records that explicitly state they have been georeferenced by other herbaria using a variety of methods. We omitted records from this dataset if the coordinate uncertainty was listed as greater than 1 km. The PG dataset includes 525 unique herbarium records (Figure 1), after outliers and duplicates were omitted.

The “Newly Georeferenced” (NG) dataset includes all historical herbarium records that have been georeferenced to a 1 km or finer resolution using the SAGA methods defined below. The NG dataset only includes herbarium records with a confidence of 1-3 (Table 2) for a total of 1104 unique historical herbarium records (Figure 1).

New Georeferencing Methods: The SAGA Protocol

We developed a novel method, the Spatial Analysis Georeferencing Accuracy (SAGA) protocol (Table 2) to improve and standardize the process of georeferencing. The SAGA protocol is an improvement over other georeferencing practices in terms of both accuracy and straightforward implementation. We meticulously and manually georeferenced each herbarium record in the O dataset for *S. austromontana*, verifying written site descriptions using Google Earth, USGS Topographic Maps, and the Atlas of Canada to ensure accurate geographic coordinates. Each record was reviewed, either through the online database or by physically examining the herbarium specimen. We transformed everything into the WGS 1984 coordinates. We created a standardized ordinal accuracy ranking of 1-5 to classify the spatial resolution of the occurrence data, which can be easily interpreted for use in spatial analysis. Other methods, including the GeoLocate georeference calculator, also assign coordinate uncertainty, but they are frequently misleading. Our method is more meticulous, thus producing higher accuracy coordinates, and our ordinal scale makes it easier to interpret.
The downside of our approach is the amount of time involved: we estimated that manual georeferencing required approximately 5-20 minutes per sample. Georeferencing large datasets with the SAGA protocol is thus less appealing than georeference calculators with batch settings that can process hundreds of samples automatically. Time is a tradeoff for accuracy, and with increased use of “big” datasets and increased model resolution, quality control will become increasingly more critical.

*Species Distribution Models*

We intentionally did not use all SDM approaches or an ensemble approach, but rather a widely-used robust method to demonstrate the need for and utility of the standardized georeferencing protocol we present. We built SDMs using the MAXENT Software (Phillips et al., 2006), one of the most, if not the most, widely-used SDM platforms (Merow et al., 2013; Fourcade et al., 2014; Guillera-Arroita et al., 2015). MAXENT is built on machine learning and Bayesian statistics of maximum likelihood (Elith et al., 2011; Halvorsen et al., 2015), and is especially popular because it outperforms other methods based on predictive accuracy and is relatively easy to use (Merow et al., 2013).

The model inputs include a list of presence points, a set of environmental predictors (i.e., climate variables), and a defined background landscape. In contrast to a true presence-absence model, MAXENT estimates habitat suitability by contrasting environmental factors at presence points with thousands of randomly selected background points throughout the study region (Guillera-Arroita et al., 2015). We followed MAXENT best practices (Merow et al., 2013) to build SDMs for *S. austromontana* using three categories of georeferenced data. Our models are intentionally simple to demonstrate the underlying importance of georeferencing.
Climate Variables

We used monthly PRISM data (Daly et al., 2008) for the reference period (1961-1990) to define the bioclimatic envelope of *S. austromontana*. The PRISM methods utilize Digital Elevation Models to refine interpolation between climate stations by including factors such as location, elevation, and aspect (Daly et al., 2008). The climate data for this study were further downscaled to a resolution of 1 km² using the ClimateNA v5.10 software package, available at http://tinyurl.com/ClimateNA (Hamann et al., 2013; Wang et al., 2012). We selected seven final variables for use in SDMs (Table 3 and Table S3). Variables were pre-selected for ecological relevance to our taxa, and further reduced to eliminate highly correlated parameters (Pearson’s r>|0.75|), Table 3. We also downscaled projected values of these variables for a 30-year period centered on 2080. Future climate projections were obtained from ClimateNA using an ensemble of 23 Atmosphere-Ocean General Circulation Models (AOGCMs) of the Coupled Model Intercomparison Project phase 3 (CMIP3) under the A2 emission scenario, selected based on validation rank (Hamann et al., 2013).

Background Selection

We limited the geographic background to locations within the likely dispersal range of *S. austromontana*. We trimmed the region extent for the reference period to the northern border of British Columbia, the southern border of the United States, and 150 km east of the Rocky Mountains. *Saxifraga austromontana* has been extensively collected across its range and is not found more than 150 km east of the Rocky Mountains crest, except for small isolated mountain ranges that we included in our extent. This area allowed us to include a potential northern range-expansion, expected for cold-adapted species (Forester et al., 2013).
Climate Space Analysis

To assess whether our three models captured the same climatic envelopes, we quantitatively compared the climatic niche space for each dataset using Analysis of Variance (ANOVAs) and Principal Component Analysis (PCA). We ran one-way ANOVAs to compare the variation between to the variation within each dataset for the values of seven climate variables extracted at each presence point. We used a Bonferroni correction to account for multiple testing, dividing the alpha of 0.05 by 3 for a final alpha of 0.017. We used an unrotated PCA to evaluate the climate space represented by the three levels of georeferenced data. We incorporated all climate variable values at all presence locations for each georeference category in our PCA and extracted the first two principal components. All statistics were run using R ver. 3.1.2 (R Core Team, 2015), and plotted using ggplot2 (Wickham, 2009).

MAXENT Model Settings

All SDMs were run using the version 3.3.3k of MAXENT (http://www.cs.princeton.edu/~schapire/maxent/). In order to compare model outputs, all runs were computed with the default features (Linear, Quadratic, Product, Threshold and Hinge), and a logistic output which results in a map of habitat suitability values ranging from 0-1 (Fourcade et al., 2014) per 1 km grid cell, defined by the resolution of the input climate data. We set MAXENT to train each SDM to a random subsample of 75% of species presence points, with the remaining 25% of the data used for model evaluation. We increased the default maximum iterations to 5000, and ran 20 replicates of each model.
Model Evaluation

We evaluated the models using the area under the receiver operating curve (AUC) because it is a generally accepted and widely used metric for model evaluations (Merow et al., 2013). The AUC score is the probability that a randomly chosen presence point is ranked higher than a random background point, and is penalized for predictions outside of presence locations (Merow et al., 2013). A high AUC value (>0.8) indicates that models can properly distinguish between presences and random background samples. Though the AUC has been highly criticized as a metric of model performance (Lobo et al., 2008), there are few alternatives for presence only models (Merow et al., 2013).

To quantify the geographic differences between models created using occurrence records of varying accuracy, we used the 10% cumulative logistic threshold to define a binary response of suitable or non-suitable habitat. We compared area of suitable habitat for the reference and future predictions across the three georeferencing categories. Cartography and spatial comparisons were performed in ArcGIS 10.3.

Results

Climate Space Analysis

The NG dataset captures a significantly different range of environmental conditions than the other two datasets. The ANOVAs revealed that values extracted at each presence point in the NG dataset capture significantly different values for 6 of the 7 climate variables compared with the O dataset, and for 5 of 7 variables compared with the PG dataset (Figure 2 and Table S2). The O and the PG dataset do not significantly differ from each other in any of the climate
variables. Effectively, O and PG capture the same climate envelope or the range of values within datasets are too large to detect a difference between groups.

The differences between the climate envelopes captured by the three datasets are clearly visible when the presence points are plotted by their location in climate space, as represented by principal components (PC) axes 1 and 2. PC1 and PC2 extracted from all climate variables at all presence locations explain 49.71% and 27.26% of the total variance, respectively (Figure 3). Ecologically, increasing PC1 can be interpreted as representing greater growing season moisture availability (more precipitation as snow (PAS), higher summer moisture index (cmiJJ), lower annual heat moisture index (AHM), and lower mean temperature of the warmest month (MWMT)). Higher values on PC2 represent increasing cold season length and severity (later start to the frost-free period (bFFP), greater difference between summer and winter temperatures (TD), and colder winter temperatures (MCMT)). The O dataset unequivocally captures the largest niche space, while the PG and NG are subsets of the O data. PG occupies most of the O dataset, whereas the NG dataset represents a much tighter ecological niche (Figure 3).

Species Distribution Models

All MAXENT models were statistically valid (AUC >0.88), however the models predicted very different areas of suitable habitat, especially for future scenarios (Figure 4 and Figure 5, Table 4). The SDMs for the reference period (1960-1990) constructed using NG data resulted in the smallest area of suitable habitat, equivalent to 84.3% of the area of the SDM constructed using PG data and 71.5% of the area of the SDM constructed using O data (Figure 5a). The 2080 SDM results for the three categories of georeferenced data differed even more drastically (Figure 4, Figure 5b, Table 4). The SDM constructed using NG data predicted the
smallest area of suitable habitat, equivalent to 50% of the area of the SDM trained using PG data and 37.1% of the area of the SDM trained using O data. The future SDM using NG data estimated the greatest loss and smallest gain in suitable habitat by 2080. The models also differed in the relative contribution of each climate variable (Table 3). The larger geographic ranges predicted by the O and PG models are a natural outcome of the larger climatic ranges captured by those datasets. Varying accuracy of occurrence records results in considerable differences in how SDMs project the location of this species in both climatic space and geographic space.

Discussion

A standardized process is needed to ensure consistent spatial accuracy of species occurrence records for use in SDMs. We employed the most commonly used SDM tool, MAXENT, and our findings are broadly applicable to correlative SDMs. The method used to georeference museum records greatly influences the spatial accuracy of those points, and thus the results of SDMs. Georeferencing manually increased the number of valid presence points available, with the NG model incorporating more than twice the number of points compared to the PG model (1104 vs. 525). A standardized georeferencing protocol can thus increase both the accuracy and number of available species occurrence records, simultaneously expanding the geographic coverage of those records and refining the climatic envelope they capture.

Although all three of our SDMs had high validation statistics (AUC > 0.88), the SDMs constructed using the O and PG datasets captured significantly different climatic envelopes for S. austromontana than the SDM trained using NG data. This adds additional evidence to the argument that AUC scores are not a reliable metric for model accuracy (Lobo et al., 2008). The O and PG dataset include many points that are clearly beyond the range of S. austromontana.
Although these points are outside the species’ range, at first glance they may not be considered extreme outliers, and would likely be used in an analysis that does not preprocess with manual georeferencing. For example, on the Olympic Peninsula of Washington State both the O and PG dataset include a point on the shore of Lake Crescent near the town of Piedmont at an elevation of 198 meters (WS-VP-70650), where the site description states the sample was collected on Mt. Storm King at an elevation between 1311-1829 meters. The incorrectly estimated point is over 6 km off, and captures a completely different elevation and climate space than the actual collection site. Another example on the Olympic Peninsula is a point less than 500 meters from the west coast at an elevation of 104 meters (WTU-VP-90424), included in both the O and PG dataset (Figure 1). This point was estimated, quite inaccurately, by the WTU herbarium using the GeoLocate calculator. Our laboratory, which has conducted extensive surveys on the Olympic Peninsula and works closely with Olympic National Park, has not recorded any *S. austromontana* in coastal or low elevation sites.

Numerous other inaccurate records were corrected during our manual georeferencing protocol, SAGA. Common errors were coordinates taken at the trailhead or in one instance the latrine, often with a GPS, rather than the actual collection site. Consequently, we feel confident stating that the NG dataset captured a more accurate representation of the species’ geographic range. Thus, the NG dataset provides a more realistic estimate of the climatic conditions in which *S. austromontana* exists: a cooler, wetter environment with a shorter growing season (Figure 3). Those conditions are more consistent with the known habitat of this high elevation plant, compared to the climate envelopes of the O and PG datasets. The models run using the O and PG datasets did not capture significantly different climate space compared with each other.
(Figure 2). This indicates that the PG dataset is not much better than the O dataset at defining the specific niche of *S. austromontana*.

The differences in climate space among our models led to drastically different SDM outputs and strikingly different predictions of current and future ranges. Using the 10% cumulative logistic threshold to define a binary response of suitable or non-suitable habitat, the O and PG models resulted in suitable habitat covering geographic areas 1.4 and 1.2 times larger than the NG dataset for the reference period. Erroneously placed presence locations, such as WTU-VP-90424 circled in Figure 1, create a broader envelope for the target taxon. For example, the O and PG dataset show suitability across most of the Olympic Peninsula and southern Vancouver Island including coastal regions that have been well-documented botanically and do not currently contain *S. austromontana*. Interestingly, the O dataset is more accurate than the PG in predicting the range on the Olympic Peninsula and Vancouver Island, probably because it includes more reference points. The NG SDM captures a much more accurate and tighter representation of the current range of *S. austromontana*, which is abundant primarily in the northeastern arc of basaltic peaks in the Olympics (Figure 4 and Figure 5a).

It is important to note that all models (O, PG, and NG) predict habitat outside of the known range of *S. austromontana*, including the Sierra Nevada, Uinta, and Wind River ranges. These regions are within the climate envelope of the species, yet for alternative reasons (e.g., dispersal and competition dynamics) the species is not known to occur there, despite extensive botanical surveys. Overall, the O and PG datasets create SDMs that appear to over-predict suitable habitat in comparison to the NG data based on our current understanding of this species’ ecology. These results clearly demonstrate the shortcomings of un-validated datasets in the use of SDMs.
Differences in predicted area of suitable habitat among the O, PG, and NG datasets are even more pronounced for future predictions. The NG SDM estimates a 65.7% reduction in suitable habitat by 2080, while the SDMs constructed using the other datasets estimate a 32-40% reduction by 2080, under the A2 emission scenario. The NG models are more consistent with other studies on alpine taxa that forecast 40-80% reduction in suitable habitat by the end of the century (Dirnböck et al., 2011; Dullinger et al., 2012; Forester et al., 2013). Further, the NG model predicts a relatively small gain in habitat by 2080, equivalent to 21-29% of the area of gain predicted by the other two models, explained by limited upslope habitat for alpine taxa. High elevation species are disproportionately affected by climate change (Gottfried et al., 2012). Alpine environments are essentially mountain-top “sky-islands” surrounded by a matrix of non-suitable habitat (DeChaine & Martin, 2005; Esposito et al., 2015), and there is little room for upward range expansion (Jackson et al., 2015).

Relying on potentially inaccurate presence records when modeling alpine species could lead to serious overestimation of the area in which these species can persist, misleading conservation and management efforts. SDMs can be developed to their full potential only when they are trained using many high-precision occurrence records for a species (Randin et al., 2009). Our results demonstrate that there is no alternative for highly accurate presence data that have been meticulously georeferenced by a human, not a machine. Many SDMs are built using historical museum or herbarium records. In fact, for many taxa these datasets are the only available records of their distribution. We found that geographic coordinates published on reputable herbaria sites often do not match the site description. These coordinates may have been recorded inaccurately by the collector, estimated by the collector using a coarse scale topographic map, recorded in a different geographic coordinate system than present systems (i.e.,
NAD27 vs. WGS84), georeferenced incorrectly by a curator, or estimated using a Georeference Calculator.

We have found the results of Georeference Calculators to be frequently misleading, often adding an element of sampling bias by assigning coordinates for collections taken in the mountains to the nearest town. For example, we tested the utility of the GeoLocate Web Application Standard Client to assign a coordinate to the locality string “West Ute Lake, Weminuche Wilderness”, Country: “United States of America,” State: “Colorado,” County: “Hillsdale.” The program assigned a coordinate with an uncertainty code of 301m to 37.466673, -106.978932, which is more 30 miles southeast of the true location of West Ute Lake. These calculators are popular because they are easy to use and allow for batch processing of CSV files with many listed localities, but the spatial accuracy of these outputs is questionable.

Conclusion and Future Efforts

Understanding the present and future distributions of species is critical for applications in conservation, ecology, biogeography, phylogenetic analysis, phenology, landscape ecology, and beyond (Lenoir et al., 2008; Newbold, 2010; Forester et al., 2013; Davis et al., 2015; Fois et al., 2015). SDMs, especially those implemented in MAXENT, are the most common tools used to determine habitat suitability. As these tools become more and more popular and public access to species occurrence data increases, it is paramount to remember that convincing SDMs can be produced from dubious data (Lozier et al., 2009). Museum and herbaria databases are invaluable archives of occurrence information, yet must be used with caution, especially when applied to spatial analyses. Our results indicate that SDMs built using low accuracy location data capture a significantly broader climate envelope, predict a more widespread spatial distribution, and
predict less loss under climate change scenarios than SDMs trained on accurate collection records. Conservation and management decisions could vary considerably depending on which model’s output they were based on.

This study highlights the importance of meticulously georeferencing all records manually before use in SDMs, as varying levels of georeferencing result in significantly different models of habitat suitability for the same species, *S. austromontana*. The tradeoff of manual georeferencing is the time it takes to analyze each record. As datasets increase in size, the feasibility of georeferencing each record becomes increasingly daunting. Batch georeferencing calculators may be desirable for large datasets, but reliable technology is not yet available. As the resolution of historical and projected climate data increases, more advanced and accurate SDMs become possible, but only if species occurrence records are also available at an increasingly fine scale. Field collectors must record accurate coordinates and detailed site descriptions, assuming use in future spatial analyses. Curators of databases must only make available accurately georeferenced occurrence records, or explicitly state otherwise. Lastly, end users must suspect occurrence records to be inaccurate and georeference before performing spatial analyses using a protocol such as SAGA. All parties should share the improved data, ultimately improving publicly available datasets and resulting science.
Tables and Figures

**Table 1:** Examples of methods used to georeferenced species occurrence records as described in species distribution modeling (SDM) papers. Georeferencing practices are not standardized, and often the resolution of the resulting SDM is finer than the historical records used to train the model. Without accurately georeferenced presence points, it is impossible to create a credible SDM.

<table>
<thead>
<tr>
<th>Authors:</th>
<th>Occurrence Records source:</th>
<th>SDM resolution:</th>
<th>Georeference description:</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Jackson et al., 2015)</td>
<td>Field measured GPS localities and opportunistic citizen science sightings</td>
<td>100m</td>
<td>For the field survey dataset, all locations were recorded with GPS. For citizen science program, summer observations filtered by location accuracy, retaining those with precise GPS or map coordinates (accurate to within 100 m).</td>
</tr>
<tr>
<td>(DeChaine et al., 2014)</td>
<td>Herbarium records</td>
<td>800m</td>
<td>“Georeferenced” herbaria samples</td>
</tr>
<tr>
<td>(Chardon et al., 2014)</td>
<td>Consortium of California Herbarium</td>
<td>800m</td>
<td>Authors employed three criteria on herbarium records: 1) Omitted occurrences with GPS error larger than 1000 m; 2) If GPS error was not included in the occurrence file, only used specimens collected since the year 2000; 3) Omitted points that were clearly planted or outside of the species’ distribution.</td>
</tr>
<tr>
<td>(Lentz et al., 2008)</td>
<td>Herbarium records from the United States, United Kingdom and Mexico</td>
<td>30 arc-seconds (ca. 1 km²)</td>
<td>If the coordinates were not specified on herbarium records, the authors georeferenced using 1:100,000 topographic maps. Locality data was only used if the location of the collection could be accurately pinpointed.</td>
</tr>
<tr>
<td>(López-Alvarez et al., 2015)</td>
<td>Herbarium records and field measured</td>
<td>30 arc-seconds (ca. 1 km²)</td>
<td>Field collections and georeferenced collections</td>
</tr>
<tr>
<td>(Smith &amp; Donoghue, 2010)</td>
<td>Labels on herbaria specimens, relevant herbaria databases and other databases.</td>
<td>30 arc-seconds (ca. 1 km²)</td>
<td>No mention of georeferencing.</td>
</tr>
<tr>
<td>(Forester et al., 2013)</td>
<td>Online herbarium records</td>
<td>50 km</td>
<td>“georeferencing was evaluated for accuracy”</td>
</tr>
</tbody>
</table>
Table 2: Standardized confidence rankings for determining the spatial accuracy of species occurrence records using the Spatial Analysis Georeferencing Accuracy (SAGA) protocol. SAGA requires manual georeferencing of each occurrence record by interpreting the site location and verifying or assigning a location in the form of WGS 1984 geographic coordinates. The SAGA protocol uses an ordinal accuracy ranking of 1-5 to classify the spatial resolution of the occurrence data. Confidence ranks of 1-3 may be useful for constructing Species Distribution Models using 1 km or coarser climate data. Ranks of 4 and 5 are not appropriate for spatial analysis and should be omitted.

<table>
<thead>
<tr>
<th>Confidence</th>
<th>GPS</th>
<th>Resolution (radius)</th>
<th>Description</th>
<th>Example Accession #s</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Required</td>
<td>1-30m</td>
<td>Records with an accurate GPS reading, listed coordinate uncertainty, and a detailed written description that matches coordinates.</td>
<td>WTU-VP-5827, RM-VP-740775</td>
</tr>
<tr>
<td>2</td>
<td>Sometimes</td>
<td>30-100m</td>
<td>Records can be georeferenced to a fine resolution based on a detailed written description that can be verified, and in many cases a GPS reading. For example: summits of peaks, fire lookouts, intersections of creeks or trails.</td>
<td>WTU-VP-185106, WTU-VP-90419</td>
</tr>
<tr>
<td>3</td>
<td>Sometimes</td>
<td>100-500m</td>
<td>Record coordinates can be georeferenced to a moderate resolution based on a written description that can be verified. For example: small lakes, mountain passes, small named meadows.</td>
<td>MONTU-VP-3979, WS-VP-101352</td>
</tr>
<tr>
<td>4</td>
<td>Often not</td>
<td>N/A</td>
<td>Record cannot be triangulated to a 1 km grid. The site description may still be useful for collections, yet cannot be used in SDMs. For example: large lakes, entire mountains or peaks, ridgelines, trail names, well-known geologic or historic landmarks.</td>
<td>MONTU-VP-27436, RM-VP-815188</td>
</tr>
<tr>
<td>5</td>
<td>Often not</td>
<td>N/A</td>
<td>Poor site description and coordinates cannot be verified. These data cannot be used accurately for SDMs and may not even be useful for collections. For example: town names, county names, state names, and mountain ranges.</td>
<td>MONT-VP-50930 MONT-VP-50961</td>
</tr>
</tbody>
</table>
Table 3: Climate variables selected for SDMs of *Saxifrage austromontana*, and percent contribution to MAXENT models for each of three levels of georeferencing: Newly Georeferenced (NG), Previously Georeferenced (PG) and Original (O). Top three contributing variables for each model are in bold. Climate data made available by ClimateNA for the reference period (1960-1990) and 2080 future projections based on an ensemble of 23 CMIP3 coupled atmosphere-ocean general circulation models (Hamann et al., 2013).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>NG</th>
<th>PG</th>
<th>O</th>
</tr>
</thead>
<tbody>
<tr>
<td>AHM:</td>
<td>Annual heat moisture index, calculated as (MAT+10)/(MAP/1000)</td>
<td>4.6</td>
<td>8.9</td>
<td>.9</td>
</tr>
<tr>
<td>bFFP:</td>
<td>The Julian date on which the frost-free period begins</td>
<td><strong>26.3</strong></td>
<td><strong>17.9</strong></td>
<td><strong>16.5</strong></td>
</tr>
<tr>
<td>cmiJJA:</td>
<td>Hogg's summer (Jun to Aug) climate moisture index</td>
<td><strong>21.2</strong></td>
<td><strong>26.5</strong></td>
<td><strong>35.4</strong></td>
</tr>
<tr>
<td>MCMT:</td>
<td>Mean temperature of the coldest month (°C)</td>
<td>10.3</td>
<td>7.8</td>
<td><strong>14.6</strong></td>
</tr>
<tr>
<td>MWMT:</td>
<td>Mean temperature of the warmest month (°C)</td>
<td>13</td>
<td>2.3</td>
<td>9.8</td>
</tr>
<tr>
<td>PAS:</td>
<td>Precipitation as snow (mm)</td>
<td>10.3</td>
<td><strong>23.9</strong></td>
<td>9.5</td>
</tr>
<tr>
<td>TD:</td>
<td>Difference between MCMT and MWMT, as a measure of continentality (°C)</td>
<td><strong>14.3</strong></td>
<td>12.7</td>
<td>13.1</td>
</tr>
</tbody>
</table>
Table 4: The results of MAXENT models for *Saxifraga austromontana* trained on presence points from three levels of georeferenced data: Original (O), Previously Georeferenced (PG), and Newly Georeferenced (NG) with the SAGA protocol. All models were run with the same features and climate covariates. The total percent reduction of the future area of suitable habitat relative to the reference period is presented in bold. The O and PG models over predict present suitable habitat with respect to the more accurate NG model, and the shortcomings of the O and PG models are exacerbated for the future projection. All models have high validation statistics using the area under the receiver operating curve (AUC) value, providing additional evidence to the argument that AUC scores are not a reliable metric for model accuracy.

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Original</th>
<th>Previously Georeferenced</th>
<th>Newly Georeferenced</th>
</tr>
</thead>
<tbody>
<tr>
<td>AUC</td>
<td>0.888</td>
<td>0.914</td>
<td>0.914</td>
</tr>
<tr>
<td>Reference Period (km²)</td>
<td>913,695</td>
<td>775,270</td>
<td>653,898</td>
</tr>
<tr>
<td>Future 2080s (km²)</td>
<td>623,044</td>
<td>462,658</td>
<td>231,376</td>
</tr>
<tr>
<td>Lost (km²)</td>
<td>477,235</td>
<td>447,353</td>
<td>461,758</td>
</tr>
<tr>
<td>Gained (km²)</td>
<td>186,584</td>
<td>134,741</td>
<td>39,236</td>
</tr>
<tr>
<td>Maintained (km²)</td>
<td>436,460</td>
<td>327,917</td>
<td>192,140</td>
</tr>
<tr>
<td><strong>Total Reduction (%)</strong></td>
<td><strong>31.8</strong></td>
<td><strong>40.3</strong></td>
<td><strong>65.7</strong></td>
</tr>
</tbody>
</table>
Figure 1: The distribution of *Saxifraga austromontana* for three categories of georeferenced historical herbarium records: Original data (O), Previously Georeferenced (PG), and Newly Georeferenced (NG). The circled point on inset map displays a species occurrence record on the coast of the Olympic Peninsula. The coordinate was incorrectly assigned using the georeference calculator: GeoLocate (WTU-VP-90424), and is included in both the O and PG dataset. Data are in a Lambert conformal conic equal area projection.
Figure 2: Range of values for seven climate variables extracted using each set of presence points for the three categories of georeferenced data: Newly Georeferenced (NG), Original (O), and Previously Georeferenced (PG). The plot displays the median, first and third quartiles, range, and extreme outliers. Different letters indicate a significant difference between datasets at a conservative alpha of 0.017, corrected with a Bonferroni.
Figure 3: Principal Component Analysis (PCA) built on seven climate variables. Plots of niche space illustrate environmental differences and similarities among the three data sets: Newly Georeferenced (NG), Original (O), and Previously Georeferenced (PG). Principal component (PC) axes 1 and 2 account for 49.71% and 27.26% of the total variance. Ecologically, increasing PC1 can be interpreted as representing greater growing season moisture availability (more precipitation as snow (PAS), higher summer moisture index (cmiJJA), lower annual heat moisture index (AHM), and lower mean temperature of the warmest month (MWMT)). Higher values on PC2 represent increasing cold season length and severity (later start to the frost-free period (bFFP), greater difference between summer and winter temperatures (TD), and colder winter temperatures (MCMT)). Cluster ellipses delineate 95% confidence intervals. For PCA loadings see Table S1.
Figure 4: Species Distribution Model (SDM) of *Saxifraga austromontana* for the reference period (1960-1990) and 2080’s under the A2 climate scenario for three categories of georeferenced data: Original (O), Previously Georeferenced (PG), and Newly Georeferenced (NG). Suitability is set at the 10-percentile training presence logistic threshold. Projected for 2080, the O and PG models predict a relatively small reduction of 31.8% and 40.3%, respectively. The more NG model predicts a 65.7% reduction, more consistent with previous studies on alpine taxa (Table 4). The NG SDM does a good job of predicting present and future suitable habitat for *Saxifraga austromontana*. The O and PG SDMs over-predict suitable habitat outside of the known range of the target taxa, including locations on the coast of the Olympic Peninsula and Vancouver Island (see inset map). Inaccurate predictions of the O and PG dataset are exacerbated for future SDM outputs. Data are in a Lambert conformal conic equal area projection.
Figure 5: SDMs built using the three categories of georeferenced data (Original (O), Previously Georeferenced (PG), and Newly Georeferenced (NG)) result in notably different areas of suitable habitat for the (A) reference period (1960-1990) and (B) 2080 under the A2 emission scenario. SDM results based on the NG dataset are overlaid on top of SDM results using the O and PG datasets to visualize the differences in predicted niche space. The O and PG datasets greatly over-predict suitable habitat for the target taxa into regions it is known to be absent, including the coast of the Olympic Peninsula and Vancouver Island. This is due to the inclusion of inaccurate presence points such as WTU-VP-90424, displayed in Figure 1. Data are in a Lambert conformal conic equal area projection.
Table S1: PCA loadings for niche space analysis of *Saxifraga austromontana*. Principle component (PC) axes 1 and 2 account for 49.71% and 27.26% of the total variance, respectively. The top contributing variables for PC1 and PC2 are in bold.

<table>
<thead>
<tr>
<th>Variable</th>
<th>PC1</th>
<th>PC2</th>
<th>PC3</th>
<th>PC4</th>
<th>PC5</th>
<th>PC6</th>
<th>PC7</th>
</tr>
</thead>
<tbody>
<tr>
<td>AHM</td>
<td>-0.47</td>
<td>0.15</td>
<td>0.19</td>
<td>0.19</td>
<td>0.83</td>
<td>0.03</td>
<td>0.00</td>
</tr>
<tr>
<td>bFFP</td>
<td>0.28</td>
<td>0.45</td>
<td>0.52</td>
<td>-0.40</td>
<td>0.07</td>
<td>-0.53</td>
<td>0.00</td>
</tr>
<tr>
<td>cmiJJA</td>
<td>0.44</td>
<td>-0.22</td>
<td>-0.24</td>
<td>0.56</td>
<td>0.23</td>
<td>-0.58</td>
<td>0.00</td>
</tr>
<tr>
<td>MCMT</td>
<td>-0.27</td>
<td>-0.59</td>
<td>0.19</td>
<td>-0.23</td>
<td>-0.03</td>
<td>-0.30</td>
<td>-0.63</td>
</tr>
<tr>
<td>TD</td>
<td>-0.18</td>
<td>0.57</td>
<td>-0.57</td>
<td>-0.02</td>
<td>-0.06</td>
<td>-0.16</td>
<td>-0.54</td>
</tr>
<tr>
<td>PAS</td>
<td>0.41</td>
<td>-0.19</td>
<td>-0.40</td>
<td>-0.60</td>
<td>0.49</td>
<td>0.17</td>
<td>0.00</td>
</tr>
<tr>
<td>MWMT</td>
<td>-0.48</td>
<td>-0.12</td>
<td>-0.34</td>
<td>-0.28</td>
<td>-0.09</td>
<td>-0.49</td>
<td>0.56</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>1.87</td>
<td>1.38</td>
<td>0.91</td>
<td>0.64</td>
<td>0.48</td>
<td>0.38</td>
<td>0.00</td>
</tr>
<tr>
<td>Proportion of Variance</td>
<td>0.50</td>
<td>0.27</td>
<td>0.12</td>
<td>0.06</td>
<td>0.03</td>
<td>0.02</td>
<td>0.00</td>
</tr>
<tr>
<td>Cumulative Proportion</td>
<td>0.50</td>
<td>0.77</td>
<td>0.89</td>
<td>0.95</td>
<td>0.98</td>
<td>1.00</td>
<td>1.00</td>
</tr>
</tbody>
</table>
Table S2: Results from ANOVA analyses comparing the variation between to the variation within each dataset for the values of seven climate variables extracted at each presence point. The Newly Georeferenced (NG) dataset differs significantly from the Original (O) and Previously Georeferenced (PG) dataset for 6 of 7 and 5 of 7 climatic variables, respectively. The O and PG datasets do not significantly differ for any one variable. We used a Bonferroni correction to account for multiple comparisons across the three datasets. Significance code: p < 0.017*.

<table>
<thead>
<tr>
<th>Variable</th>
<th>NG vs. O</th>
<th>NG vs. PG</th>
<th>PG vs. O</th>
</tr>
</thead>
<tbody>
<tr>
<td>AHM</td>
<td>1.49e-10*</td>
<td>0.005*</td>
<td>0.02</td>
</tr>
<tr>
<td>bFFP</td>
<td>1.23e-08*</td>
<td>2.57e-05*</td>
<td>0.85</td>
</tr>
<tr>
<td>cmiJJA</td>
<td>8.76e-07*</td>
<td>1.4e-08*</td>
<td>0.094</td>
</tr>
<tr>
<td>PAS</td>
<td>9.49e-05*</td>
<td>.056</td>
<td>0.24</td>
</tr>
<tr>
<td>MCMT</td>
<td>0.022</td>
<td>.0055*</td>
<td>0.28</td>
</tr>
<tr>
<td>MWMT</td>
<td>8.5e-10*</td>
<td>2.3e-07*</td>
<td>0.81</td>
</tr>
<tr>
<td>TD</td>
<td>1.9e-03*</td>
<td>.059</td>
<td>0.33</td>
</tr>
</tbody>
</table>
**Table S3:** All bioclimatic variables made available by ClimateNA
[http://ualberta.ca/~ahamann/data/climatena.html](http://ualberta.ca/~ahamann/data/climatena.html).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>MAT</td>
<td>mean annual temperature (°C)</td>
</tr>
<tr>
<td>MCMT</td>
<td>mean temperature of the coldest month (°C)</td>
</tr>
<tr>
<td>MWMT</td>
<td>mean temperature of the warmest month (°C)</td>
</tr>
<tr>
<td>TD</td>
<td>difference between MCMT and MWMT, as a measure of continentality (°C)</td>
</tr>
<tr>
<td>MAP</td>
<td>mean annual precipitation (mm)</td>
</tr>
<tr>
<td>MSP</td>
<td>mean summer (May to Sep) precipitation (mm)</td>
</tr>
<tr>
<td>AHM</td>
<td>annual heat moisture index, calculated as (MAT+10)/(MAP/1000)</td>
</tr>
<tr>
<td>SHM</td>
<td>summer heat moisture index, calculated as MWMT/(MSP/1000)</td>
</tr>
<tr>
<td>DD.0</td>
<td>degree-days below 0°C (chilling degree days)</td>
</tr>
<tr>
<td>DD.5</td>
<td>degree-days above 5°C (growing degree days)</td>
</tr>
<tr>
<td>NFFD</td>
<td>the number of frost-free days</td>
</tr>
<tr>
<td>bFFP</td>
<td>the Julian date on which the frost-free period begins</td>
</tr>
<tr>
<td>eFFP</td>
<td>the Julian date on which the frost-free period ends</td>
</tr>
<tr>
<td>PAS</td>
<td>precipitation as snow (mm)</td>
</tr>
<tr>
<td>EMT</td>
<td>extreme minimum temperature over 30 years (°C)</td>
</tr>
<tr>
<td>Eref</td>
<td>Hargreave's reference evaporation</td>
</tr>
<tr>
<td>CMD</td>
<td>Hargreave's climatic moisture index</td>
</tr>
<tr>
<td>CMI</td>
<td>Hogg's climate moisture index</td>
</tr>
<tr>
<td>cmiJJA</td>
<td>Hogg's summer (Jun to Aug) climate moisture index</td>
</tr>
<tr>
<td>Tave_wt</td>
<td>winter (Dec to Feb) mean temperature (°C)</td>
</tr>
<tr>
<td>Tave_sm</td>
<td>summer (Jun to Aug) mean temperature (°C)</td>
</tr>
<tr>
<td>PPT_wt</td>
<td>winter (Dec to Feb) precipitation (mm)</td>
</tr>
<tr>
<td>PPT_sm</td>
<td>summer (Jun to Aug) precipitation (mm)</td>
</tr>
</tbody>
</table>
Figure S1: The specimen database made publicly available by the Consortium of the Pacific Northwest Herbaria. This figure displays the results of a search for “Saxifraga bronchialis,” a taxonomic synonym of Saxifraga austromontana. Most historical records include a written site description and often a pair of geographic coordinates. Each orange dot on the map represents coordinates assigned to a specific herbarium record. We found many of these coordinates to be incorrect.
References


Chapter 3
The Compounding Consequences of Climate Change and Wildfire for a High
Elevation Wildflower (*Saxifraga austromontana*)

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Abstract

Climate change disproportionally affects high elevation plants. As temperatures continue to rise, the amount of available alpine habitat in the Rocky Mountains will decrease, likely resulting in local extinctions of plant species that exist nowhere else. In addition to the direct effects of climate-driven habitat loss, alpine plants must also respond to indirect effects, such as changes in disturbance regimes. One of the most tangible changes in disturbance regime is the increase in wildfire frequency in regions in which fire was previously rare or absent, including the alpine. We studied the response of *Saxifraga austromontana*, a wildflower endemic to the Rocky Mountain Floristic Region, to the direct effects of climate change and the indirect effect of increased wildfire frequency. Our approach involved integrating historical herbarium records, a four-month field study, Species Distribution Models (SDMs), and wildfire predictive models. We hypothesized that direct climatic changes compounded with increased wildfire frequency will reduce the future suitable habitat of *S. austromontana* more than if climate was considered alone. The results of our field study indicate that wildfire significantly reduced the abundance and increased the likelihood of extirpation six-fold for *S. austromontana*, compared to paired unburned sites. Increased fire frequency compounded with direct climatic changes will reduce
the range of the species by 42.56% by 2050 compared to 37.88% due to climate alone, under a moderate emission scenario. The effect of wildfire is highly regional. The greatest impact is observed in the Middle Rockies, where an additional 15.6% of suitable habitat may be lost due to fire, on top of 58.39% lost due to climate, resulting in an overall reduction of 73.98%. Other regions are relatively unimpacted by fire, and the northern range of the species may provide both climate and fire refugia. Our work provides novel evidence that increased wildfire frequency will compound the impact of climate change on already imperiled alpine taxa in North America.
Introduction

Direct and Indirect Effects of Climate Change

Climate change is expected to lead to habitat range shifts and species extinctions (Dirnböck et al., 2011; McKelvey et al., 2011; Flower et al., 2013; Forester et al., 2013; Jackson et al., 2015), yet the future distribution of species is not dictated by climate alone (Serra-Diaz et al., 2015). Climate change will result in a suite of “direct effects” such as increased temperatures and changes in precipitation, coupled with profuse “indirect effects.” Indirect effects include changes in biotic interactions such as pathogen outbreaks, biological invasions, interspecific competition, changes in phenology, as well as shifts in environmental disturbance patterns, such as extreme weather events: i.e. flooding and wildfire (Dale et al., 2001; Littell et al., 2010; Loehman et al., 2011; Dale et al., 2016). Disturbance events may act more rapidly than gradual climate forcing to determine the future range of species (Littell et al., 2010). Because the direct effects alone may not accurately predict the full threat to species, there is an immediate need to better understand how variations in disturbance patterns may compound the future impacts of climate change (Loehman et al., 2011; Serra-Diaz et al., 2015).

One of the major indirect effects of climate change that could impact species’ distributions is increased wildfire frequency and intensity (Schumacher and Bugmann, 2006). The fire regime in the mountainous region of Western North America (WNA) is acutely sensitive to changes in climatic oscillations (Higuera et al., 2014; O’Leary et al., 2016). In WNA, historically rare, large fire disturbances are becoming more frequent (Westerling et al., 2014). Furthermore, the average area burned per year by large wildfires has increased six-fold since the 1970s and is predicted to escalate further (Westerling et al., 2006). Fire predictive models
forecast at least a two-fold increase in the area burned across the entire Rocky Mountains and Pacific Northwest by 2050 (Spracklen et al., 2009; Yue et al., 2013).

Wildfire occurrence is correlated to many factors including snowmelt timing, summer temperatures, and ultimately fuel moisture content during the fire season (Westerling et al., 2006; Spracklen et al., 2009; Higuera et al., 2015; O’Leary et al., 2016). Since 1970, the average length of the fire season in WNA has increased 78 days with the largest changes occurring at high elevations in the U.S. Northern Rockies (Westerling et al., 2006). As summer temperatures rise and fuel moisture decreases, wildfire may become as influential as direct effects of climate change in the persistence of high elevation vegetation (Westerling et al., 2011), including in alpine regions where wildfire rarely occurs under current conditions (Schumacher & Bugmann, 2006).

As wildfire dynamics change over the next century, the composition of plant communities will shift in response (Westerling et al., 2011). Vegetation can be strongly mediated by wildfire intensity and frequency (Agee, 1993; Hu et al., 2006; Sugihara et al., 2006; Gavin et al., 2013). The fire regime of the mountain west is characterized by a long mean fire return interval (MFRI) followed by infrequent high severity stand-replacing fires (Baker, 2009), often maintaining a community of late-successional plant species for hundreds of years post fire (Gavin et al., 2013). The past 100 years of fire suppression likely did not drastically impact fuel loading at high elevations, due to the long MFRI (150-400+ years) of the ecosystem (Baker, 2009; Coop et al., 2010). The historical fire rotation of the high alpine may exceed 1000 years (Baker, 2009). Because the high elevation environment of WNA was relatively unaffected by suppression (Dennison et al., 2014), it is an ideal laboratory to isolate and investigate the vegetative response to the interaction between climate and fire (O’Leary et al., 2016).
High Elevation Ecosystems and Climate Change

Mountain ecosystems, similar to arctic tundra, are disproportionately affected by climate change (Dirnböck et al., 2011; Gottfried et al., 2012; DeChaine et al., 2013; Jackson et al., 2015). Cold adapted species must either migrate north or up in elevation to track warming temperatures, yet risk extinction if they are already at the limit of their range or fail to migrate (Forester et al., 2013; Jackson et al., 2015). Mountain ranges are rich biodiversity hotspots harboring many endemic species unique to a single range, or at times a single peak (Körner, 1995; Jackson et al., 2015; Dirnböck et al., 2011). Alarmingly, a ~44-80% habitat loss for alpine species in the mountains of WNA and the European Alps is projected by the end of the century under conservative climate change predictions (Dirnböck et al., 2011; Dullinger et al., 2012; Forester et al., 2013). Effective conservation of these shrinking biodiversity hotspots will require better monitoring and sophisticated climate forecasting at high elevations (Dirnböck et al., 2011; Jackson et al., 2015).

The distributions of high elevation plant species are defined by steep climatic gradients, and are limited by available habitat (Lenoir et al., 2008). High elevation environments are effectively islands surrounded by a matrix of non-suitable habitat (Riebesell, 1982; DeChaine & Martin, 2005; Galbreath et al., 2009; Esposito et al., 2015). Many plant species are restricted to these mountaintop ‘sky islands.’ Mountains are inherently conical in shape, and as treeline moves up in elevation the sky island shrinks and becomes more isolated (Dullinger et al., 2012). Cold adapted alpine species forced to migrate up in elevation are at risk of being squeezed off the mountain (Jackson et al., 2015), resulting in local extinctions as populations become smaller and highly fragmented (Loehman et al., 2011; Forester et al., 2013; Jackson et al., 2015). Micro-refugia, habitat patches that are buffered from increased temperature, may provide sanctuaries
but the number and effective patch-size of micro-refugia are also decreasing for cold-adapted species (Jackson et al., 2015; Serra-Diaz et al., 2015).

*Fire Effects on High Elevation Plants*

Change in fire regime may compound the direct effects of climate in the mountains of WNA, and further threaten species that are not adapted to frequent disturbances. Plants can be classified as fire adapted, fire resistant, or fire avoiders. Fire adapted plants are reliant on wildfire to reproduce, with certain adaptations including serotinous cones (ex. *Pinus contorta*) (Agee, 1993; Keeley, 2012; Feduck et al., 2015). Fire resistant plants adapt to frequent fire with thick bark (ex. *Pseudotsuga menziesii*) (Cocking et al., 2014) or deep tap roots that survive surface burns (ex. *Prosopis glandulosa*) (Ansley et al., 2015). Fire avoiders are plants adapted to habitats with very infrequent MFRIs, typically have no adaptations to fire (Agee, 1993), and can be extirpated by rare fire disturbances. Because of the long MFRIs in the alpine, there is reason to suspect many species there are fire avoiders; however, this supposition has not been tested directly. Doing so is essential to understanding how high elevation plant species in WNA will respond to the direct effects of climate change compounded with increased wildfire frequency.

To date, the best evidence for the powerful synergistic effect of climate and increased wildfire frequency in mountains come from studies on trees, not herbaceous alpine species. In conjunction with direct effects of climatic change, increased fire frequency and size will likely significantly threaten Whitebark Pine, (*Pinus albicaulis*) in Glacier National Park by the end of the century (Loehman et al., 2011). This cold adapted tree species is especially sensitive to a reduced MFRI, which inhibits effective re-colonization prior to the next disturbance (Loehman et al., 2011). In another study, all scenarios predicted a significant range reduction and decline in
micro-refugia for cold-adapted tree species, and the effects were further compounded by increased fire frequency (Serra-Diaz et al., 2015). Finally, in a comprehensive study addressing the direct and indirect effects of climate change on the future distribution of Douglas-fir (Psuedotsuga menziesii) in Washington State, Littell et al. (2010) predicted that changes in species composition may be more rapidly driven by dynamic disturbance events than gradual climatic range shifts.

The response of non-forested high elevation vegetation to wildfire is poorly documented (Douglas & Ballard, 1971; Agee, 1993; Sugihara et al., 2006) At small wildfire scales (<250 m) in Washington, rapid re-colonization from nearby populations led to an increase in subalpine plant diversity (Douglas & Ballard, 1971). In Colorado, plant species richness roughly doubled 29-years post fire in subalpine forests, and species richness rose with distance into burns, but decreased with increasing elevation (Coop et al., 2010). This work clearly highlights the importance of infrequent fires in maintaining diverse plant communities in the subalpine, yet it is still unclear how higher-elevation plants that exist in regions with very long MFRIs respond to fire.

Uncharacteristic wildfires have already had disastrous impacts on certain mountain plants, especially those that are rare or endemic. For instance, the Idaho Department of Fish and Game noted that the Tobias’ Saxifrage (Saxifraga bryophora var. tobias), one of the rarest plants in Idaho, was extirpated from three locations by the 1994 Blackwell Fire (Mancuso, 2003). The Camarillo Springs fire in California (2011) wiped out 93% of the already rare Verity’s liveforever (Dudleya verity) reducing the population to only 300 known individuals (Akpan, 2014). Perennial cushion plants constitute most of the biodiversity near or above treeline in WNA. In contrast to plants at lower elevations, cushion plants restricted to alpine environments
likely did not evolve adaptations to wildfire, due to extremely low historical fire frequencies (Sugihara et al., 2006) that may exceed 1000 years (Baker, 2009). As the climate warms, and fires move higher in elevation, alpine plants will face increased fire frequency. Already stressed by increases in temperature, the decline of unique alpine plant communities may be exacerbated by changes in wildfire regime. This is the first study to test wildfire as a mechanism for population level extirpation in high elevation flowering plants.

The Study System

The Rocky Mountain Floristic Region (RMFR) encompasses most of the mountainous regions of WNA and is defined as the area from Kodiak Island of Alaska south along the roughly 5000 km parallel coastal and interior cordillera to New Mexico and California, delimited to the west by the Pacific ocean and to the east by the Great Plains (Takhtajan et al., 1986). As such, the RMFR has been the focus of many wildfire studies (Westerling et al., 2006, 2011; Baker, 2009; Loehman et al., 2011; Higuera et al., 2015), with a noted increase in large fire frequency over the past several decades. Furthermore, this region contains the highest diversity of conifers in the new world along with numerous endemic flowering plant genera and species (Thorne, 2008). One such species is Saxifraga austromontana Wiegand (syn. S. bronchialis L. subsp. austromontana (Wiegand) Piper [DeChaine 2014]), also known as the Prickly Saxifrage or Spotted Saxifrage, which occurs exclusively in high elevation and cold micro-refugia sites. This plant is an ideal taxon to investigate the combined impact of climate change and wildfire on the persistence of high elevation plants species in the RMFR for several reasons. First, this plant is well distributed across, yet restricted to, the subalpine/alpine of the RMFR. Second, it has an extensive dataset of occurrence records with over 1000 historical herbarium records. Further,
there is circumstantial evidence that it is a fire avoider (Pers. obs. Bloom & DeChaine) and thus not adapted to frequent wildfires.

*Saxifraga austromontana* exhibits the typical growth form of many alpine flowering plants in North America, and as such may serve as model taxon for studying their response to the combined effects of climate and fire. It is a perennial evergreen herb with a cushion growth habit, low matted clusters of basal rosettes, and shallow roots that cling to rocky, gravelly, or sandy habitats in the high subalpine to alpine zone, and occasionally in lower elevation cold-air micro-habitats (Pojar & Mackinnon, 2013; DeChaine, 2014). The 5-petals of the cream colored flower are brilliantly spotted with yellow, orange, and red dots (McGregor, 2008), Figure 1, for attracting pollinators. Like many high-elevation plants, *S. austromontana* produces a seed that is wind dispersed. It can also reproduce vegetatively when a plant is broken apart by rock fall. Perennial cushion plants such as this, can live decades, often centuries, and constitute a majority of the plants present at high elevations (Huntly et al., 1986; Körner, 1995). The life history, growth form, tightly defined observed niche, and fact that it persists primarily in regions with a historically long MFRI all suggest that *S. austromontana* may not be well adapted to changes in climate and wildfire. Because it is representative of the greater alpine plant community, the response of *S. austromontana* can serve as a broader model for understanding the synergistic effect of climate and wildfire on high elevation ecosystems.

*Experimental Overview*

In this study, we combined field observations and computer modeling to explore the response of the high elevation wildflower *S. austromontana* to the direct and indirect effects of climate change. This research utilizes historical herbarium records, Species Distribution Models
(SDMs), and wildfire predictions to investigate how the interaction between climate change and wildfire has and may further impact S. austromontana across the latitudinal range of the RMFR.

First we employed MAXENT to build current and predictive SDMs of the target taxa to answer the following question: **Q1: Will the available suitable habitat of S. austromontana change by 2050 relative to the current distribution, based on climate variables alone?** We hypothesized that the available suitable habitat for S. austromontana will be reduced ~40% by the 2050s comparable to the findings of other studies conducted on high elevation species (Dirnböck et al., 2011; Dullinger et al., 2012; Forester et al., 2013).

Next we implemented an exhaustive field study, investigating historical populations of S. austromontana located using herbarium records to test our hypotheses to the following three questions. **Q2: Do historical populations of S. austromontana have a greater likelihood of extirpation in areas that have been burned, versus populations without recent wildfire history?** We hypothesized an increased likelihood of extirpation for populations that have burned versus those without recent wildfire history. **Q3: Do historical populations of S. austromontana have a reduced abundance in areas that have burned versus those without wildfire history?** We hypothesized that wildfire will reduce the abundance of S. austromontana compared to unburned populations. **Q4: Is there detectable re-colonization or re-growth post fire, when looking at burn sites that range from 0-21 years old?** We hypothesized that the abundance of S. austromontana will increase as year since fire increases, indicating regrowth or recolonization.

Lastly, we integrate our 2050 SDM results, our knowledge on the fire ecology of the species based on the field study, and future wildfire predictions to address our primary research question; **Q5. What are the synergistic effects of climate change and increased fire frequency on the future distribution of S. austromontana?** We hypothesized that the compounding impacts of
climate change and wildfire would further reduce the range of *S. austromontana*, compared to predictions based on climate data alone.

**Methods**

We used 1107 georeferenced historical herbarium records of *S. austromontana* and 148 new collections (this study) to build SDMs and to establish the field experiment. The SDMs were designed to predict the current and future distribution (2050s) of the species under a moderate climate change scenario (A1B), which assumes that technology will become more efficient and that there will be regional cooperation to balance the use of renewable and non-renewable energy sources. In the field, we investigated the species response to wildfire through extensive observations at paired burned and unburned sites. We integrated our findings from the climate modeling, field analyses, and wildfire predictions to estimate the overall impacts of the direct and indirect (wildfire) effects of climate change on *S. austromontana*.

**Herbarium Records**

We compiled a comprehensive dataset of historical herbarium records for *S. austromontana*. In May 2015, we downloaded all search records for “Saxifraga austromontana” and “Saxifraga bronchialis” from the Consortium of the Pacific Northwest Herbarium, Consortium of Intermountain Herbarium, Consortium of Rocky Mountain Herbarium, Southwest Environmental Network (SEINet), and Canadensys. We also included additional, undigitized records from regional herbaria, including the Pacific Northwest Herbarium (WWB), University of Washington Herbarium (WTU), Washington State University Herbarium (WS), University of
Oregon Herbarium (ORE), Oregon State University Herbarium (ORC), Mount Rainer National Park Herbarium, Reed College Herbarium (REED), Boise State Snake River Plains Herbarium (SRP), Royal BC Museum (V), University of British Columbia Herbarium (UBC) and the B.A. Bennett Herbaria (BABY).

The dataset was edited to omit duplicate records and extreme outliers clearly outside the species’ observed range. We meticulously georeferenced each herbarium record in the edited dataset, following the Spatial Analysis Georeferencing Accuracy (SAGA) protocol described in Bloom et al. 2016 (Chapter 2). This is a manual georeferencing approach specifically designed to prepare historical records for use in spatial analysis. For our analyses, we only included herbarium records rated 1-3 (those with a location accuracy <1km) to facilitate field collections and to match the resolution of our climate models. The original dataset included 1355 unique historical herbarium records, which were further reduced to 1107 after editing and georeferencing. To the 1107 accurate records, we added an additional 148 collections with GPS coordinates and uncertainty measures that were sampled 2013 through 2015 by the authors Bloom and DeChaine, as well as other members of the Pacific Northwest Herbarium (WWB).

Species Distribution Models

We used MAXENT (Phillips et al., 2006), the most widely implemented SDM platform in current literature (Merow et al., 2013; Fourcade et al., 2014; Guillera-Arroita et al., 2015) to generate reference and future SDMs. The MAXENT software is built on machine learning and Bayesian statistics of maximum likelihood to build SDMs with high predictive accuracy, using a list of occurrence records, a set of environmental predictor variables, and a defined background landscape. Instead of utilizing true absence records, MAXENT estimates suitability by
contrasting factors at occurrence points with 10000 randomly selected points throughout the background landscape (Guillera-Arroita et al., 2015). We followed MAXENT best practices (Merow et al., 2013) to build SDMs for *S. austromontana* under reference conditions (1960-1990), and for the 2050s (average conditions for 2041-2070). We used an ensemble projection of 23 CMIP3 models for the 2050s under the A1B moderate emission scenario, to match the scenario and timeframe of the previously published fire predictions we used (Spracklen et al., 2009; Yue et al., 2013).

We utilized monthly PRISM data (Daly et al., 2008) for the reference period (1961-1990) to define the bioclimatic envelope of *S. austromontana*. The climate data for this study were downloaded in May 2016 from ClimateWNA (tinyurl.com/ClimateWNA) and downscaled to a resolution of 1km² using the ClimateWNA v5.10 software package (Hamann et al., 2013; Wang et al., 2012). We selected 7 final variables for use in SDMs, pre-selected for ecological relevance to our taxa, and further reduced to eliminate highly correlated parameters (Pearson’s r>|0.75|), Table 2. We defined the background extent for the reference period to include all EPA Ecoregions Level 3 that contain >1 occurrence record of *S. austromontana*, plus a 150km buffer around each included ecoregion. We did not refine the geographic space for future projections, in order to estimate and observe potential range expansion.

Our model was run using the version 3.3.3k of MAXENT (http://www.cs.princeton.edu/~schapire/maxent/) and computed with the Linear, Quadratic, Product, Threshold and Hinge features. We used a logistic output to calculate a range of suitability from 0-1 (Fourcade et al., 2014) per 1km grid cell. We set MAXENT to train each SDM to a random subsample of 75% of species presence points, with the remaining 25% of the data used to calculate an AUC score, averaged over 10 model runs. We used the 10% cumulative
logistic threshold to define a binary response of suitable or non-suitable. We calculated areas of suitability for five ecological regions 1) the Southern Rockies 2) The Middle Rockies 3) The Pacific Northwest 4) Vancouver Island and 5) The Northern Range, Figure 2. Cartography and spatial comparisons were performed in ArcGIS10.3.

Fire Records

Fire data in the United States were sourced from the Monitoring Trends in Burn Severity (MTBS) National Burn Area Boundaries data from 1984-2013 (MTBS Data Access 2015). This is a standardized dataset of all wildfires >400 hectares in the Western U.S. maintained by the United States Forest Service. MTBS data are in the form of polygon shape files that include internal heterogeneity of the wildfire severity at a fine-scale (30m) resolution (MTBS Data Access 2015), though the accuracy of the internal severity mapping varies and is contested (Kolden et al., 2015).

We used the most comprehensive fire database available for Canada, the Canadian Wildland Fire Information System (CWFIS) Data Mart (CWFIS 2013). There are inconstancies between the methods and metrics of the CWFIS dataset in comparison to MTBS (Whitman et al., 2015). For the field sampling we only identified a single “burn” site within Canada, using the methods described below. For reasons of data quality and sample size, we omitted the single Canada record in our field study analysis to allow for accurate comparisons among paired sites. We did use both the MTBS and CWFIS dataset for all fires 1984-2013 (>400 ha) to inform our Fire and Climate Predictive Spatial Analysis, to model the synergistic impact of climate and wildfire on the overall range of *S. austromontana*.

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Determining Field Sites

We designed a field study to investigate the impact of wildfire on the persistence and abundance of historical populations of *S. austromontana*. To select sites for fieldwork we used ArcGIS 10.3 to run an intersect between MTBS fire perimeters (polygons) and herbarium records (points), pinpointing localities where fires mapped from 1984-2013 in the U.S. (MTBS Data Access 2015) had burned over previous herbarium collection records. Our analysis revealed 30 total potential “burn” sites in the western U.S. where historical populations of *S. austromontana* may have been impacted by fire since last collection.

Each burn site was paired *a priori* with an “unburned” site exhibiting similar environmental conditions and collection histories, to isolate the effect of wildfire on the abundance and presence/absence of *S. austromontana* by controlling alternative variables. We paired burn sites with unburned sites that were in close proximity geographically (+/- 50km), in the same mountain range, at similar elevations (+/- 500m), found at similar aspects, and in comparable habitats (i.e. ridge tops, summits, streamside cliff faces). We further considered the history and quality of the historical herbarium records, specifically pairing sites with comparable collection dates and georeference confidence, Table 1. Every site was paired to at least one other site, and in a few cases two, if suitable sites were available.

Field Observations and Collections

During the summer of 2015, 57 historical herbaria record locations were revisited for a total of 24 paired burned and unburned sites across the range of *S. austromontana*, including 7
sites in New Mexico, 21 in Colorado, 6 in Idaho, 4 in Wyoming, 12 in Montana, and 5 in Washington, Figure 3. We visited all possible burn sites identified by our GIS analysis except for three in Montana that were inaccessible due to past or present fires (two in the Bob Marshall Wilderness and one near Eureka).

At each site (burned and unburned) we travelled to the exact coordinates listed on the herbarium record, and conducted a 1-hour time-based search for evidence of the species within a 500m radius. If *S. austromontana* was present, we located the population center, defined as the highest density of plants within a 5-meter radius. Individuals were defined as plants that were not connected to the same cushion mat and did not share roots. At the population center we recorded abundance in a 5-meter radius, GPS coordinates, habitat description, vegetative community, geologic substrate, aspect, elevation, phenology, search time, and other notes. We also made observations of fire evidence (burned vegetation, scorched rocks, etc.) and took soil samples. Soil samples were collected at 1 and 2 cm depths at the population center, 5 meters north, and 5 meters south, and subsequently analyzed in the lab for the presence or absence of macro-charcoal following previously established methods (Welch, 1999; Hart & Buchanan, 2012; Horn & Underwood, 2014). At each site, we collected 1-3 voucher specimens for curation at the Pacific Northwest Herbarium (WWB), and DNA samples from 1-10 individuals for use in future phylogenetic analysis. If we did not find any plants within the 1-hour search-time, we recorded *S. austromontana* as absent, abundance as zero, and collected all relevant site details at the original coordinate provided by the herbarium record.
Computational Analyses

We performed a series of multiple linear regression analyses in R ver. 3.1.2 (R Project for Statistical Computing, 2015) and the lme4 package (Bates, Maechler & Bolker, 2012) to identify the factors that had the greatest predictive power on the abundance of *S. austromontana*. We ran a Poisson generalized repeated-measures linear mixed-effect regression model (GLMER) on the abundance count data to satisfy the assumption of normality. Paired sites were considered as a single random repeating factor; for example, site TWA1 (burned) and TWA2 (unburned) were both classified as site 1. We tested abundance of *S. austromontana* (\(y\)) as a function of wildfire treatment (\(\beta_1 x\)) classified binomially as burned or unburned, elevation (\(\beta_2 x\)), and year since collection (\(\beta_3 x\)), using the following equation (\(y = \beta_0 + \beta_1 x + \beta_2 x + \beta_3 x + (1|\text{site})\)) across the entire data set (n=55, 23 pairs), and only using locations where *S. austromontana* was present, omitting all sites without a population detected (n=41, 16-burn, 25-unburned). A second analysis was run to determine if wildfire treatment (burn/unburned) increased the likelihood of extirpation of *S. austromontana*. We used a similar model as in the previous analysis using the entire dataset (n=55, 23 pairs), treating the response (\(y\)) as binomial Presence/Absence (0,1). The predict function was employed to determine the likelihood of extirpation in burn and unburned sites.

A final set of analyses was run using only the burn data set (n=27) to test for the effect of fire on population abundance. First, a linear regression was run to determine if “year since fire” accurately predicted the abundance of *S. austromontana*. Year since fire values ranged from 2-21. Second, we tested abundance (\(y\)) as a function of Fire Severity, using the MTBS severity scale from 0-6; where 0=outside fire perimeter, 1=Low to Unburned, 2=Low, 3=Moderate, 4=High, 5=Increased Greenness, and 6=Inside Burn Perimeter yet No Severity Data Available.
We only included burn sites with an MTBS score between 1-4 (n=24), although we did observe fire evidence at three sites with the rating of 6. The MTBS classified severity product is notoriously limited in its utility and consistency among sites (Kolden et al., 2015), so we interpreted these results with caution.

For all analyses, visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. P-values were obtained by Analysis of Variance (ANOVA) likelihood ratio tests of the full model with the effect in question against the model without the effect in question. We compared Akaike’s Information Criterion (AIC) values between full and reduced models to determine the most accurate and parsimonious model.

Fire and Climate Predictive Spatial Analysis

We used the results of the SDMs, MTBS and CWFIS perimeter data, and existing fire predictions in WNA to build models that predict how wildfire may compound the impact of climate change on the future distribution of S. austromontana. Assuming fire will conservatively double by 2050 in WNA (Spracklen et al., 2009; Yue et al., 2013), we calculated a total area within the future distribution of S. austromontana that will likely burn by 2050; considering the 43% post-fire extirpation rate observed in the field, we estimate the area of future suitable habitat that will be “lost due to fire” (Area Burned x 0.43). The area lost due to fire is subtracted from the total area of “maintained” habitat in the 2050 SDM, and is not spatially explicit.

To estimate a total area of suitable habitat “lost due to fire”, we first dissolved the MTBS and CWFIS perimeter datasets into a single polygon feature for fires within a 30-year timeframe (1984-2013), similar to methods described by Whitman (2015). We did not account for areas that experienced re-burn, although this is certainly an important topic and warrants further
investigation. Any extent that was burned was counted once. Next, we clipped the dissolved MTBS and CWFIS dataset to the area of future suitable habitat (2050s) in each ecoregion, to quantify the amount of future habitat that already has been burned (reference area burned). Next we made the conservative estimate that area burned will remain the same for the time centered around the 2020’s (1x reference area burned). Then, assuming area burned will double by the 2050s, we calculated area burned for that time-period as 2x reference area burned. To consider the compounding effect of fire, we added area-burned for each time-period (reference, 2020s, and 2050s) for a total “future area burned” that was four times the reference area burned. This value was then multiplied by the 43% extirpation rate observed for *S. austromontana* post-fire, to determine the final value of habitat “lost due to fire” to be subtracted from the total area of maintained habitat in 2050 SDM, Table 3. We combined this value with habitat “lost due to climate” to predict the compounding impact of climate change and fire on the future distribution of *S. austromontana*, Table 3.

Both fire and climate predicative models make tremendous assumptions, and are not true forecasts. Fire predictive models are in their infancy, and it is exceptionally challenging to predict future fire behavior across a large landscape due to changes in vegetation, impact of re-burn, human influence, ignition sources, topography and more (Littell et al., 2010; Higuera et al., 2015; Whitman et al., 2015). The fire predictions we used (Spracklen et al., 2009; Yue et al., 2013), are at a much coarser resolution than our models and were not intended to inform biogeographic spatial analyses. Further, our models do not explicitly account for fire severity, an important variable when considering future fire impacts. Interestingly, as fire frequency increases, the severity of future fires, especially reburns, may decrease by the end of the century (Parks et al., 2016). Thus, we attempt a low-resolution, somewhat qualitative, approach to
estimate the combined influence of climate change and wildfire on the future distribution of *S. austromontana*. That said, we err on the side of caution and make a rather conservative estimate, best-case scenario, given we assume area burned for the 2020’s will match the reference period, rather than increase. Further, fires at high elevation may become more common (Schumacher & Bugmann, 2006), and the total area burned in future suitable habitat could increase more than projected in our models.

**Results**

*Species Distribution Models*

The findings of our SDM support our hypothesis to Q1, indicating a substantial decrease in suitable habitat due to climate alone. The SDM for the reference period (1960-1990) predicts 659,292 km² of suitable habitat for *S. austromontana*, while the SDM for 2050, under the A1B climate scenario, predicts 409,548 km² of suitable habitat, indicating a range-wide reduction of 37.88% by 2050, Figure 4 and Table 3. All ecoregions, aside from the Northern Range will lose >58% by 2050, Table 3. The greatest net reductions will occur in the Southern Rockies, the PNW, and Vancouver Island, which all stand to lose upwards of 65-80% of suitable habitat by 2050. Additional suitable habitat will potentially become available at the northern end of the species’ range. Our MAXENT models are statistically valid through interpretation of the area under the receiver operating curve (AUC >0.85), calculated using 10-fold cross validation. AUC is a generally accepted metric for model evaluation (Merow et al., 2013), although its utility is contested (Lobo et al., 2008).
Charcoal Analysis

Most burn sites exhibited evidence of recent wildfire, through the presence of macro-charcoal in the topsoil. Soil samples were taken at 25 burn sites and 24 unburned sites. Burn sites are defined as sites within MTBS fire perimeters 1984-2013. Macro-charcoal was present at 84% of all burn sites: 72% of 1 cm samples and 76% of all 2 cm samples contained charcoal >2 mm. Macro-charcoal was present at 8.6% of 1 cm samples and 26% of 2 cm samples in unburned sites, indicative of historic fires likely prior to 1984.

Population Comparisons

We tested the effect of wildfire treatment and alternative factors (elevation and year since collection) on the presence/absence and abundance of *S. austromontana*. The results support our hypothesis to Q2, that wildfire significantly increased the likelihood of complete extirpation of *S. austromontana* (*p*=0.0016), Figure 5. The likelihood of extirpation of a historical population in an unburned site is 7.4%. The likelihood of extirpation in a burn site is 42.8%. Thus extirpation is 5.8 times more likely in a burned versus unburned population.

The treatment (burned/unburned) significantly affected the abundance of *S. austromontana* (*p*<<0.001), and removal of the treatment factor greatly increased the AIC score compared to the full model, Figure 6, supporting our hypothesis to Q3. *Saxifraga austromontana* is 3.5x more abundant in unburned (mean = 52.5, standard error = 6.0) versus burned (mean = 15.1, standard error =6.0) sites, when considering the entire dataset (n=55, 23 pairs). When only observing locations where *S. austromontana* was present (n=41, 16-burn, 25-unburned), we still found the abundance significantly lower (*p*=0.005) in burned (27.37, standard error = 8.0) versus unburned (56.92, standard error = 6.4) populations. Collection year (*p*=0.59) and elevation
(p=0.88) had no significant effect on the abundance of *S. austromontana*. Other variables including collection year and elevation were not predictors of population presence or abundance.

There was no clear observed relationship between ‘year since fire’ and abundance ($r^2=0.045$, $p=0.61$), Figure 7, or presence/absence ($r^2=0.007$, $p=0.70$). These findings do not support our hypothesis to Q4, where we expected to see increased abundance as year since fire increased, potentially due to post fire recolonization. There is tremendous site to site variation in response to fire, indicative of a stochastic response to wildfire rather than a clear time-series trend.

Fire Severity as recorded by MTBS did not predict the abundance or presence/absence of *S. austromontana*. No extirpation occurred in Low to Unburned severity wildfires; whereas any fire recorded by MTBS (Low-High) resulted in many complete extirpations of historical populations. Likewise, ‘Elevation’ and ‘Collection year’ failed to predict abundance within the burn data set only ($p>0.05$).

*Fire and Climate Predictive Spatial Analysis*

Our fire predictive models forecast that the overall range of *S. austromontana* will be further reduced from 659,292 km\(^2\) to 378,665 km\(^2\) by the 2050’s when both climate and wildfire are considered. This is a 42.56% reduction in suitable habitat, compared to a 37.88% reduction when climate is considered alone. The impact of fire varied greatly among ecoregions (Table 3; Figure 4). Combined, climate change and wildfire will reduce the future suitable habitat of *S. austromontana* by >70% for all ecoregions, except the Northern Range (Table 3; Figure 4). The greatest compounding effect of wildfire is in the Middle Rockies, which on top of a 56% reduction in suitable habitat due to climate alone, may lose an additional 15.6% to fire, resulting
in an 71% reduction overall. Per our methods, wildfire did not have much of a compounding impact on the Southern Rockies, the Northern Range, or Vancouver Island. Estimates of area burned for Canada made using the CWFIS dataset may understate the true impact of fire, due to missing fire data.

**Discussion**

Our results provide further evidence that high-elevation plant species may lose the majority of their range by the end of the century under moderate climate change predictions (Dirnböck et al., 2011; Dullinger et al., 2012; Forester et al., 2013). What is less clear is how indirect effects such as increased wildfire frequency will compound the direct effects of climate change for alpine taxa. Ours findings suggest that *S. austromontana* will lose 37.88% of its habitat due to climate and an additional 5% due to wildfire, under a moderate emission scenario and a conservative forecast of increased area burned centered on the 2050s. The compounding impact of fire is regionally specific, with the largest effect detected in the Middle Rockies that stands to lose an additional 15.6% of habitat due to fire, resulting in a 71% reduction overall. Other regions are relatively unaffected by fire. Unlike slow climatic changes that can take decades to centuries, disturbance events can act rapidly (Littell et al., 2010) expediting the extermination of alpine plant populations.

*Direct Effects of Climate Change*

*Saxifraga austromontana* stands to lose most of its suitable habitat by 2050. The results of the SDM analyses support our initial hypothesis to Q1, suggesting that suitable habitat for *S. austromontana* will greatly decline due to direct changes in climate alone.
Changes in suitable habitat differ greatly across ecoregions, yet all ecoregions other than the
Northern Range may lose most suitable habitat by 2050 (>58%) under the conservative A1B
emission scenario, Table 3. The greatest reductions (>75%) are observed in Vancouver Island
and the Southern Rockies. Effectively the alpine of the western United States and southern
British Columbia will shrink dramatically, and many populations, forced upwards, risk being
pushed off the summits resulting in local extirpation. As the climate envelope of \textit{S.}
austromontana becomes increasingly reduced, populations become more isolated into smaller
and more fragmented patches, limiting their resiliency to survive or recolonize post-disturbance.

\textit{Saxifraga austromontana} is currently found across most of the Rocky Mountain Floristic
Region, but that is likely to change soon. In future climate scenarios, the suitability in the
northern portion of the species’ range is either maintained or increased. The predictions for \textit{S.}
austromontana mirror those of other cold adapted species: as climate continues to warm,
populations will migrate northwards (Forester et al., 2013). Although suitable habitat is
theoretically gained in the north, the availability of climatically suitable habitat, especially
outside of a species’ known range, does not guarantee colonization or establishment (Zhu et al.,
2012). Range expansion is limited by the dispersal ability of the species and competition among
other species (Case et al., 2000). North of 55 degrees’ latitude, the observed niche of \textit{S.}
austromontana is primarily replaced by its sister species, \textit{S. tricuspidata} Rottb. Northward
migration may be impeded by a limitation of space and resources already used by other species
that occupy similar niches. Further, our models do not take topography into account. Upward
expansion in the Rocky Mountains may be limited by topographic constraints or substrate
(Malanson et al., 2007). Our results bolster the concept that, based solely on direct changes in
climatic conditions, alpine species face tremendous habitat loss over the coming century (Dirnböck et al., 2011; Dullinger et al., 2012; Forester et al., 2013; Jackson et al., 2015).

Effect of Wildfire

The results of our field study support the hypotheses that *S. austromontana* is not well adapted to wildfire, and should be classified as a fire avoider by definition (Agee, 1993). Extirpation of historical populations is greatly increased in burned versus unburned sites. Out of a total of 27 unburned sites, we failed to relocate only two historical populations of *S. austromontana*; one of which was at the southern edge of its distribution (Intermountain Herbarium #99901), possibly indicating that the southern-most range is already becoming unsuitable climatically. In contrast, when visiting burn sites, *S. austromontana* was absent 42.8% of the time. Further, abundance is lower in sites that have burned. Under the current fire regime, populations are experiencing partial to full extirpation, and as fire frequency increases (Spracklen et al., 2009; Yue et al., 2013), it will likely worsen.

The role of MFRI is critically important to understanding the full effect of fire on high-elevation ecosystems. A historically long MFRI (300+ years) likely facilitated slow colonization and establishment of alpine communities. Our results do not support our hypothesis of re-colonization or regrowth up to 21 years post-fire. We found no statistical pattern that abundance increases post-fire, although we did observe a weak positive relationship between abundance and year since fire (Figure 7). The power of our linear regression model may be limited by sample size and a relatively short time-interval. There is clearly lots of site-to-site variability, indicating that some locations fare better than others in maintaining populations post-fire. We observed certain sites to essentially contain “fire refugia,” where populations persisted on steep rocky cliff
faces or near streams that were more often spared by the mosaic nature of fire. Furthermore, colonization of *S. austromontana*, may experience a lag effect. Further information on the natural history of this species is needed.

Colonization or regrowth of burned sites clearly occurs, as we found evidence of charcoal at 2cm depths at one quarter of the unburned sites, indicative of older fires. The age of the charcoal is unknown, and carbon-14 dating is beyond the scope of this study. Deposition of soil at high elevation sites varies, yet typically occurs very slowly. Alpine communities could take centuries to recover post-fire (Baker, 2009). Future work could use carbon dating to reconstruct the wildfire history and investigate the response of high elevation cushion plants to wildfire at incrementally older burn sites, as 21 years is a small fraction of the predicted MFRI of these ecosystems (Baker, 2009).

*Compounding Impacts of Climate and Fire*

Large and uncharacteristic wildfires are expected to increase across North America (Dennison et al., 2014). The largest increases in area burned are projected across the entire Rocky Mountain and the Pacific Northwest region (Spracklen et al., 2009; Yue et al., 2013), which encompass much of the habitat for *S. austromontana*. Our results indicate that increases in fire frequency compounded with direct climatic changes will intensify local extinctions of *S. austromontana*, and possibly other fire-avoider taxa with similar growth habits. Following the conservative estimate that area burned will double by 2050, wildfire could reduce suitable habitat for the 2050s by an additional 5% across the range, on top of a projected 37.88% reduction based on direct climate variables alone (Table 3; Figure 4).
Fire does not impact the entire range of *S. austromontana* equally (Table 3; Figure 4). The Middle Rockies, which includes the Greater Yellowstone Ecosystem (GYE), is the most highly impacted by wildfire. From 1984-2013, nearly a quarter of classified suitable habitat for *S. austromontana* burned. The results of our Fire and Climate Predictive Models indicate that the Middle Rockies could lose an additional 15.6% of its range due to fire by 2050, resulting in a total reduction of 71%. This is especially interesting, because typically habitat loss due to climate occurs at the periphery, either the latitudinal or elevational boundary of the range, not in the core of the distribution. The response to indirect effects is much more stochastic than direct effects. Climate is relatively predictable on a spatial scale, while fire is not. A fire event could completely miss a population, or by chance, wipe out the entire population. Furthermore, humans have much more control over wildfire prevention, mitigation, and suppression than we do over climate, making these core regions a valuable focus of conservation efforts.

The MFRI for the GYE may decrease from 100-300 years down to 30 years by the end of the century, which will dramatically alter the plant and animal communities of the region (Westerling et al., 2011). We did not observe a pattern of re-colonization of *S. austromontana* up to 21 years post wildfire. If in fact the MFRI of the region is reduced to 30 years, wildfire will certainly drive increased habitat reduction for this species and many others. In the time-frame of the MTBS wildfire dataset (1984-2013), the Middle Rockies experienced many large fire events including the 1988 fires in Yellowstone (Turner et al., 1994; O’Leary et al., 2016), which certainly impacted our results.

Habitat loss is of special concern in the Southern Rockies, due to their unique biogeographic history and high degree of endemism. The high elevations of the Southern Rockies harbor the greatest diversity of endemic flowering plants in the RMFR (Fowler et al.,
2014), with at least 38 alpine taxa found nowhere else. Initial phylogenetic analyses by our lab indicate that *S. austromontana* likely originated in the Southern Rockies, and then through a series of dispersal and isolation events diversified into the entire *Saxifraga* sect. *Bronchiales* clade (DeChaine et al. 2013; DeChaine 2014). The Southern Rockies are disjunct from other ranges by the relatively flat Wyoming Basin to the north, making long distance dispersal in current and future climates very difficult. As habitat patches decrease in size and become increasingly fragmented, the Southern Rockies may experience many local extinctions over the coming decades. Because of the Southern Rockies’ geographic location and topographic limitations for upslope migration, we predict >75% reduction of suitable habitat for *S. austromontana* by 2050, primarily driven by climate. Thus, for this species and a host of endemic alpine taxa, the flora of the Southern Rockies is critically important yet gravely imperiled.

For a high elevation forb, *S. austromontana* has a relatively large distribution across WNA and occupies a range of elevations from high subalpine to alpine. Expansion and maintenance of suitable habitat in the Northern Range provides a climate and fire refuge for this species. Highly fragmented, small populations may be at the greatest risk of extinction by wildfire as there are no nearby populations to recolonize. More geographically restricted and rare taxa, such as the Tobias’ Saxifrage (*Saxifraga bryophora var. tobias*), discussed previously, may be at even greater risk of population or even species level extinction under the combined influence of fire and climate by mid-century. Rising temperatures and increased wildfire frequency is not negative for all species. Many flowering plants and conifers will benefit from longer growing seasons and wildfire at high elevation, yet the overall composition of
communities will shift (Westerling et al., 2011). During our field study, we observed more
generalist species such as *Ribes spp.* and *Sedum lanceolatum* colonizing recent burns.

Subalpine species may outcompete alpine taxa and eventually, a new “more generalist”
community may replace many existing high elevation ecosystems. A decreased MFRI could
prevent re-colonization of slower growing species, and favor early successional species. Our
findings suggest that a long fire rotation is required for establishment and maintenance of *S.
austromontana*, and similar to Whitebark Pine (Loehman et al., 2011), a highly reduced MFRI
could be detrimental. As disturbances increase and populations become more fragmented, re-
colonization will become increasingly challenging. Future climate conditions may also determine
the speed of recovery of alpine communities post-wildfire. Recovery may be more rapid if there
is adequate moisture and snowpack in the subsequent decades, and may be very long (centuries)
if warmer, drier decades occur (Baker, 2009). Together, climate and disturbance regimes will
determine future alpine community composition.

*Model Limitations and Future Work*

Models can serve as important tools to prioritize conservation efforts. We take the first
pioneering steps to forecast the combined direct and indirect effects of climate change on a high
elevation forb. This is the first study of its kind for non-forested vegetation, and merits future
investigations. We focused on a single species, and although the response of *S. austromontana*
may be representative of other taxa, future studies should investigate multiple alpine species to
gain a community level understanding of the direct and indirect effects of climate change.

It is impossible to accurately predict when, where, and at what scale wildfires will occur.
Modeling future wildfire activity is extremely challenging (Higuera et al., 2015), and the wide
range of predictions are the result of varying degrees in fire prediction schemes, model sensitivity to changing greenhouse gases, and the choice of climate change scenarios. Further, wildfire is only partially driven by climate (Littell et al., 2010; Higuera et al., 2015). Area burned cannot increase indefinitely, and is limited by the finite amount of fuels available. More mechanistic models of wildfire behavior that take into account fuels, vegetative response, weather, climate, and topography are needed to fully understand the role of fire in particular ecosystems (Littell et al., 2010). We use the best available predictions (Spracklen et al., 2009; Yue et al., 2013), and make broad inferences to highlight the need for future, more complex spatial models that integrate wildfire predictions and SDMs.

Both SDMs and fire predictive models are limited by the resolution of the input data available and the assumptions they make regarding future climatic conditions. As these models improve, they will become increasingly more useful for management applications. Further, our research uses the moderate A1B emission scenario (Nakicenovic & Swart, 2000). Less conservative emission scenarios will predict greater impacts of climate change than presented here (Bloom et al. 2016, Chapter 2).

Mountain environments are highly complex topographically (Coop et al., 2010; Dobrowski, 2011). They contain myriad micro-habitats, that we are only beginning to understand ecologically (Dobrowski, 2011; Jackson et al., 2015; Serra-Diaz et al., 2015). Slope, aspect, elevation, geologic substrate, cold-air drainages, and other variables create localized climates (Scherrer & Körner, 2011), influencing both fire behavior (Baker, 2009) and species distributions. Due to the complexity of *S. autromontana*’s habitat, micro-refugia will persist, and downslope migration may be possible (Crimmins et al., 2011). We observed tremendous site-to-site variation in response to fire. Many populations of *S. austromontana* were spared from the
effect of wildfire because they persisted on steep rocky terrain, or on moist cliffs bordering mountain streams or lakes that did not burn even in fire-affected sites. Identifying refugia for mosaic disturbances, such as wildfire, is especially challenging (Keppel et al., 2012) and warrants extensive further investigation. There is an increasing need for higher resolution data to build more informative disturbance and Species Distribution models in complex spatial and temporal landscapes.

Conclusions

Global climate is changing, and species must adapt to rapid transformations or risk extinction. *Saxifraga austromontana* may serve as an appropriate indicator species for the alpine in WNA, foreshadowing the response of a greater community of high elevation taxa that must cope with both direct climate variation and increases in fire frequency. Many lower elevation, subalpine species are well adapted to fire (Agee, 1993; Coop et al., 2010), and may move into high elevation niches both as temperatures warm, and fire disturbance events increase in frequency. Fire adapted species may gain an increased advantage over fire avoiders, and the diversity of plants may even increase but with the loss of alpine natives. We reveal that the Middle Rockies, the core of *S. austromontana*’s distribution, may experience significant range reduction when indirect effects are considered. Typically, reduction occurs at the periphery of the distribution, not the core, indicative that indirect effects such as fire are essential to understanding range shifts for high elevation species in WNA. Furthermore, managers may have greater control over indirect effects such as wildfire mitigation than over direct climate changes, providing an opportunity for valuable targeted conservation efforts in regions of great
importance. Ultimately, when considering the synergistic impact of climate change and wildfire, the fate of certain high elevation species is likely worse than previously predicted.
Tables and Figures

Table 1: Georeferencing methods for determining the spatial resolution of herbaria records using the SAGA approach, described in detail in Bloom et al. 2016 (Chapter 2). We used records with a confidence of 1-3 for both the field experiment and SDMs.

<table>
<thead>
<tr>
<th>SAGA Rank</th>
<th>GPS</th>
<th>Resolution (radius)</th>
<th>Example Descriptions</th>
<th>Example Accession #s</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Required</td>
<td>1-30m</td>
<td>Records with GPS + listed coordinate uncertainty.</td>
<td>WTU-VP-5827, RM-VP-740775</td>
</tr>
<tr>
<td>2</td>
<td>Sometimes</td>
<td>30-100m</td>
<td>Summits of peaks, fire lookouts, intersections of creeks or trails.</td>
<td>WTU-VP-185106, WTU-VP-90419</td>
</tr>
<tr>
<td>3</td>
<td>Sometimes</td>
<td>100-500m</td>
<td>Small lakes, mountain passes, small named meadows.</td>
<td>MONTU-VP-3979, WS-VP-101352</td>
</tr>
<tr>
<td>4</td>
<td>Often not</td>
<td>N/A</td>
<td>Large lakes, entire mountains or peaks, ridgelines, trail names.</td>
<td>MONTU-VP-27436, RM-VP-815188</td>
</tr>
<tr>
<td>5</td>
<td>Often not</td>
<td>N/A</td>
<td>Town names, county names, state names, mountain ranges.</td>
<td>MONT-VP-50930, MONT-VP-50961</td>
</tr>
</tbody>
</table>
Table 2: Climate variables selected for SDMs of *S. austromontana*, and percent contribution to MAXENT models. Climate data made available by ClimateNA for the reference period (1960-1990) and 2050 and 2080 future projections based on an ensemble of 23 CMIP3 AOGCMs for A1B emission scenario (Hamann et al., 2013).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Description</th>
<th>Contribution (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>AHM:</td>
<td>Annual heat moisture index, calculated as ((\text{MAT}+10)/(\text{MAP}/1000))</td>
<td>5</td>
</tr>
<tr>
<td>bFFP:</td>
<td>The Julian date on which the frost-free period begins</td>
<td>26.3</td>
</tr>
<tr>
<td>cmiJJA:</td>
<td>Hogg's summer (Jun to Aug) climate moisture index</td>
<td>19.7</td>
</tr>
<tr>
<td>MCMT:</td>
<td>Mean temperature of the coldest month (^\circ\text{C})</td>
<td>9.3</td>
</tr>
<tr>
<td>MWMT:</td>
<td>Mean temperature of the warmest month (^\circ\text{C})</td>
<td>19.2</td>
</tr>
<tr>
<td>PAS:</td>
<td>Precipitation as snow (mm)</td>
<td>9.6</td>
</tr>
<tr>
<td>TD:</td>
<td>Difference between MCMT and MWMT, as a measure of continentality (^\circ\text{C})</td>
<td>11.0</td>
</tr>
</tbody>
</table>
Table 3: Results of Species Distribution and Fire Predictive Models for *Saxifraga austromontana* for the Reference Period (1960-1990) and the 2050s (average conditions for 2041-2070). We calculated Maintained, Lost, and Gained suitable habitat for five ecological regions: 1) the U.S. Middle Rockies (Middle); 2) the Southern Rockies (Southern); 3) The Pacific Northwest (PNW); 4) the Northern Range (Northern); and 5) Vancouver Island (Van. I). Values are presented both as area of suitable habitat (Km²) and as a percent (%) of the Reference Period. We also predicted the area of future suitable habitat that may be lost due to wildfire. The indirect effect of wildfire will compound the direct impacts of climate change and further reduce suitable habitat for *S. austromontana* by an additional 4.8% across the entire range. The effect of fire, as with climate, varies greatly by region with the greatest impact in the Middle Rockies which may lose an additional 15.6% of suitable habitat due to increased area burned, on top of 58.39% lost due to climate alone resulting in an overall reduction of 73.98%. Species distribution models were built with MAXENT, and spatial analyses performed in ArcGIS10.3.

<table>
<thead>
<tr>
<th>Region</th>
<th>Reference Period</th>
<th>Maintained due to Climate (2050s)</th>
<th>Lost due to Climate (2050s)</th>
<th>Lost due to Fire (2050s)</th>
<th>Maintained due to Climate and Fire (2050s)</th>
<th>Lost due to Climate and Fire (2050s)</th>
<th>Total Area (2050s) Climate only</th>
<th>Total Area (2050s) Climate and Fire</th>
</tr>
</thead>
<tbody>
<tr>
<td>Middle</td>
<td>4791 km²</td>
<td>29.9%</td>
<td>0.7%</td>
<td>12.7%</td>
<td>40.9%</td>
<td>43.2%</td>
<td>37.8%</td>
<td>75.7%</td>
</tr>
<tr>
<td>Southern</td>
<td>10871 km²</td>
<td>25.9%</td>
<td>1.7%</td>
<td>12.3%</td>
<td>41.2%</td>
<td>42.7%</td>
<td>35.7%</td>
<td>71.4%</td>
</tr>
<tr>
<td>PNW</td>
<td>52175 km²</td>
<td>10.3%</td>
<td>0.1%</td>
<td>5.5%</td>
<td>15.8%</td>
<td>16.9%</td>
<td>13.3%</td>
<td>26.6%</td>
</tr>
<tr>
<td>Northern</td>
<td>377922 km²</td>
<td>6.3%</td>
<td>0.1%</td>
<td>5.5%</td>
<td>10.9%</td>
<td>12.0%</td>
<td>9.0%</td>
<td>18.0%</td>
</tr>
<tr>
<td>Van. I</td>
<td>659292 km²</td>
<td>5.0%</td>
<td>0.1%</td>
<td>5.5%</td>
<td>10.9%</td>
<td>12.0%</td>
<td>9.0%</td>
<td>18.0%</td>
</tr>
</tbody>
</table>

Values are presented both as area of suitable habitat (Km²) and as a percent (%) of the Reference Period.
**Figure 1:** *Saxifraga austromontana*, also known as the Spotted Saxifrage, is endemic to the Rocky Mountain Floristic Region, and exhibits typical alpine growth habits. Shown in flower near Longs Peak, Rocky Mountain National Park.
Figure 2: Ecological regions (ecoregions) used in this study: 1) the Northern Range (Northern) 2) Vancouver Island (Van. I.), 3) the Pacific Northwest (PNW), 4) the Middle Rockies (Middle) and 5) the Southern Rockies (Southern).
Figure 3: Overview of field study to test the response of *S. austromontana* to wildfire: a) the distribution of *S. austromontana* across WNA. In the field study, burned sites (black triangles) are paired with unburned sites (green circles), with similar alternative environmental variables. New collections are displayed as blue octagons. The inset map displays the MTBS fire severity b) unburned site, Willow Lake, CO c) burned site, Medano Pass, CO.
Figure 4: Species Distribution Model (SDM) for *Saxifraga austromontana*, displaying suitable habitat that is Maintained, Gained, Lost due to Climate, and Lost due to Fire by the 2050s (average conditions for 2041-2070 under the moderate A1B emission scenario) relative to the Reference Period (1960-1990), see Table 3 for all values. The Southern Rockies, the Pacific Northwest, and Vancouver Island stand to lose most of their suitable habitat by 2050, due to climate alone. The Middle Rockies could lose an additional 15.6% of suitable habitat due to fire by 2050, resulting in a total reduction of 71%. This is especially interesting, because typically habitat loss due to climate occurs at the periphery, either the latitudinal or elevational boundary of the range, not in the core of the distribution. The Northern Range maintains a large amount of suitable habitat, and is the only region with any notable potential gain. The initial SDM informed only by climate variables, was built using MAXENT and trained with seven selected climate variables (Table 2), and 1256 occurrence records georeferenced to a 1 km resolution (Table 1). Suitability is set at the 10-percentile training presence logistic threshold. The black polygons on the map are MTBS fire records within the Maintained 2050 habitat. We used these values to compute the area burned in these regions, and calculated a value of habitat lost due to fire by 2050, which was removed from the total Maintained value. Data are in a Lambert conformal conic equal area projection, and model resolution is 1 km².
Figure 5: The probability of finding a historical population of Saxifraga austromontana in paired unburned and burned sites. In the field, we recorded presence, and measurements of abundance if present, at 23 paired burned and unburned sites, based on historic occurrence records in herbarium collections, across the Rocky Mountains from New Mexico north through 6 states into central British Columbia, Canada. We found S. austromontana to be absent (or extirpated) at only 2 unburned populations, one being the southern-most record known in New Mexico, possibly an indication of direct climate effects. In contrast, S. austromontana was extirpated at 42.8% of all burned populations, supporting our premise that S. austromontana is not well adapted to fire.
Figure 6: Abundance as a function of wildfire, for *S. austromontana*, in 23-paired burned and unburned sites (p=2.3e⁻⁵). The chart displays the mean and standard error for the abundance across the treatment types, across the entire geographic range of the species. The mean abundance of *S. austromontana* was measured as the number of plants within a five-meter radius at the population center. Abundance is significantly lower in sites that were recently burned (15.1) in comparison to sites without a recent history of wildfire (52.5), although there is much site to site variability.
Figure 7: Abundance plotted as a function of year since wildfire, for burned sites only. The low $r^2$ suggests that year since fire does not accurately predict abundance, likely due to a relatively short time-series of available data and large variability among sites. This data does not support our initial hypothesis that abundance would increase as a function of year since fire. There is great site to site variability, indicative of the mosaic nature of fire and diverse topographic variation of the mountain sites, potentially indicative of microsite fire refugia.
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