A SPATIOTEMPORAL ANALYSIS OF CLIMATE CHANGE IN THE GREATER YELLOWSTONE ECOSYSTEM AND ITS EFFECTS ON *PINUS ALBICAULIS*

by

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of

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DEDICATION

I dedicate this to my parents who endured the hardships of immigration to provide an opportunity for their son to accomplish more than he even thought possible for himself.

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ABSTRACT

Climate change is arguably the biggest challenge facing humanity. Successful mitigation and adaption planning vitally requires more science in regard to its impacts on ecological systems. To address knowledge gaps regarding climate change impacts within the regional level, I performed a series of analyses on an "early responder" species in the Greater Yellowstone Ecosystem and examine how its distribution may be impacted by biotic and abiotic factors. My research aids in decision making processes for regional land managers that must address climate change in their policy decisions and increases ecological understanding at a landscape level.

This manuscript includes a detailed analysis of past, present, and projected climate in the Greater Yellowstone Ecosystem. I addressed the expected impacts of present and future climate shifts on the distribution of the sub-alpine tree species, whitebark pine (*Pinus albicaulis*) and its main disturbance agent, mountain pine beetle (*Dendroctonus ponderosae*). This research found a major reduction of suitable climate habitat for *P.albicaulis* within the Greater Yellowstone Ecosystem under multiple Global Circulation Models and Representative Concentration Pathway futures. Finally, this research determined that the recent *D.ponderosae* outbreak driven by climate effects in 2000-2010, that resulted in an unprecedented mortality event on *P.albicaulis* was more than double the risk area size of any previous outbreak since 1951. Although more studies are necessary to reduce uncertainty and make assertive recommendations for management actions, this research suggests that future sub-alpine stand structure and composition may be radically different than anything in recent history due to range shifts of suitable climate habitat and disturbance agents, and advocates for land managers to apply a multifaceted approach of competitor thinning and controlled burning to ensure the resilience and persistence of *P.albicaulis*.

PREFACE

This dissertation is presented in a journal manuscript format, consisting of four chapters that have or will be submitted for publication in scientific journals. Therefore, there is some redundancy between chapters. It is noted that the term Greater Yellowstone Ecosystem (GYE) and Greater Yellowstone Area (GYA) appear several times in this dissertation and are used synonymously.

INTRODUCTION

In 1957, G. Evelyn Hutchinson introduced the concepts of the realized and fundamental niches, which helped set the framework for landscape ecology and species distribution modeling. Hutchinson provided the idea that one could expect to find a particular species in a location given a number of environmental characteristics in that location, or as he described "the n-dimensional hypervolume" of ecological factors [3]. These environmental factors can exert direct or indirect effects on species, but can generally reflect three main types of influences on the species as defined by Guisan and Thuiller [2]: (1) limiting conditions, defined as factors controlling species eco-physiology such as abiotic factors associated to climate and soil (e.g. temperature, precipitation, soil composition); (2) disturbances, defined as all types of perturbations affecting environmental systems (e.g., fire, insects and disease, logging); and (3) resources, defined as all local nutrients that can be consumed and assimilated by the species (e.g., chemical nutrients and water). The fundamental niche defines the full range of climate conditions and food resources that permits the individuals in a species to live permitted by their anatomy and physiology. The realized niche, represents the actual range of habitats that species can occupy as a result of competition with other species for available resources and stochastic processes such as dispersal and disturbance. The spatial patterns that result from interactions between organisms and the environment can change as one observes from different scales in a hierarchical manner [6]. For instance, a potential distribution of a species observed over a large extent and at a coarse resolution is likely to be controlled by climatic regulators. One would expect a continental scale analysis to find continuous stretches of rainforest

palm trees at the equator and conifer species towards the higher latitude regions. At a more local area, analyses at fine resolutions are more likely to result in a patchy distribution of resources, driven by micro-topographic variation or habitat fragmentation and thus a patchy distributions of the species of interest. Given this understanding, one would expect that changing environmental factors that involve climate at a global or regional scale to have a profound impact on species distributions.

In the past 30 years, emissions of carbon have increased the Earth's carbon concentration above 400 ppm, which exceeds levels observed in the last 20 million years [1]. At the global scale, the climate change resulting from elevated CO_2 levels are expected to cause sea level rise, reduce sea ice, and cause shifts in ecosystem composition and structure. At the regional scales, there are projected to be a variety of impacts, with the Southwest US expecting to see more drought, greater potential for extreme weather in the Southeast, and drier and hotter conditions in the Pacific Northwest [5]. These changing precipitation patterns and increasing temperatures are likely to be major determinants of changes of plant species' distributions. Within the Greater Yellowstone Ecosystem, temperatures have risen in the last 40 years and changes have occurred in water availability, with less snowpack in mid-elevations and increases in precipitation in the form of rain rather than snow [7]. These changes may already had a profound effect on the high elevation species, whose ecology are adapted to a very specific climate regime, thus suggesting evidence of the first manifestations of climate impact on our ecological system [4].

Whitebark pine, *Pinus albicaulis*, is one particular species that has experienced a drastic impact in its distribution due to gradually shifting climate conditions. The unprecedented mortality to *P.albicaulis* from the thermally dependent mountain pine beetle, *Dendroctonus ponderosae*, has raised awareness of a potential "early responder" species to climate change. This body of research examines the climate

change in the Greater Yellowstone Ecosystem through a species distribution model approach for *P.albicaulis* and the disturbance agent, *D.ponderosae*.

Chapter 2 is an analysis of historical and projected climate change in the Greater Yellowstone Ecosystem that was published in the non-peer reviewed science journal, Yellowstone Science in March 2015. It should be noted that this article was written with language (and units) for a non-science audience and may be inconsistent with the rest of the dissertation. I investigated the current available regional climate datasets and global circulation models that describe the area's past, present, and future trends. I also conduct a literature review that describes the current and expected changes within the system's ecosystems that are of concern to local stakeholders.

Chapter 3 describes the patterns and variability of projected bioclimate habitat for *P.albicaulis* in the Greater Yellowstone Ecosystem under different climate models, and was published in *PLoS ONE* in 2014. The study focuses on improving past *P.albicaulis* distribution models by using a regional scale design, expansive local datasets, inclusion of high resolution climate and dynamic water balance variables, and selective projection under the latest AR5 General Circulation Models (GCMs). The results of this study report spatially explicit suitable climate habitat projections for *P.albicaulis* for 2010-2099 across nine different GCMs and two Representative Concentration Pathways, to better assist land resource managers in strategizing restoration plans for keeping whitebark pine in the system.

Chapter 4 is an application of a predictive model approach to reconstruct past *D.ponderosae* outbreaks within the Greater Yellowstone Ecosystem to be submitted for publication in the coming months. This chapter reconstructs historic *D.ponderosae* host tree probabilities of mortality within the GYE using a predictive model approach based on outputs from mechanistic equations of *D.ponderosae* physiology to identify and compare previous outbreaks with the current 2000-2010 *D.ponderosae*

outbreak. This analysis provides quantification of a disturbance event associated with recent climate change on the sub-alpine ecosystem and provides measures of spatial extent/severity that have ramifications for future disturbance and forest structure.

Conclusions are drawn in Ch. 5. I summarize the utility of this body of work and make recommendations to land managers and stakeholders on what can be done in regards to the loss of a dominant tree species in the Greater Yellowstone Ecosystem. I also outline next steps that need to be considered to address uncertainty in these models.

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HISTORIC AND PROJECTED CLIMATE CHANGE IN THE GREATER YELLOWSTONE ECOSYSTEM

Contribution of Authors and Co-Authors

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Contributions: Helped conceive the study design. Provided feedback on early drafts of the manuscript and contributed text in discussion section.

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Introduction

Evidence of the Earth's shifting climate patterns has become more perceptible from sea and surface temperature monitoring, satellite technology, and improvements in climate modeling. At a relevant human scale, these changes are highlighted by recent hurricane events, glacial retreat, and droughts at new, unprecedented frequencies and magnitudes that have begun to reshape the landscapes. Within the Greater Yellowstone Ecosystem (GYE), regional managers and citizens have already experienced major disturbance events that have changed the system's ecology, such as increased mountain pine beetle attacks, wildfire events, and reduced annual snowpack. The fifth annual Intergovernmental Panel for Climate Change (IPCC) and the latest U.S. National Climate Assessment report a decadal global temperature increase of 1-1.2^{o}F and a continuing upward trend. From paleoclimate records of the GYE, changing climate has occurred before due to the natural variability of the Earth's position relative to the sun. The last major warm period occurred during the late Pleistocene and early Holocene (12,000-8,000 years ago), when the world saw the end of the last glacial maximum. The first major vegetation to move in was Engelmann spruce, followed by subalpine fir and whitebark pine, creating a widespread subalpine forest across the region. As conditions grew warmer and glaciers reached their minimum (9,500-7,500 years ago), the region became characterized by drier and warmer conditions than present day. At this period, lodgepole pine and Douglas-fir moved in from southern landscapes, pushing sub-alpine species to higher elevations [19]. Around 5,000 years ago, temperatures dropped and precipitation increased, converging towards the climate we recognize the GYE as having today.

Methods

Greater Yellowstone Ecosystem is a complex and fascinating region to study climate. The GYE encompasses approximately 58,000 square miles with an elevational gradient from 1,713-13,800 ft. representing 14 mountain ranges. Due to the complex mountain topography and steep elevational gradients, weather is highly variable across the region, allowing events where specific mountain ranges can encounter snowfall in one area while another experiences warm, clear skies. The region is home to some of the longest running records of temperature and precipitation anywhere in the U.S., with some weather stations initiated in 1895. Interest in snow science and variability across these mountain landscapes led to the installation of 92 active SNOwpack TELemetry (SNOTEL) stations across the GYE. SNOTEL stations are automated climate and snowpack sensors distributed across sites within the western U.S. and operated by the Natural Resource Conservation Service. These sites provide scientists with some of the highest density records of long-term weather data of anywhere in the U.S. Although weather stations provide excellent information regarding their local site, scientists often need to know what the weather was like at higher elevation sites, in shaded valleys, or places different from where the weather stations are established. We draw on two separate data sets called the Parameter-elevation Relationships on Independent Slopes Model (PRISM) [3], and Topography Weather (TopoWx) [10] to characterize past climate for the GYE. PRISM and TopoWx use mathematical equations based on the relationship between weather and elevation, aspect, and other factors to estimate the temperature and precipitation that occurred in locations without weather stations. The result is a weather data set of temperature and precipitation every month since 1895 (PRISM) and 1948 (TopoWx) for every 800 m square (grid) in the continental U.S. We use

these data to calculate the mean annual temperatures and precipitation since the earliest available period in the GYE. Using these two gridded climate data sets, we are able to utilize their individual strengths and summarize climate for sub-areas of interest within the GYE.

Results

How Has Climate Changed Within the GYE

Since 1948, annual temperatures across the GYE have averaged slightly above 39°F (Fig 2.1) with an annual precipitation averaging 21.4 in/year (Fig 2.2). Current trends indicate annual temperatures have increased by 0.31^{o}F/decade, echoing the increasing temperature changes seen globally. Similarly, mean annual minimum and maximum temperatures have been increasing at the same rate of 0.3^{o}F/decade for the GYE (Table 2.1). At a sub-regional level, we considered the temperature and precipitation averages and rates of change from 1948 to 2010, for the following areas (Fig 2.3):

1. Yellowstone and Grand Teton national parks (YELL/GRTE)
2. Absaroka/Beartooth/N. Absaroka Wilderness Area (NA/ABT WA)
3. Washakie/Teton Wilderness Area (WA/TE WA)
4. Bridger/Fitzpatrick/Popo Agie Wilderness Area (BR/FI/PO WA)

Analysis at the sub-regional level reveal high variability across the entire GYE, with a general tendency for warming in the high elevation northern ranges of the Absaroka/Beartooth and Northern Absaroka wildernesses (0.39^{o}F/decade) compared to the southern Wind River Range wildernesses (0.28^{o}F/decade). Yellowstone and Grand Teton national parks as a whole followed a similar trend of warming to the

entire GYE of $\sim$0.3^{o}F per decade (Fig. 2.4, Table 2.1). It should be noted that considering smaller areas of interest within the GYE possess more challenges. When we consider small regions, there is a reduction of actual stations from which the algorithms for TopoWx and PRISM can utilize to fill in the unknown areas, so there is increased uncertainty regarding sub-regional analyses, despite these data sets representing our best estimates of climate change. To overcome such uncertainty, local field observations from stream gauge and weather stations can verify some of the warming trends, and describe potential microsite conditions the ecological system may be responding to [15]. One example of this is the observed temperature changes influencing stream flow and temperature over the past century. Stream discharge has declined during 1950-2010 in 89% of streams analyzed in the Central Rocky Mountains, including those in the GYE [6]. Reduced flows were most pronounced during the summer months, especially in the Yellowstone River. Stream temperatures have also changed across the range of the Yellowstone, observing a warming of 1.8^{o}F over the past century [1]. This stream warming during the 2000s exceeded that of the Great Dust Bowl of the 1930s and represents the greatest rate of change over the past century. Continued warming could have major implications to the management and preservation of the many aquatic resources we have today.

The Projected Climate of the GYE

General Circulation Models (GCM), or global climate models, have been in development since the mid-1950s and are currently our best method of understanding and predicting the impacts of humans and natural variability on the Earth. Originally produced to computationally investigate weather patterns, rapid advances in computing allowed physics-based modeling of atmospheric patterns on the entire Earth. As computer processing speeds increased, higher modeling resolution and increased levels

of complexity were able to create models with the levels of sophistication that exist today. However, despite the differences of past and present GCM complexity, they all model the same underlying general principles of motion and laws of thermodynamics that have been understood for centuries. Today, climate models simulate not only the atmosphere but also surface and deep ocean dynamics. When ocean and atmosphere models are linked together, we refer to the GCM as "coupled", which result in a more realistic simulation of our planet's climate. Determination of "realism" for GCM tend to be quantified in their ability to accurately predict the movement and evolution of disturbances, such as frontal systems and tropical cyclones. Common recognizable metrics include the ability to detect the El Niño Southern Oscillations and Pacific Decadal Oscillation. As more institutions began climate system modeling, questions regarding the impact of increased carbon emissions on temperature became prevalent. To address these questions, climate modelers generate scenarios of future potential atmospheric/ocean chemical compositions and investigate the impacts they have on the Earth's climate. In 2013, the IPCC released the most recent projections of future climate under scenarios of greenhouse gas emissions [2]. Some 46 global climate models were used to project climate under four Representative Concentration Pathways (RCP). RCPs are designed to characterize feasible alternative futures of the climate considering physical, demographic, economic, and social changes to the environment and atmosphere. Here we report results from two scenarios for an analysis of the GYE: RCP 4.5, which assumes stabilization in atmospheric CO_2 concentration at 560 ppm by 2100; and RCP 8.5, which assumes increases in atmospheric CO_2 concentration to 1370 ppm by 2100. Actual measured rates of greenhouse gas emissions since 2000 have been consistent with the RCP 8.5 scenario [4, 13]. Thrasher et al. [16] downscaled these GCM outputs to an 800-m pixel size so regional level analysis could be possible. For this GYE summary, we referenced the

Rupp et al. [14] analysis of GCMs that best represents the Pacific Northwest region. Within the GYE, mean annual temperature is projected to rise under each of the climate scenarios. By 2100, temperature is projected to increase 6-13°F above the average for the reference period of 1900-2010 (Fig. 2.5a). Mean annual precipitation is projected to vary between 2-4 inches by 2100 (Fig. 2.5b). While temperature is projected to rise at similar rates across seasons, precipitation increases most rapidly in spring and decreases slightly in summer. Changes in aridity are projected to increase moderately under RCP 4.5 and more substantially under RCP 8.5. This suggests the current climate changing pattern we have experienced for the last 30 years will likely continue and become more severe.

Discussion

Current & Projected Impacts on Ecosystems

A consequence of warming during the winter and spring months and seasonally high summer aridity has been an outbreak of forest pests causing forest die-off. Mild winter temperatures in alpine regions have been found to directly relate to the survivorship of overwintering broods of mountain pine beetle, the major disturbance agent acting on whitebark pine species [7, 8]. Arid summers (high temperatures, low precipitation) likely provide a compounding effect of increasing pine beetle development rates and increasing resource stress on whitebark pine. This reduction in mortality of overwintering broods,increased development rates, and reduced tree defense can result in an expansion of the dispersal and colonization effectiveness of insect pests. Since 1999, an eruption of mountain pine beetle events has been observed that exceed the frequencies, impacts, and ranges documented during the last 125 years [9, 12]. Aerial assessment of whitebark pine species populations within the GYE has indicated a 79% mortality rate of mature trees. These dramatic changes

may be the first indicators of how GYE vegetation communities are to shift due to changed climate patterns. Projected changes in climate are expected to continue to influence ecosystem processes, such as soil moisture, runoff in streams and rivers, and terrestrial net primary productivity through shifts in vegetative communities. The projected warming results in April 1 snowpack declining 3.2-4.3 inches by 2100. The reduction in snowpack is most pronounced in spring and summer, with the GYE projected to be largely snow free on April 1 by 2075 under RCP 8.5. Average annual soil water projections show considerable inter-annual variability, but have a shallow positive trend, increasing about 0.4 inches by 2100 with increases mostly in spring and a slight decline in summer. Mean annual runoff increases more rapidly, with pronounced increases in spring and decreases in summer. The projected pattern for gross primary productivity also increases annually in spring and decreases in summer. Stream temperatures are projected to increase between 1.4-3.2^{o}F by 2050 to 2069 [1]. Yellowstone cutthroat trout are projected to decline by 26% in response to this temperature increase due to its positive influence on nonnative species [17]. In uplands, warming temperatures are projected to result in severe wildfires becoming more common within the GYE [18], which could result in major changes in vegetation type and seral stage. One way to gauge potential effects of projected climate change on vegetation is to determine the climate conditions within which a vegetation type currently occurs and map locations projected to be within this range of climate conditions in the future. While dispersal limitations, competition from other species, disturbances, etc., may prevent vegetation from establishing in areas with newly suitable climates, this method is a meaningful way to interpret climate from a vegetation perspective. Piekielek et al. [11] projected suitable climatic conditions to decrease for the subalpine conifer forest and alpine tundra biome types and increase largely for Great Basin montane scrub biome type and slightly increase

for montane conifers such as Douglas-fir [5]. If vegetation changes in parallel with these climates, these results suggest snowpack, runoff, and net primary productivity would be substantially reduced.

A New Status Quo

These results indicate climate has and will continue to change substantially. Our summary of projected climate suggests the future will experience temperatures higher than any time in the warm periods of the Holocene. This rapid temperature change can result in substantial reductions in snowpack and stream runoff and increases in stream temperature, fire frequency, and mortality of currently dominant tree species. One possible future is for the system to move into a new state with little summer snow, very low stream flows, frequent and severe fire, and switch from forest-dominated vegetation to desert scrub vegetation. Such changes will challenge resource managers in the effort to ensure the health and integrity of this complex natural system while still providing the recreational experiences the public has come to expect. Strategies for adaptation and mitigation in natural resource management should be considered given the magnitude of potential future ecosystem impacts.

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Tables and Figures

	GYE	**YELL/GRTE**	**NA/ABT WA**	**WA/TE WA**	**BR/FI/PO WA**
T_{mean} average (^oF	37.8	34.1	33.5	33.3	32.0
T_{max} average (^oF)	49.4	45.7	42.7	43.5	42.6
T_{min} average (^oF)	26.1	22.4	24.3	23.1	21.4
Ppt average (in)	24.8	34.8	34.5	34.1	31.3
T_{mean} trend ($^oF/decade$)	0.31	0.29	0.39	0.31	0.28
Ppt trend ($in/decade$)	0.19	0.32	0.19	0.38	0.09

Table 2.1: Summary of the regional and sub-regional mean climate conditions and median rates of change using the TopoWx data set for temperature and PRISM data set for precipitation 1948-2010

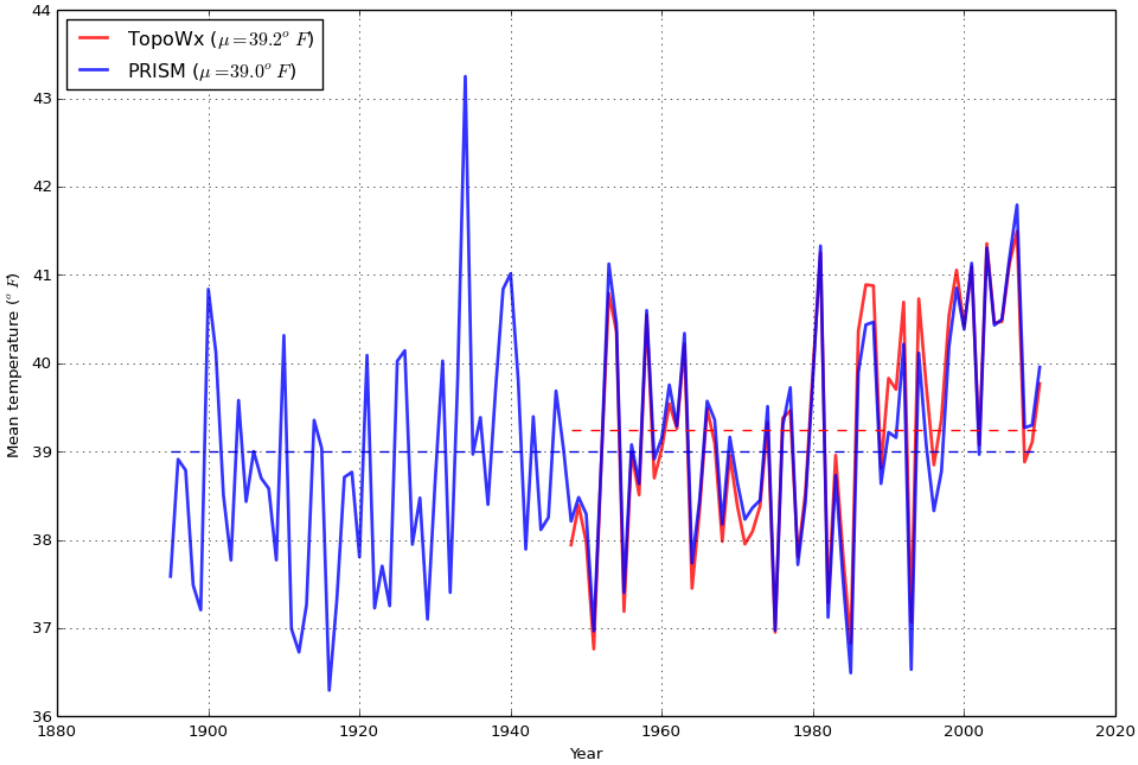

Figure 2.1: Mean annual temperatures averaged across the entire GYE for the past century. Dashed lines indicate the average since 1895-2010 (blue) and since 1948-2010 (red), using the PRISM and TopoWx gridded climate data sets respectively

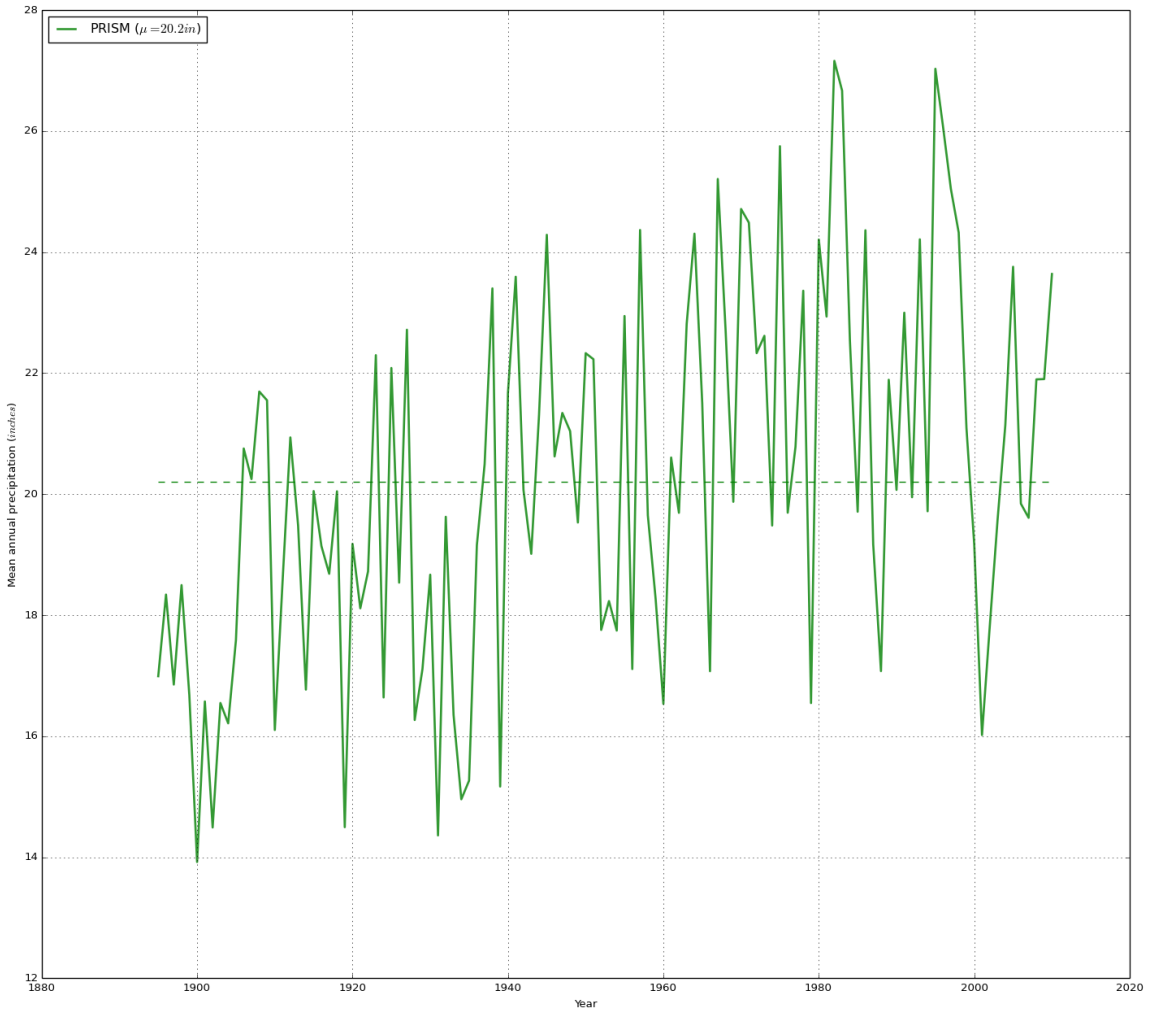

Figure 2.2: Mean annual precipitation averaged across the entire GYE for the past century. Dashed lines indicate the average since 1895-2010 using the PRISM gridded climate data sets. Data indicate a slight increase in precipitation over the past century at the rate of 0.4/in century

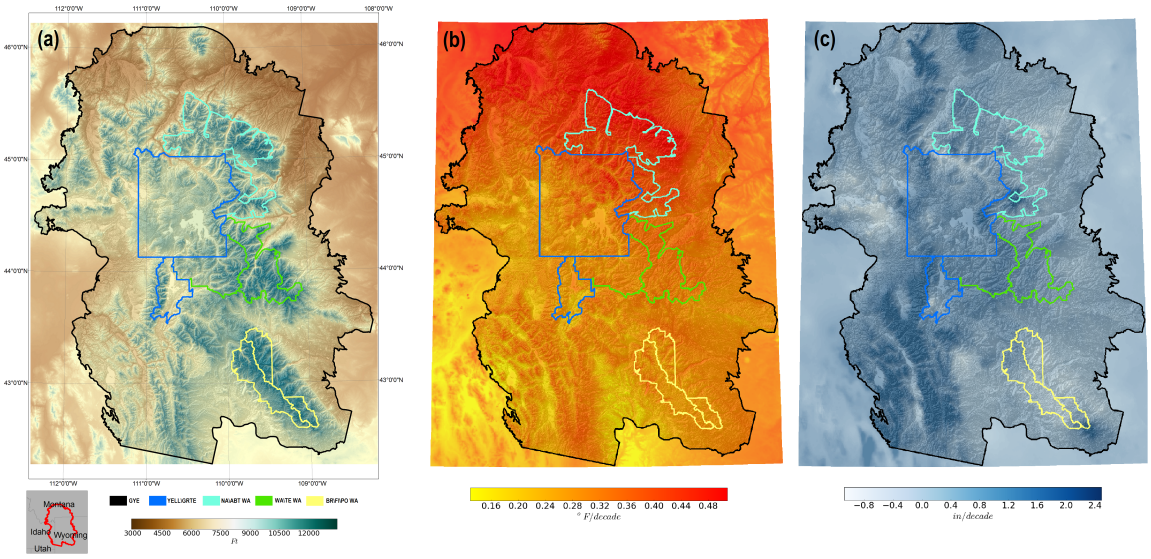

Figure 2.3: The Greater Yellowstone Ecosystem (58,186 square miles) and the surrounding wilderness and national park sub-regions for historic climate analysis: (a) illustrates the complex elevation gradient within the GYE region ranging from 3,000-13,800 ft, (b) TopoWx rate of change of mean annual temperatures between 1948-2010 within the GYE and sub-regions, and (c) PRISM rate of change of mean annual precipitation between 1948-2010 within the GYE and sub-regional areas

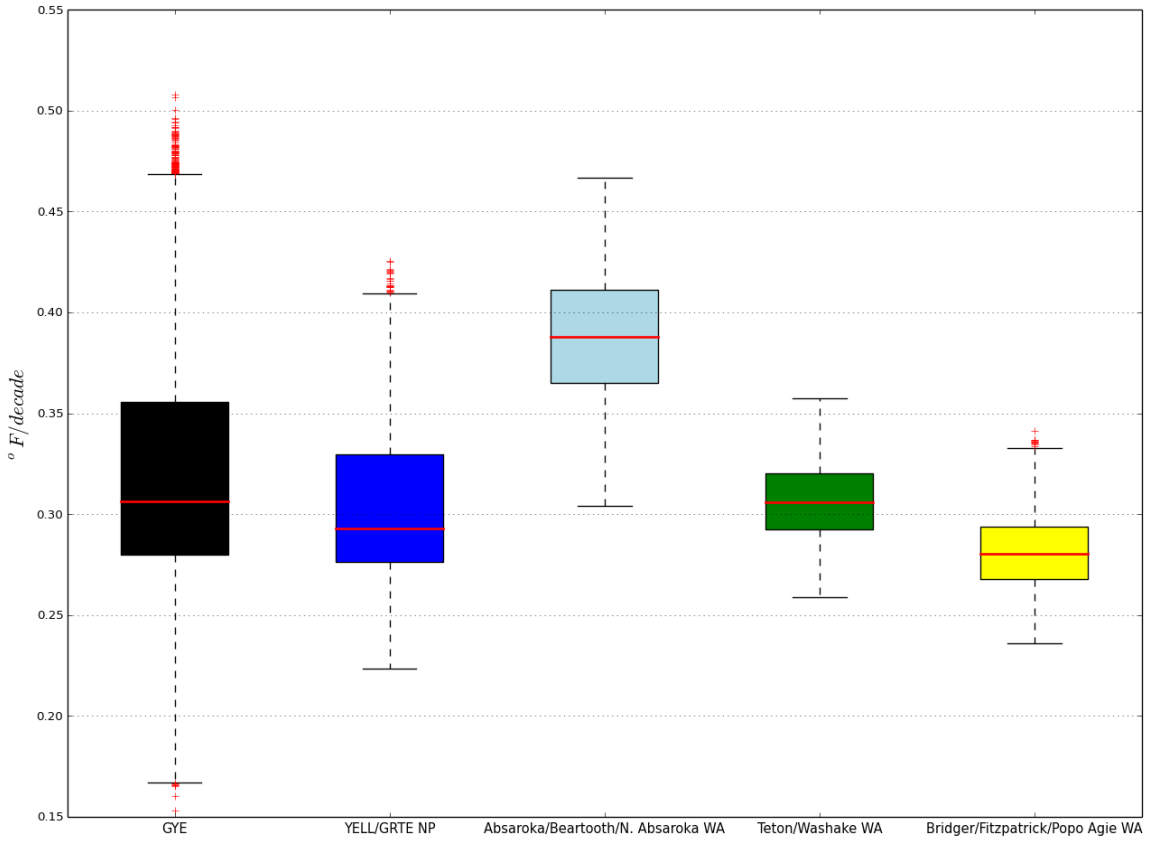

Figure 2.4: Box and whisker plots of warming trends across the GYE and 4 sub-regions. Northern range wilderness areas depict the greatest level of warming over 1948-2010 compared to the southern wilderness areas of the Wind River range

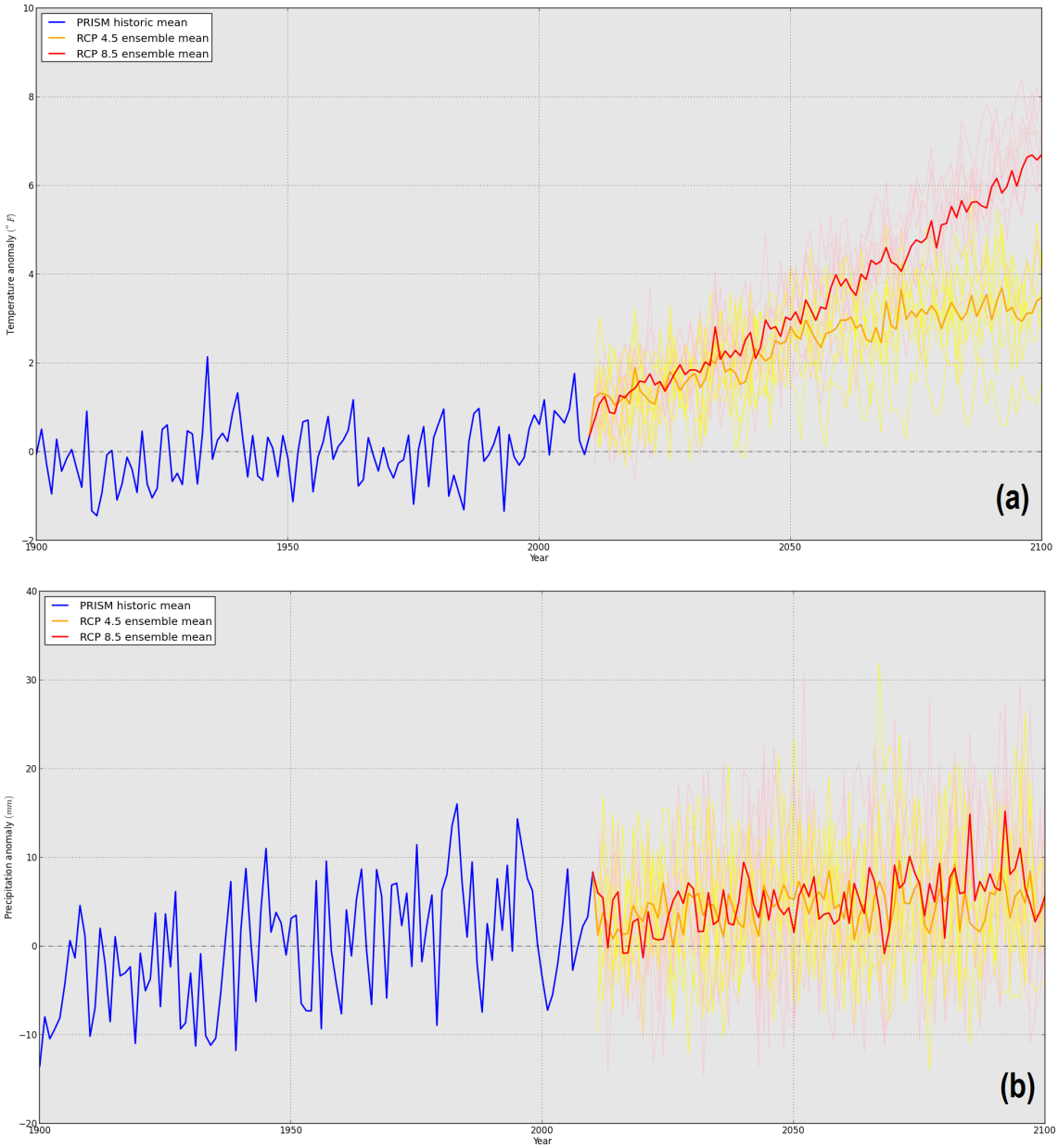

Figure 2.5: GYE projections from ensemble GCMs of the Coupled Model Intercomparision Project 5 (CMIP5), the latest set of models from the IPCC Fifth Assessment Report, from 2010 to 2099 (a) mean annual temperatures, and (b) mean annual precipitation anomaly from long-term average

PATTERNS AND VARIABILITY OF PROJECTED BIOCLIMATIC HABITAT FOR *PINUS ALBICAULIS* IN THE GREATER YELLOWSTONE AREA

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: Tony Chang

Contributions: Conceived and implemented the study design. Collected and analyzed data. Wrote and edited the manuscript.

Co-Author: Andrew J. Hansen

Contributions: Helped conceive the study design and analysis. Provided research funding and support throughout study.

Co-Author: Nathan Piekielek

Contributions: Assisted in Forest Inventory and Analysis data allocation and provided support in water balance model conception.

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Abstract

Projected climate change at a regional level is expected to shift vegetation habitat distributions over the next century. For the sub-alpine species whitebark pine (*Pinus albicaulis*), warming temperatures may indirectly result in loss of suitable bioclimatic habitat, reducing its distribution within its historic range. This research focuses on understanding the patterns of spatiotemporal variability for future projected *P.albicaulis* suitable habitat in the Greater Yellowstone Area (GYA) through a bioclimatic envelope approach. Since intermodel variability from General Circulation Models (GCMs) lead to differing predictions regarding the magnitude and direction of modeled suitable habitat area, nine bias-corrected statistically down-scaled GCMs were utilized to understand the uncertainty associated with modeled projections. *P.albicaulis* was modeled using a Random Forests algorithm for the 1980-2010 climate period and showed strong presence/absence separations by summer maximum temperatures and springtime snowpack. Patterns of projected habitat change by the end of the century suggested a constant decrease in suitable climate area from the 2010 baseline for both Representative Concentration Pathways (RCPs) 8.5 and 4.5 climate forcing scenarios. Percent suitable climate area estimates ranged from 2-29% and 0.04-10% by 2099 for RCP 8.5 and 4.5 respectively. Habitat projections between GCMs displayed a decrease of variability over the 2010-2099 time period related to consistent warming above the 1910-2010 temperature normal after 2070 for all GCMs. A decreasing pattern of projected *P.albicaulis* suitable habitat area change was consistent across GCMs, despite strong differences in magnitude. Future ecological research in species distribution modeling should consider a full suite of GCM projections in the analysis to reduce extreme range contraction/expansion predictions. The results suggest that restoration strageties such as planting of seedlings and

controlling competing vegetation may be necessary to maintain *P.albicaulis* in the GYA under the more extreme future climate scenarios.

Introduction

Over the next century, it is expected that most of North America will experience climate changes related to increased concentrations of anthropogenic greenhouse gas emissions and natural variability [31]. At regional scales these changes are highly variable and can result in areas of increased mesic, xeric, or even hydric habitat conditions relative to present day. These shifting climates in turn also transform the suitable habitat for individual species that may result in changes in species composition and dominant vegetation types.

Whitebark pine (*Pinus albicaulis*) is a native conifer of the Western U.S. that is considered a keystone species in the sub-alpine environment. It provides a food source for animals such as the grizzly bear (*Ursus arctos*), red squirrel (*Tamiasciurus hudsonicus*), and Clark's nutcracker (*Nucifraga columbiana*) [71]. It also serves the ecosystem functions of stabilizing soil, moderating snow melt and runoff, and facilitating establishment for other species [71, 12]. Whitebark pine has experienced a notable decline in the past two decades within the U.S. Northern Rockies due to high rates of infestation from the mountain pine beetle (*Dendroctonus ponderosae*) and infections from white pine blister rust (*Cronartium ribicola*), resulting in an 80% mortality rate within the adult population [44, 34, 42, 41]. Given the potential loss of important ecosystem functions that *P.albicaulis* contributes to the landscape under this mortality event, there is an emphasis to understand the climate characteristics of its habitat to identify the restoration strategies and locations that may aid the persistence of the species under future climates.

One method of understanding species response to climate change is through bioclimate niche modeling, which has become a common practice for assessing potential vegetation shifts under new environmental conditions [59, 58, 70, 32, 28, 11]. Ecological niche theory proposes there exists some range of bioclimatic conditions within which a species can persist [30]. In bioclimatic niche modeling, the realized niche is modeled by empirical relationships between the presence or absence of a species and the associated abiotic, and sometimes biotic, variables that describe the niche space. Bioclimatic models assume that species are in equilibrium with their environment and that the current abiotic relationships reflect a species' environmental preferences which may be retained into the future [4, 5]. At macro scales, bioclimatic approaches have demonstrated success at predicting current distributions of species [55, 79]. Most bioclimatic models do not explicitly consider the many additional ecological factors that ultimately influence a species distribution such as dispersal, disturbance, or biotic interaction. Thus the approach does not predict where a species will actually occur in the future, but rather it predicts locations where climatic conditions will be suitable for the species.

Bioclimatic niche methodology has demonstrated utility in modeling historic ranges of species for conservation and management applications. By modeling the present day suitable habitat and then projecting those habitats into the future, bioclimatic niche models can serve as the first step filter for conservation action plans, such as mapping suitable species reintroduction sites or habitat reserve selection [2, 21, 54]. For *P.albicaulis*, McLane and Aitken [48] utilized bioclimate niche models to successfully implement experimental assisted migration on persisting climate habitat in British Columbia. Additionally, models of *Pinus flexilis*, a closely related species of five needled pine, have been used to evaluate management options in Rocky Mountain National Park [49]. Given these examples, an effort to model and project

suitable climate habitat for *P.albicaulis* within a regional domain can provide valuable insight to land resource managers.

In this study, we present a bioclimatic habitat model for *P.albicaulis* within the Greater Yellowstone Area (GYA). Although *P.albicaulis* has a range-wide distribution that is split into two broad sections, one along Western North America: the British Columbia Coast Range, the Cascade Range, and the Sierra Nevada; and the other section in the Intermountain West that covers the Rocky Mountains from Wyoming to Alberta [3, 71]; the GYA was selected as the primary geographic modeling domain for three reasons: 1) evidence that the *P.albicaulis* sub-population in the GYA is genetically distinct from other regional populations with different climate tolerances [45]; 2) the high regional investment in *P.albicaulis* conservation in the area [42]; 3) the high density of climate stations within the region. Climate within the GYA is highly heterogenous due to complex topography, and sharp elevational gradients. Current knowledge of the region expects climate to shift towards increased mean annual temperatures and earlier spring snowmelt [56, 76]. This shift is expected to have an impact on the total suitable habitat area for *P.albicaulis*. Modeling at a regional scale can provide a finer resolution spatially explicit description of the bioclimatic envelope of *P.albicaulis* in the GYA.

Here we also present an opportunity to investigate the effect of future climate variability on projected species distributions. In 2013, the World Climate Research Programme Coupled Model released the new generation General Circulation Model (GCM) projections through the Coupled Model Intercomparison Project Phase 5 (CMIP5) [66]. These new GCM projections also include four possible climate futures are modeled with each GCM under the Representative Concentration Pathways (RCP) of greenhouse gas/aerosol. These RCP scenarios designate four different levels of radiative forcing (2.6, 4.5, 6.0 and 8.5 W/m^2) that may occur by the year 2099

[29]. In practice, research of future species suitable climate generally use a small suite of GCM/RCP combinations to project future climate [59, 43, 32]. However, internal variability in these GCMs that arise from modeled coupled interactions among the atmosphere, oceans, land, and cryosphere can result in atmospheric circulation fluctuations that are characteristic of a stochastic process [17]. Such intrinsic atmospheric circulation variations from model structure induce regional changes in air temperature and precipitation on the multi-decadal time scale [17]. For the GYA specifically, this GCM variability has be observed with mean annual temperatures projected to increase by $2 - 9$ ^{o}C and mean annual precipitation to change by -50 to +225 mm (Fig. 3.2). This suggests that the magnitude and direction of projected species distributions at a regional scale can vary depending on the GCM selected and the modeled species response to more xeric or mesic future climate conditions [7].

To summarize, this study presents a bioclimate niche model for *P.albicaulis* based on historic climate observations and field sampling of *P.albicaulis* presence and absence. Using this modeled bioclimate envelope, projections of future total climate suitable habitat area under nine GCMs and two RCP scenarios will be estimated. Since different GCMs may project a diverging spectrum of climates, it is expected that measures of total suitable habitat will reduce with varying degrees of area loss. It is also expect that number and size of continuous patches of *P.albicaulis* habitat will be reduced due to the limited available number of sub-alpine areas distributed within the landscape. This research provides an analysis of the variability of biotic response under a large suite of GCMs to provide managers/researchers with a measure of the uncertainty associated with future species distribution models. Furthermore, this analysis explicitly describes the spatial patterns of bioclimatic niches for *P.albicaulis* to gain a better understanding of topographic characteristics, such as elevation, on

suitable habitat. Changes in these spatial patterns are examined through quantifying landscape patch dynamics that may result from GCM projections to understand the species trends for persistence on the landscape.

Methods

Study area

The GYA, which includes Yellowstone National Park, Grand Teton National Park, and a number of state and federally managed forests, is a mid- to high-latitude region in the Northern Rocky Mountains of western North America. Conifers are dominant in the range, with forest types composed of *Pinus contorta*, *Abies lasiocarpa*, *Pseudotsuga menziesii*, *Pinus albicaulis*, *Juniperus scopulorum*, *Pinus flexilis* and *Picea engelmannii*, although the deciduous hardwood *Populus tremuloides*, is also widespread. Plateaus and lowlands are dominated by species of *Artemisia tridentata* and open grasslands of mixed composition. The GYA study area encompasses 150,700 km^2 with an elevational gradient from 522-4,206 m that represents 14 surrounding mountain ranges (Fig. 3.1).

Data

Biological data Field observations of *P.albicaulis* adult presences and absences were compiled from three data sources. First, 2,545 observations from the Forest Inventory and Analysis (FIA) program were assembled. FIA plots are located on a regular gridded sampling design with one plot at approximately every 2,500 forested hectares, with swapped and fuzzed exact plot locations within 1.6 km to protect privacy [63]. Gibson et al. [26] found that model accuracy to not be dramatically affected by data fuzzing, but to provide the most spatial accuracy, this study culled FIA field points where measured elevation were >300 m different from a 30 m USGS

DEM [25]. To capitalize on additional field observations of *P.albicaulis* within the study area, and because false absences are one of the most problematic data issues in constructing bioclimatic niche models [22]; supplementary points were drawn from the Whitebark/Limber Pine Information System (WLIS) [40], and long-term monitoring plots established by the National Park Service Greater Yellowstone Inventory and Monitoring Network (GYRN) [33]. The presences in these two additional datasets were collocated within predictor pixels of FIA absence to correct for false absences. In doing so, only one *P.albicaulis* presence or absence record was associated per predictor pixel, thereby avoiding issues associated with sampling bias that are common when building bioclimate niche models with data from targeted surveys [20]. This compilation of data represents an effort for "completeness" as described by Kadmon et al. [35] and Franklin [22], to capture all climate conditions where a species does exist. New data sources added 119 *P.albicaulis* presences that would have been missed by using FIA data alone, for a total of 938 presences and 1,633 absences.

Mature *P.albicaulis* were selected for modeling based on a recorded diameter at breast height (DBH) >20 cm. *P.albicaulis* within Central Montana are reported to reach 100 years of age at approximately 8-12 m in height with DBHs between 15-20 cm [74]. Given previous silvicultural studies, it was assumed that 20 cm DBH *P.albicaulis* represent adult class individuals for the GYA, with potential to reproduce [3]. Furthermore, this study focused on adult size class due to difficulties distinguishing younger age class *P.albicaulis* from *P.flexilis*.

Historic climate data Climate inputs for modeling were acquired from the 30-arc-second (∼800 m) monthly Parameter-elevation Regressions on Independent Slopes Model (PRISM), a derived product that interpolates local station measurements

across a continuous grid [16]. PRISM data include monthly average minimum temperatures (T_{min}), maximum temperature (T_{max}), mean temperature (T_{mean}), and mean precipitation (Ppt). All monthly data were averaged for the temporal extent of 1950-1980 for bioclimatic niche model fitting. The 1950-1980 temporal extent was selected for modeling since: 1) a sufficient density of weather stations were operating by 1950 to provide a reasonable network; 2) evidence of anthropogenic warming that begins in the late 1980s; 3) trees old enough to bear seeds today likely established under a similar climates to the 1950-1980 period.

Water balance A Thornthwaite-based dynamic water balance model was used to estimate a number of variables that include actual evapotranspiration (AET) and potential evapotranspiration (PET) [67, 68, 18]. The model requires only monthly mean temperatures, dew point temperatures, latitude, and precipitation (see Supporting Information). Water was stored as soil moisture or in surface snowpack, with the excess taking the form of evaporated vapor or loss through seepage/runoff. In addition to the climatic variables and physical characteristics of the soil were required to define water holding capacity. Soil attributes assigned by the Soil Survey Geographic (STATSGO) datasets were allocated from the Natural Resource Conservation Service at a 30-arc-second resolution to determine soil water holding capacity and estimated soil depth [53]. All water balance variables, which include PET, AET, soil moisture, vapor pressure deficit (VPD), and snow water equivalent (PACK), were averaged by month over 1950-1980 to match with historic climate data for bioclimate model fitting.

GCM data The general circulation model (GCM) experiments conducted under CMIP5 for the Intergovernmental Panel on Climate Change Fifth Assessment Report provided future projected climate data sets for assessing the effects of global climate

change. Using a Bias-Correction Spatial Disaggregation (BCSD) approach, an archive of statistically down-scaled CMIP5 climate projections for the conterminous United States at 30-arc-second spatial resolution was assembled by the NASA Center for Climate Simulation NEX-DCP30 [69]. For this analysis, a subset of the total GCM models available from NASA was selected that best represents the Northwestern US. Rupp et al. [61] recently presented an analysis of GCM performance versus the observed historic climate in the U.S. Pacific Northwest under 18 specified climate metrics. In their analysis, Rupp et al. ranked GCMs for accuracy using an empirical orthogonal function (EOF) analysis of the total normalized error compared to reference data. This analysis selected models with a normalized error score < 0.5 as a threshold to cull the full suite of GCMs to the top nine models. These GCMs were used to project modeled *P.albicaulis* distributions into the future (Table 3.1). Two RCP scenarios were selected to understand effects of differing carbon futures under climate change from 2010 to 2099. RCP 4.5 was the first, representing increased radiative forcing until stabilization of greenhouse emissions between 2040-2050 and total radiative forcing of 4.5 W/m^2 by 2099. RCP 8.5 was the second, representing the "business as usual" scenario, with uncontrolled radiative forcing increasing with stabilization of 8.5 W/m^2 by 2099 [24, 52].

Modeling methods

A Random Forest (RF) [10] algorithm was used to create a bioclimate niche model of *P.albicaulis* in the GYA. Random forest is an ensemble learning technique that generates independent random classification trees using a subset of the total predictor variables and classifies a bootstrap random subsample of the data. These trees are aggregated and a majority vote over all trees in the random forest defines the resulting response class. This method of random trees with subsampling ensures

a robust ensemble classification reducing overfitting and collinearity issues, especially with a large number of trees [60, 58, 38, 10]. The python programming language (Python 3.3) and the Scikit-Learn library was used to fit the random forest model and predict current habitat niche, with parameters for number of trees ($n_{estimators} = 1000$), number of variables ($max_{features} = 4$), and node size ($min_{samplesleaf} = 20$) [57].

First pass filtering of environmental covariates was performed using Principal Component Analysis (PCA) to generate proxy sets [19, 9, 64]. After the initial list was constructed, an additional filter was imposed on the variables with a 0.75 maximum correlation threshold to avoid collinearity issues (Fig. 3.3) [19]. Physiologically relevant variables for *P.albicaulis* presence were given precidence in final culling in cases of correlation above the specified maximum threshold. The final variable list selected was tmin1, vpd3, ppt4, pack4, tmax7, aet7, pet8, ppt9 (Table 3.2). The Software for Assisted Habitat Modeling (SAHM) was used to visualize correlations with the pairs function embeded in the VisTrails scientific workflow management system [23, 51].

Model evaluation was performed under a variety of methods. An out-of-bag (OOB) error estimate was calculated by comparing the modeled probability of presence using approximately two-thirds of the field data, while withholding a subset of the remainder. Accuracy was evaluated by calculating: 1) the sensitivity, representing the true positive rate (TPR), 2) the specificity, representing the true negative rate (TNR), 3) the area under the receiver operator characteristic curve (ROC AUC). The importance of a specific predictor variable was calculated by examination of the increase in prediction error within the OOB sample when the predictor variable was permuted while others were held constant [57, 39]. The rate of prediction error with permutation of a specified variable can be interpreted as the level of dependence of presence or absence response to that variable [15].

Projections for *P.albicaulis* were computed using 30 year moving climate averages for the period from 2010-2099 for both RCP 4.5 and 8.5 climate scenarios. Changes of suitable habitat area were determined using a binary classification of expected presence and absence. Binary class assignment was made under a probability of presence threshold where the ratio of sensitivity and specificity equalled 1. This method ensured an equal ability of the model to detect presence and absence. The Kappa and True Skill Statistic (TSS) were also calculated to observe how sensitivity and specificity responded under differing probability thresholds [1]. Survey plots predicted as suitable under climatic conditions in 2010 served as a reference for projections. The presence classifications were evaluated as the amount of suitable habitat changed over time, confined within specified elevational limits. To account for the need for a minimum patch size, total number of patches and median sizes using the an eight-neighbor rule for patch identification were tracked over time [72].

Results

Model evaluation

The random forest model displayed an out-of-bag (OOB) error rate of 16.1% with greater errors of commission (13.1%) than omission (10.9%) (Table 3.3). The AUC was 0.94, displaying high specificity and sensitivity (Fig. 4.4). The threshold probability of presence for a binary classification was selected at 0.421 (i.e where sensitivity = specificity). A probability threshold where TPR and TNR were equal was compared to the maximum Kappa statistic (0.538) and the maximum True Skill Statistic (TSS) (0.345) and found to be a compromise between the diagnostics (Fig. 3.5).

Estimates of variable importance plots revealed that permutation of maximum temperatures of summer months from all random trees resulted in a large drop in

mean accuracy for distinguishing presence and absence of *P.albicaulis* (0.706 decrease in mean accuracy). This was followed by spring time snowpack (0.137 decrease in mean accuracy) (Fig. 3.6). Histogram plots of July maximum temperatures and April snowpack provided evidence of discrimination for presence and absence that are consistent with the modeled probability of presence for the year of calibration (Fig. 3.7).

Spatially explicit probability plots for the 2010 climate displayed highest probability of presence values within the $\geq$ 2500 m mountain ranges of the GYA in agreement with studies employing aerial imagery and remote sensing [44, 34] (Fig. 3.8). Assuming that the modeled suitable bioclimate for *P.albicaulis* remains similar in the next century, the model demonstrated capacity to predict probable future *P.albicaulis* suitable habitat under projected climate conditions.

Model projections

Under both RCP 4.5 and 8.5, there was a predicted steady reduction of suitable bioclimate habitat for *P.albicaulis* over the course of this century, with RCP 8.5 displaying steeper declines than RCP 4.5 (Fig. 3.9). Under the RCP 4.5 and 8.5 scenarios, suitable habitat shifts from 100-85% to 2-29% by 2099, and 100-85% to 0.04-10% by 2099 respectively (Table 3.4).

CNRM-CM5, CMCC-CM, and CESM1-BGC projections showed the highest probabilities for suitable habitat area at the end of the century, while HadGEM2-AO, HadGEM2-ES, and HadGEM2-CC indicated the lowest probabilities. The standard deviations per year for both RCPs progressively decreased over time (Fig. 3.10). Among climate scenarios, standard deviations for both RCPs display low variability for the first five projection years and a rapid increase of variability peaking at 2043. For RCP 4.5, high variability existed primarily due to differing climate projections by

models HadGEM2-AO and HadGEM2-CC, resulting in uncertainties in probabilities of presence fluctuating between 8 and 15% until 2068, after which variability was between 6-8%. Under RCP 8.5, standard deviations between GCMs were consistently lower than RCP 4.5. Regardless of the GCM, by 2079 the areas of suitable habitat converged to similar values.

Spatially explicit mapping of probability surfaces presented similar contractions of *P.albicaulis* habitat suitability toward the upper elevation zones of the GYA that included the Beartooth Plateau and Wind River Ranges (Fig. 3.11). This implies that rapid warming may lead to conditions outside of the *P.albicaulis* niche in lower elevation areas, limiting the species to the alpine zones. Elevational analysis of cells within threshold presence probabilities over time estimated mean elevations of suitable bioclimates shifting from 2,875 to 3,218 m and 2,875 to 3,470 m for RCP 4.5 and 8.5 respectively. By 2099, ensemble averaged GCM projections displayed over 70% loss of habitat under both scenarios.

P.albicaulis patches from the 2010 baseline comprised 202 patches with median patch size of $\sim$180 km^2. Projected patch dynamics analysis denoted a quadratic relationship of patch size over time. Patch dynamics displayed a slow increase in number of *P.albicaulis* patches to a maximum at 2074 and 2057 for RCP 4.5 and 8.5 respectively, followed by a decreasing trend. RCP 4.5 patch numbers were more sporadic, displaying fluctuations across the time period compared to RCP 8.5 associated with the greater interannual climate variability amongst GCM models. Median patch size saw a steady decrease from 72-65 km^2 to 21-8 km^2 for RCP 4.5 and 8.5 respectively, for the projection period, suggesting habitat loss through fragmentation (Fig. 3.12).

Discussion

In this analysis, the spatiotemporal patterns for *P.albicaulis* distributions were assessed under nine climate models and two emissions scenarios. Bioclimate modeling of *P.albicaulis* illustrated that presence and absence were strongly separated by summer temperatures and spring snowpack. This was in agreement with empirical findings of *P.albicaulis* presence in cool summertime environments where July temperatures range between 4-18 ^{o}C [75]. Concordantly, these cool summer regions were synonymous with late snow melt, supporting snowpack as an important feature in distinguishing presence and absence.

Future projections by all nine GCMs suggested a contraction in suitable *P.albicaulis* climate area by the end of the century to <30% of current conditions. This was consistent with the results from various other research using either niche models or hybrid process models, predicting similar amounts of *P.albicaulis* contraction [59, 73, 58]. Variability among projected suitable habitat areas under differing GCMs decreased as all projected maximum temperatures increased above 1°C from the 100 year historic mean. This pattern of warming convergence occurred earlier for the GCMs under the RCP 8.5 scenario than those under RCP 4.5, resulting in the observed low variability of *P.albicaulis* suitable habitat area under RCP 8.5. Despite temperature variability remaining relatively constant amongst GCMs within a RCP, once mean annual temperatures increased beyond $\sim$1°C from the historic average, all bioclimatic habitat models exhibited a pattern of contracting total area and variability. These results lead to the conclusion that explicit selection of a GCM to model under may not matter for *P.albicaulis* bioclimatic niche modeling studies, especially if the direction of change is solely of concern. However, if investigation of the magnitude of change is relevant, then GCM selection may directly influence the

projected total suitable habitat area. This can be observed with RCP 4.5 habitat projection models differing by as much as 27% total suitable habitat area by the year 2099. Therefore arbitrary selection of a GCM for future projection modeling is likely inappropriate since it could lead to overly optimistic/pessimistic results for the species of concern.

Temporal patch dynamic analysis present an increase in fragmentation of the larger *P.albicaulis* suitable habitats over the next five decades, suggested through an increase in the total number of continuous patches but decreases in median size. This was followed by a contraction of small patches until they were almost absent from the system. Remaining habitat patches were smaller and less prevalent on the landscape by the end of the century. Reduced habitat patch size and density may reduce the likelihood for *N.columbiana* to disperse successful germinating seed caches, due to the limited size and area of suitable patch space. If changing climate habitats result in mortality within adult patches, genetic diversity may be lost resulting in a population bottleneck, thus reducing the robustness of the species to adapt to future disturbances. Experimental trials of P.albicaulis survival and fecundity under warmer and drier conditions outside the currently known range would provide greater confidence of the species ability to persist under future change. Limited analysis on seedling environmental conditions would also elucidate spatially explicit dispersal ranges and greater understanding of probable ranges for future establishment and survivorship.

Projected distributions of persistent *P.albicaulis* patches displayed a strong trend towards contraction into high elevation zones. Physiologically, there does not appear to be any upper elevation limit for *P.albicaulis* in the GYA. *P.albicaulis* in the region has been reported to survive in absolute temperatures as low as -36°C [75]. Lab experiments performed on *Pinus cembra*, a related five-needle pine residing in similar

climates, were able to endure cold temperature extremes as low at -70 ^{o}C without cellular tissue damage [62]. Considering the current absolute minimum temperatures the species resides in and the cold tolerance of its relatives suggests that *P.albicaulis* treeline in the GYA is not limited by lower temperatures. Controlled laboratory experimentation on *P.albicaulis* tolerances to temperatures would greatly improve this physiological understanding of cold tolerance.

Elevational habitat constriction do not imply that *P.albicaulis* will be completely gone from the region, but merely the loss of suitable climate habitat. Currently established adult age class individuals will likely persist, since projected conditions of increased temperatures and CO_2 concentrations physiologically indicate increased growth rates of *P.albicaulis* [14]. Furthermore, micro-refugia sites may exist in the GYA that support *P.albicaulis* survival into the future, but were failed to have been modeled due to the coarseness of 30-arc-second climate data resolution. Since this bioclimatic envelope modeling approach was parametrized by the realized niche from in-situ data, it was difficult to determine if lower elevation limits are driven by warmer climate conditions or competition for light, water, or nutrients [55, 4]. For example, lower treeline limits for *P.albicaulis* maybe driven primarily by competitive exclusion from late seral species *A.lasiocarpa* and *P.engelmannii*. This follows from paleoecological pollen records of competitor migration during the Early Holocene (9000-5000 yr B.P), when climate conditions were warmer and drier. Longer growing seasons allowing competitors to invade likely drove *P.albicaulis* communities +500 m in elevation [78, 77, 6]. If future climate conditions become analogous to this Early Holocene period, invasion of competitor species will likely contract *P.albicaulis* habitat to the limited high elevation zones of the GYA, specifically the Beartooth Plateau region and Wind River range [65].

Conclusion

This analysis examined the future of *P.albicaulis* suitable climate in the GYA and explicitly addressed the question of distribution variability under 9 representative GCMs and 2 emission scenarios. Increases in temperature within the GYA will likely result in a high level of contraction of suitable climate habitat for *P.albicaulis* over the next century. This contraction was consistent for all GCM projections, with approximately 20% uncertainty in total probable area. This analysis recommends that care be taken for species distribution modeling in future studies during the selection of GCMs due to their relevance for magnitudes of change. GCM ensemble averaging may be a solution to this issue, however it should be noted that averaging should take place after an individual GCM is projected in order to maintain interannual variability.

Although other studies have examined *P.albicaulis* species distribution models [8, 59, 73], this study is a step forward through its focus on relevant regional scale design, expansive local datasets, inclusion of high resolution climate and dynamic water balance variables, and selective projection under the latest AR5 GCMs. It is reiterated that the bioclimate niche model approach has high utility for understanding habitat conditions through correlative relationships with environmental variables, however, it may fail to explicitly model competitive exclusion, disturbance, phenotypic plasticity, and other complex interactions that are vital in determining a species' actual presence as it experiences changes in climate [37, 4, 27, 55]. These unmodeled factors create uncertainties suggesting that this modeling effort does not identify the full potential climatic range of *P.albicaulis* in the future. Uncertainties also exist regarding new suitable climates that may occur outside the current species range. Despite most range-wide studies confirming our results of total suitable habitat area

reduction, there is potential for previously unsuitable habitat to become available under future climate change in the Northern regions [48, 59, 73]. Caution is therefore advised to individuals interpreting these findings. Changing climate will inevitably result in impacts on biomes and community structures. As such, mitigation and adaptation for potential futures are vital to conservation of climate sensitive species [36]. Future research that combines bioclimatic niche modeling with a mechanistic based disturbance, dispersal, and competition model will likely provide greater insight to the potential range of *P.albicaulis* in a climate changing world [46, 50]. It would furthermore provide insight towards informing management options for restoration that may include controlled fire, selected thinning of competitor species, or assisted migration.

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Supporting Information

Supporting Information:

Patterns and variability of projected bioclimate habitat for *Pinus albicaulis* in the Greater Yellowstone Ecosystem

Water Balance Model

A simple bucket model utilizing a Thornthwaite-type equation will be applied in this study, following the methods described by Dingman [**?**] for water balance:

Given known climate variables, the melt factor F_m is calculated,

$$T_a \leq 0^oC : F_m = 0$$

$$0^oC < T_a < 6^oC : F_m = 0.167T_a$$

$$T_a \leq 6^oC : F_m = 1$$

where T_a is the mean monthly temperature (^oC). This allows the modeling the amount of rain and snow from the known P_m precipitation values (mm):

$$RAIN_m = F_m P_m$$

$$SNOW_m = (1 - F_m)P_m$$

From these the monthly total accumulated snow pack $PACK_m$ and snow melt $MELT_m$ can be determined:

$$PACK_m = (1 - F_m)^2 P_m + = (1 - F_m)PACK_{m-1}$$

$$MELT_m = F_m(SNOW_m + PACK_{m-1})$$

The monthly water input W_m to the system (or individual cell) is:

$$W_m = RAIN_m + MELT_m$$

Values of monthly water input are related to the maximum water holding capacity (WHC) from empirical interpolation $SOIL_{max}$, and the potential and actual evapotraspiration (PET_m) & (AET_m), as follows:

$$SOIL_m = minimum[SOIL_{max}, [(W_m - PET_m) + SOIL_{m-1}]]$$

Using the heat load (HL) equation from McCune and Keon [47], reproduced here:

$$A_f = |180 - |aspect - 225||$$

$$HL = 0.339 + 0808[cos(L)cos(S)] - 0.196[sin(L)sin(S)] - 0.482[cos(A_f)sin(S)]$$

where L is latitude, S is slope, A_f is the folded aspect. PET_m can be derived

$$PET_m = 29.8 * n_{days} * DL_m * \frac{e_a(T_a)}{T_a + 273.2} * HL$$

where, e_a is the saturation vapour pressure at T_a from Campbell and Norman [13]:

$$e_a = 0.611e^{(\frac{17.502T_a}{T_a+240.97})}$$

additionally, vapor pressure deficit can be determined by calculating the actual vapor pressure using $T_{dewpoint}$ for the temperature variable and subtracting actual

vapor pressure from saturation.

n_{days} = days in the month, and DL_m is the daylength from the 15th day of the month defined by:

$$DL_m = \frac{2cos^{-1}[-tan(\delta_m)tan(\lambda)]}{\omega}$$

for δ_m as the solar declination angle, λ is latitude, and ω is the angular velocity of the Earth's rotation ($0.2618\frac{rad}{hr}$).

AET_m can be derived as the smaller of either the sum ($\Delta_{SOIL} + W_m$) or PET_m, where Δ_{SOIL} is defined as:

$$\Delta_{SOIL} = SOIL_{m-1} - SOIL_m = SOIL_{m-1} * [1 - e^{-\frac{(PET_m - W_m)}{SOIL_{max}}}]$$

Provided this water balance model and mean monthly climate for the temporal scale of interest, this simple working model of climate and water/energy balance presents a set of predictor variables for vegetation distribution modeling.

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Tables and Figures

Table 3.1: General Circulation Models for analysis

Name	Institute	Country
CESM1-CAM5	National Center for Atmospheric Research	US
CCSM4	National Center for Atmospheric Research	US
CESM1-BGC	National Center for Atmospheric Research	US
CNRM-CM5	Centre National de Recherche Meteorologiques	FR
HadGEM2-AO	Met Office Hadley Centre Climate Programme	UK
HadGEM2-ES	Met Office Hadley Centre Climate Programme	UK
HadGEM2-CC	Met Office Hadley Centre Climate Programme	UK
CMCC-CM	Centro Euro-Mediterraneo per Cambiamenti Climatici	ITA
CanESM2	Canadian Centre for Climate Modelling and Analysis	CAN

Selection of AR5 GCMs that represent historic climate in the U.S. Pacific Northwest region for future bioclimate habitat modeling.

Table 3.2: Bioclimatic predictor variable list

Code	Predictor Variable
tmin1	Minimum Temperature January
vpd3	Vapor Pressure Deficit March
ppt4	Precipitation April
pack4	Snow Water Equivalent April
tmax7	Maximum Temperature July
aet7	Actual Evapotranspiration July
pet8	Potential Evapotranspiration August
ppt9	Precipitation September

Final predictor variable set for Random Forest modeling. All variables were calculated as a 30-year climate mean from 1950-1980.

Table 3.3: Confusion matrix from out-of-bag analysis

		Validation data set	
		Presence	Absence
Model	Presence	763 *(81.9 %)*	169 *(13.1 %)*
	Absence	176 *(10.9 %)*	1437 *(89.1 %)*

Random Forest tree estimators displays higher OOB specificity than sensitivity. Area Under Curve (AUC) value of 0.94 suggests model has high predictive capacity for projecting future suitable bioclimate habitat.

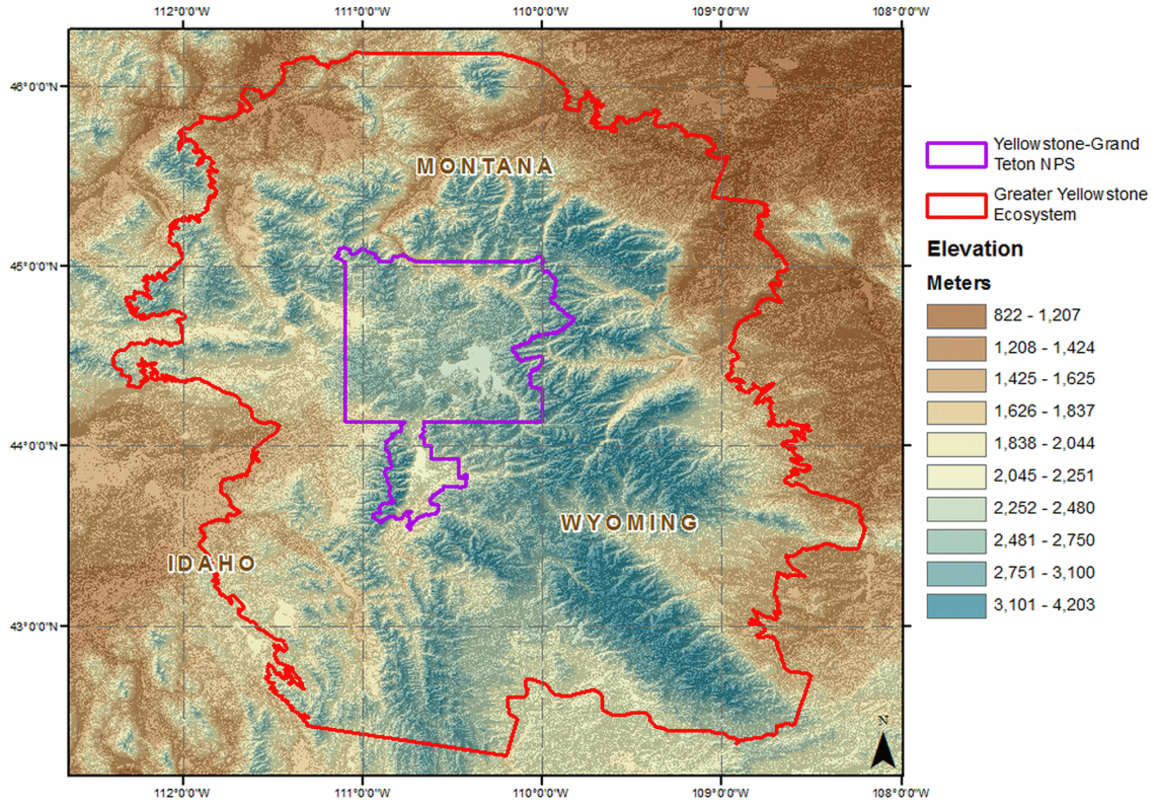

Figure 3.1: The Greater Yellowstone Ecosystem, representing an area of 150,700 km^2 with an elevational gradient from 522-4206 m

Table 3.4: Projected binary *P.albicaulis* presence area within GYE to 2099

Ensemble Average RCP 4.5	**2010**	**2040**	**2070**	**2099**
Area (km^2)	29250.9	16381.2	9151.1	5685.9
	(27134-32858)	*(6918-23359)*	*(2962-12477)*	*(763-9194)*
% Total Threshold Area*	91.3	51.1	28.6	17.8
	(85-103)	*(22-73)*	*(9-39)*	*(2-29)*
Mean Elevation (m)	2875.7	3020.2	3128.0	3217.9
	(2842-2895)	*(2938-3182)*	*(3055-3297)*	*(3114-3471)*
2.5 Percentile Elevation (m)	2356.3	2494.2	2595.0	2691.5
	(2320-2376)	*(2433-2656)*	*(2506-2758)*	*(2571-3041)*
97.5 Percentile Elevation (m)	3521.9	3603.5	3677.8	3734.6
	(3507-3530)	*(3551-3701)*	*(3636-3783)*	*(3673-3905)*

Ensemble Average RCP 8.5	**2010**	**2040**	**2070**	**2099**
Area (km^2)	29259.3	15746.0	5271.5	960.0
	(27188-32604)	*(12985-19581)*	*(1247-8850)*	*(13-3105)*
% Total Threshold Area*	91.3	49.2	16.5	3.0
	(85-102)	*(40-61)*	*(4-28)*	*(0-10)*
Mean Elevation (m)	2874.7	3022.5	3225.5	3470.5
	(2845-2893)	*(2974-3061)*	*(3116-3412)*	*(3255-3749)*
2.5 Percentile Elevation (m)	2353.1	2492.2	2691.3	3001.5
	(2322-2369)	*(2436-2547)*	*(2553-2934)*	*(2622-3401)*
97.5 Percentile Elevation (m)	3522.1	3605.7	3739.5	3908.7
	(3508-3530)	*(3576-3631)*	*(3677-3866)*	*(3775-4063)*

Summary of projection outputs under RCP 4.5 and 8.5 climate scenarios displays loss of bioclimate habitat from 2010 to 2099 (low and high probability of presence GCM summaries displayed in parentheses). Projections into 2099 under all 9 GCMs suggest rapid loss of suitable bioclimate habitat to below 70% of the current modeled distribution and shifts towards the limited high elevation zones (> 3000 m). *(*Percent threshold areas calculated from the 2010 PRISM reference probabilities of presence.*)

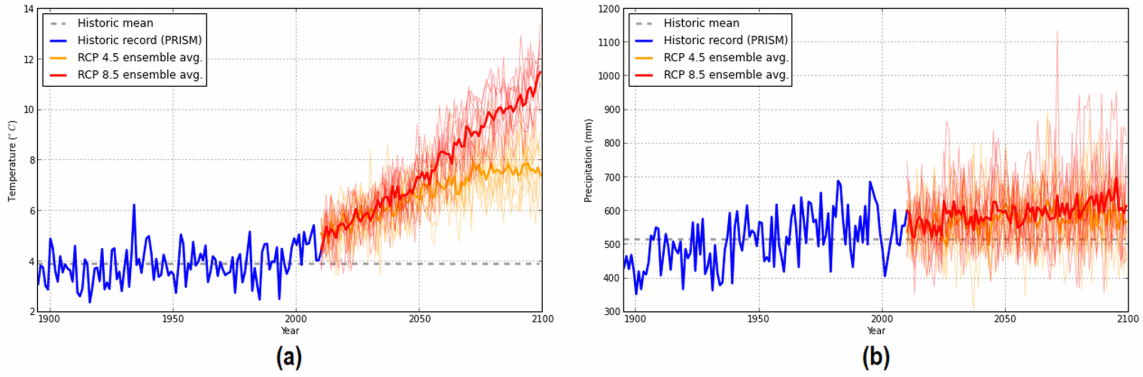

Figure 3.2: Historic and projected climates variables for the GYE from 1895-2099 under RCP 4.5 and 8.5 scenarios. Light shaded orange and red lines represent individual GCMs for RCP 4.5 and 8.5 respectively. Bold lines represent GCM ensemble average for: (a) mean annual temperature, (b) mean annual precipitation

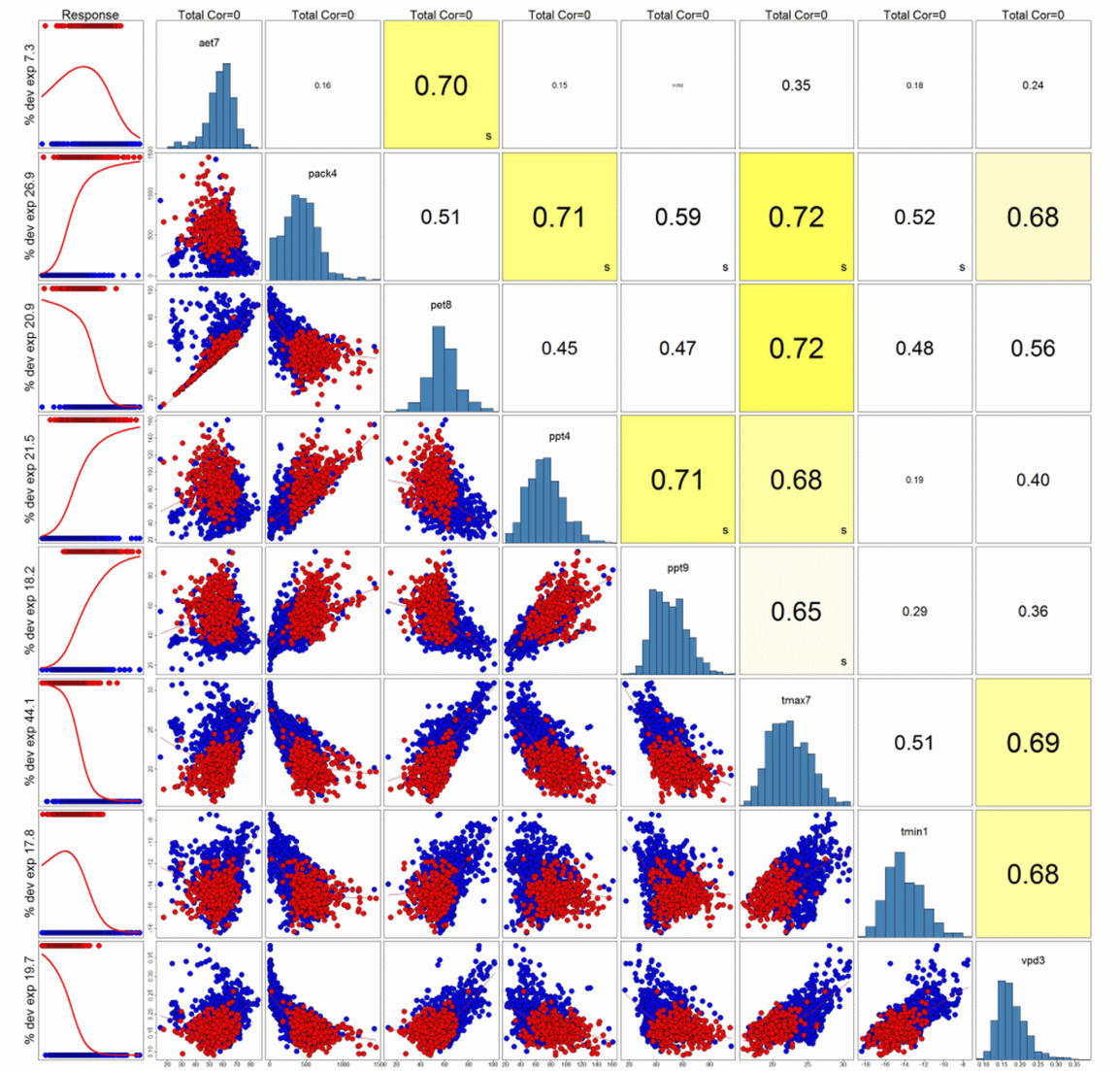

Figure 3.3: Selected predictor variables based on Principal Component Analysis and a maximum correlation filter of ≤ 0.75. Scatter plots represent one-to-one covariate plots where red points represent *P.albicaulis* presence, and blue points represent absence from field data. Far-left columns display logistic-regression of covariates from Generalized Additive Modeling using the Software for Assisted Habitat Modeling (SAHM)

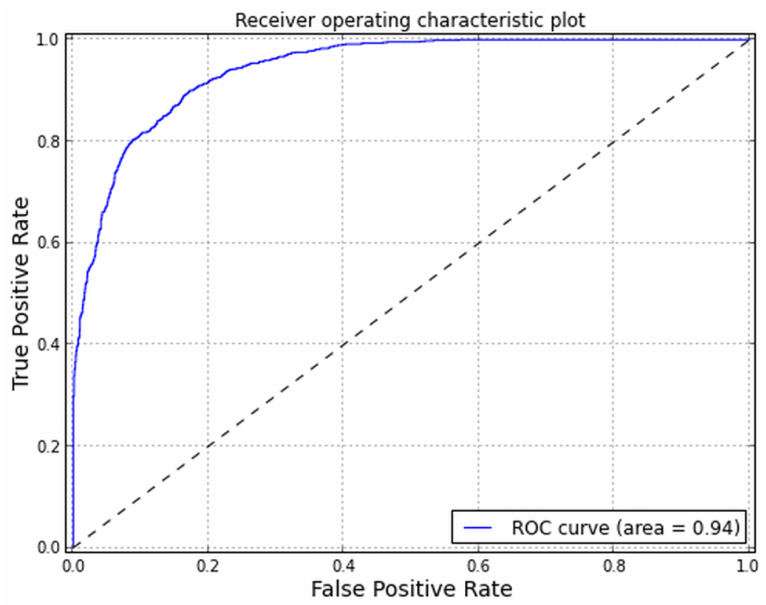

Figure 3.4: Area under curve for the receiver operating characteristic plot suggests adequate performance from the Random Forest modeling for prediction

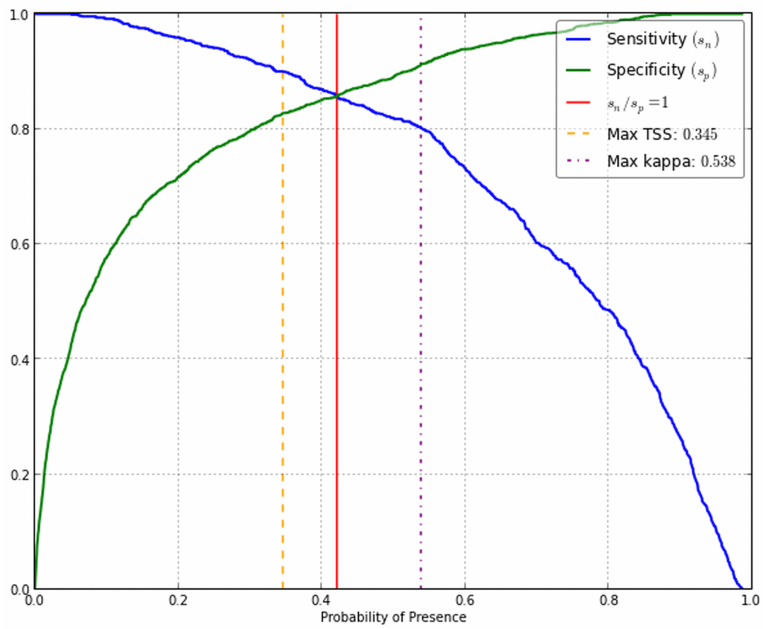

Figure 3.5: Threshold for probability of presence of 0.421 determined at the intersection of true positive rate (TPR) and true negative rate (TNR). Equivalent TPR and TNR, displayed a compromise between the maximum true skill statistic ($TSS : 0.345$) and maximum Kappa statistic ($\kappa : 0.538$)

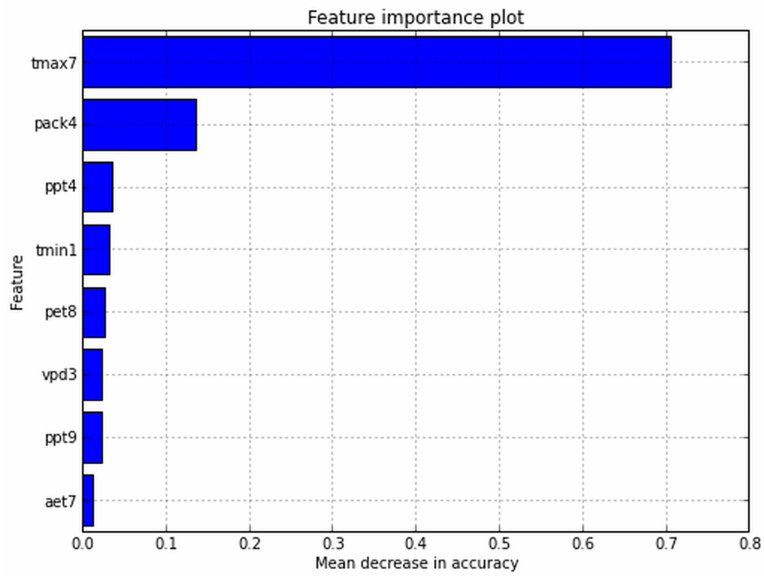

Figure 3.6: Random Forest out-of-bag variable importance plots find removal of maximum temperatures for July and April snow water equivalent to create the greatest reducing in model accuracy

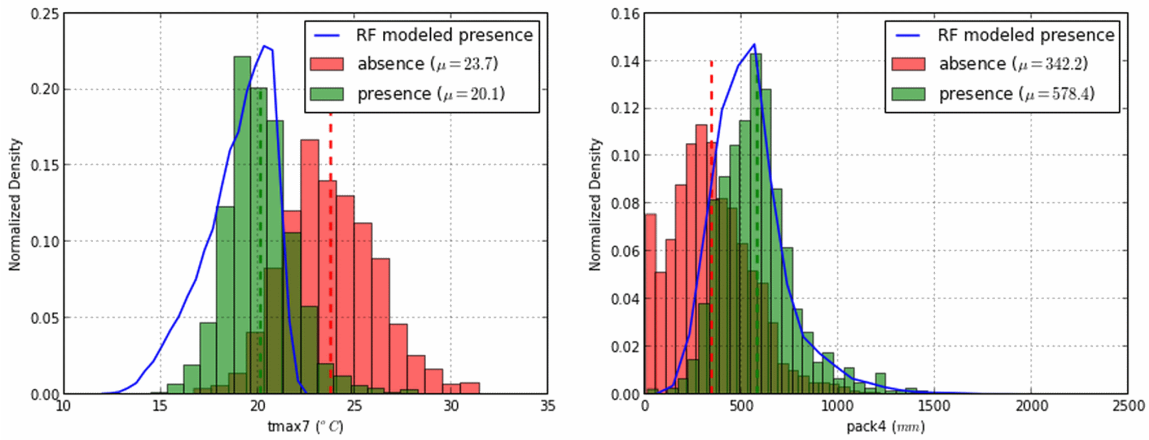

Figure 3.7: Modeled binary presence for *P.albicaulis* under 1980-2010 mean July maximum temperatures and mean April snow water equivalent bioclimate variables shows agreement with field presence data. Dotted lines designate climate means for corresponding *P.albicaulis* field points. Blue lines represent the distribution of Random Forest modeled presence within the GYE

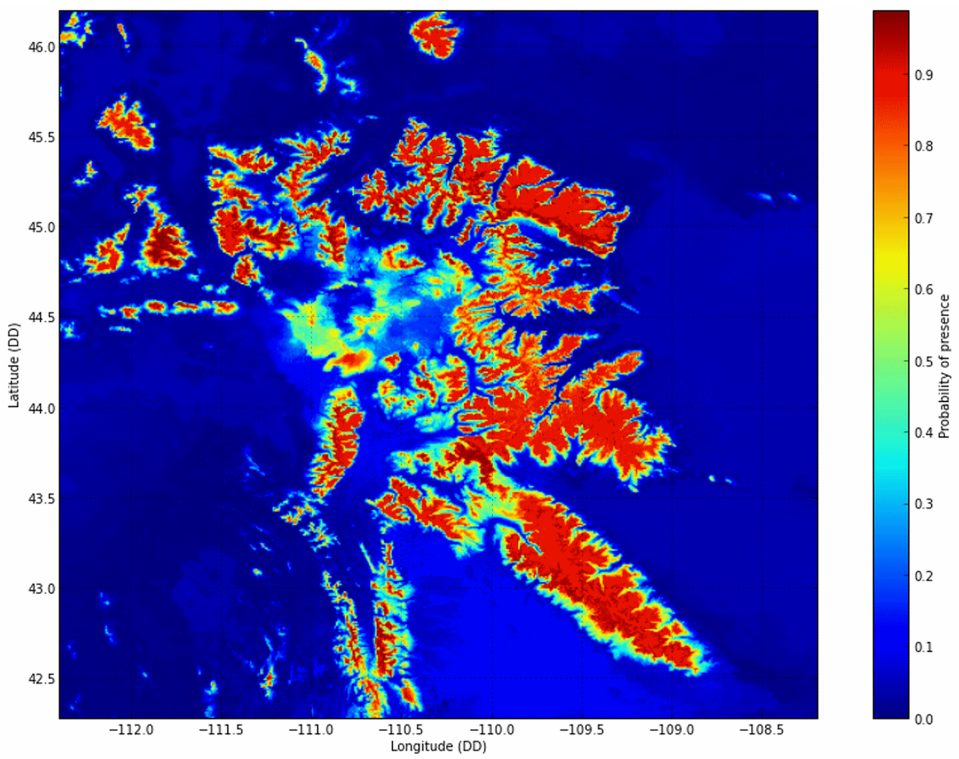

Figure 3.8: Probabiliy presence for *P.albicaulis* $\geq$ 20 cm DBH within the GYE for the 2010 climate period

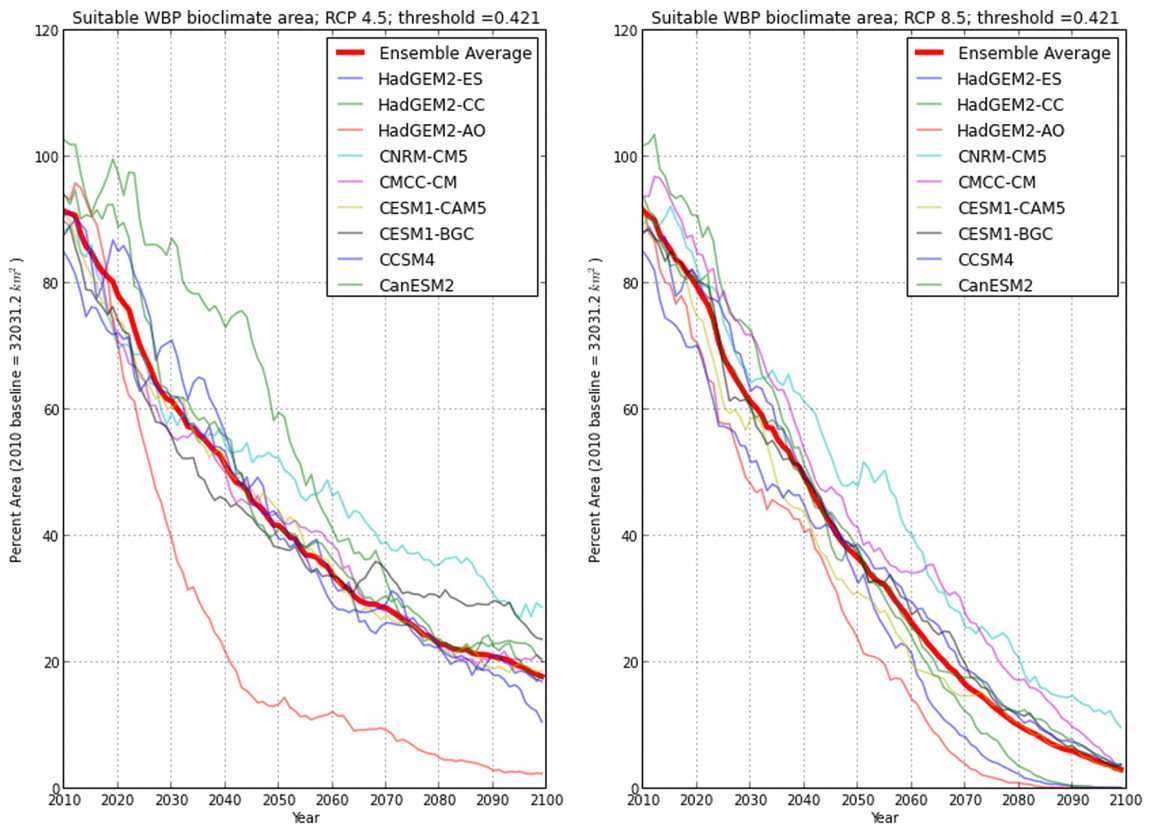

Figure 3.9: Bioclimate projections for *P.albicaulis* for 2010 to 2099 under 30-year moving averaged climates

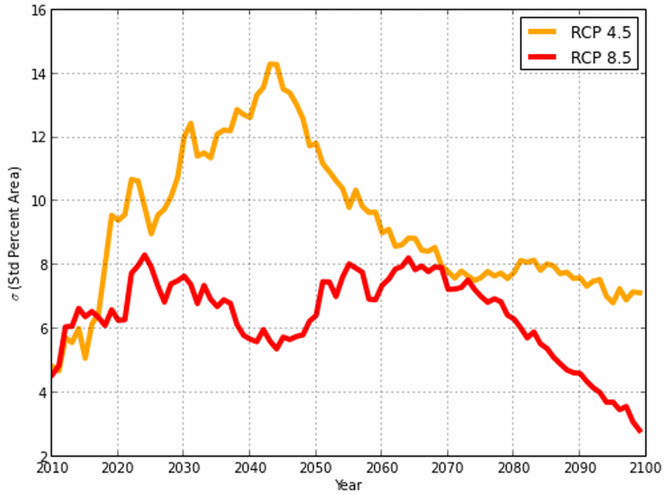

Figure 3.10: Evaluation of the standard deviation σ for percent suitable habitat area by RCP scenario

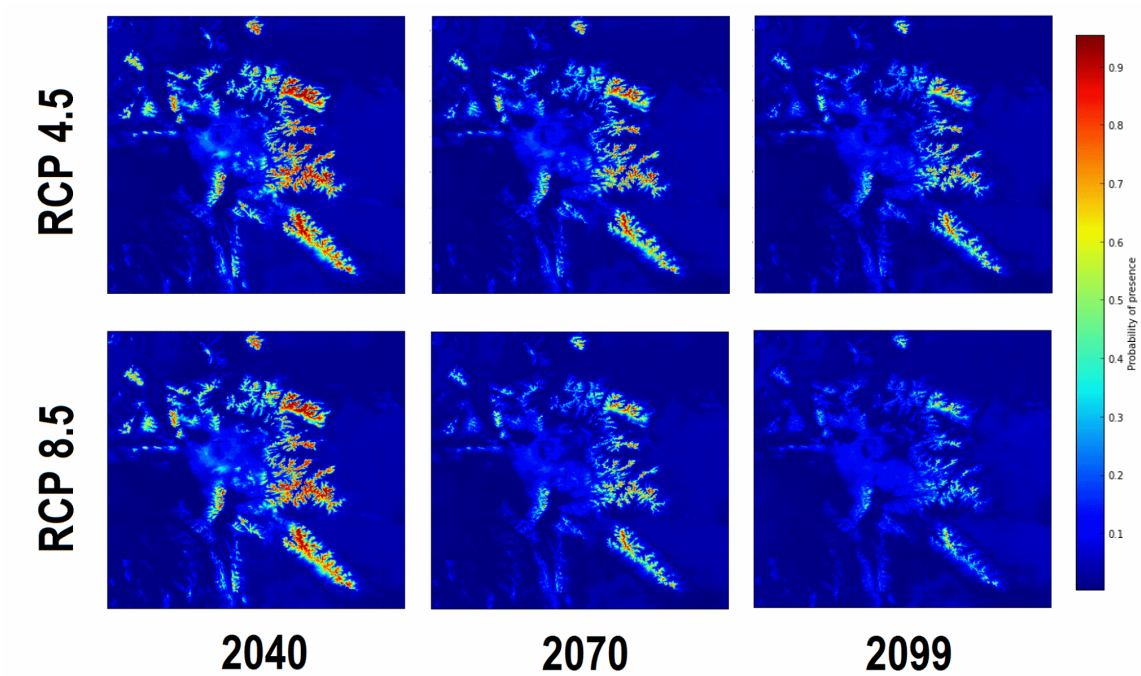

Figure 3.11: Spatially explicit probabilty surfaces for 2040 to 2099 suggest contraction of suitable bioclimatic habiatat for *P.albicaulis* into the $\geq$ 2500 m elevation zones

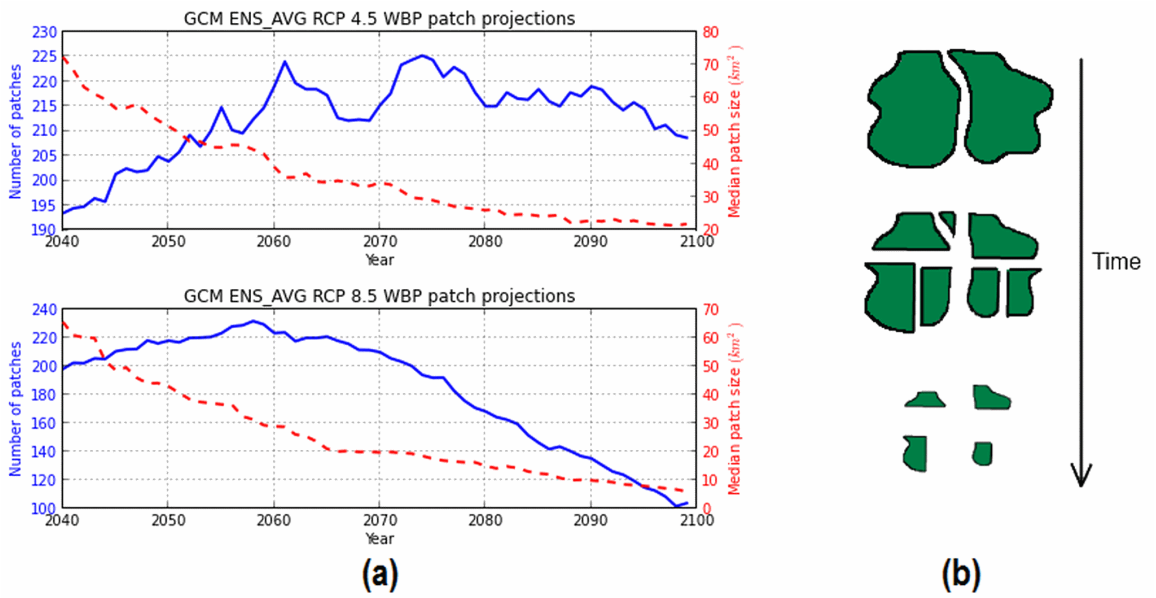

Figure 3.12: Patch dynamics of modeled *P.albicaulis*. (a) Time series of *P.albicaulis* patch projections for number of patches and median patch size to 2099. (b) Cartoon depicting projected patch dynamic displays early pattern of habitat fragmentation followed later by habitat loss under changing climate conditions

A COMPARATIVE SEVERITY ANALYSIS OF RECENT *DENDROCTONUS PONDEROSAE* OUTBREAK AND PREDICTIVE HINDCASTS WITHIN THE GREATER YELLOWSTONE ECOSYSTEM

Contribution of Authors and Co-Authors

Manuscript in Chapter 5

Author: Tony Chang

Contributions: Performed much of the data preparation, spatial analysis, and drafted the manuscript, which was approved by all authors. Wrote and edited major sections of the manuscript.

Co-Author: Andrew J. Hansen

Contributions: Provided conceptual framework for this study and consulted in direction of analysis.

Co-Author: Jesse Logan

Contributions: Provided original scripts for mountain pine beetle phenology model.

Co-Author: Mark C. Greenwood

Contributions: Provided statistical consulting for machine learning methods.

Co-Author: David W. Roberts

Contributions: Provided insightful review for statistical modeling and spatial analysis methods.

Co-Author: Jia Hu

Contributions: Provided plant physiology consultation.

Manuscript Information Page

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Abstract

Climate change at the regional scale can markedly impact forest disturbances due to its direct effect of increased survival and population development of the native insect, mountain pine beetle (*Dendroctonus ponderosae*). From 2000-2010 an eruptive outbreak in the Greater Yellowstone Ecosystem has resulted in over 400,000 hectares of severe mortality, including over 82% of catchments containing the high elevation tree species whitebark pine (*Pinus albicaulis*). Although this recent outbreak has been called unprecedented, few studies exist comparing this outbreak to the extent and spatial patterns of previous outbreaks. This study seeks to quantify how different the recent outbreak was from previous outbreaks. A predictive modeling approach based on physiological process models for *D.ponderosae* survival and phenology, as well as derived regional aridity, was used to hindcast the potential mortality risk within host species habitat from 1951-2010. Comparative analysis indicates that the last period of major outbreak risk occurred in the 1960-1969 period; which corroborates historic records. The recent 2000-2010 outbreak was found to be over twice the total area of the previous 1960-1969 outbreak, with anomalously high modeled probabilities of tree mortality representing over 40% of all *D.ponderosae* host habitat area. The modeled 2000-2010 outbreak also indicated an expansion of *D.ponderosae* elevational range to 2209-3395m, 172m higher in elevation on average compared to the 1960-1969 mean elevation. This implicates the latest outbreak was centered in the core elevational range of *P.albicaulis* suitable climate habitat. This study presents information that suggests that the scale of the recent outbreak was indeed unprecedented and could have a legacy effect on the ecosystem that may need to be addressed in forest planning under future climate change disturbance regimes.

Introduction

The impacts of global and regional climate change have become more prevalent in recent years. One manifestation of increased temperature is forest loss due to insects and disease. Mountain pine beetle, *Dendroctonus ponderosae* (Hopkins), is a poikilothermic (varying internal body temperature) species that has responded to climate change with increased winter survival and a shifted phenology [43, 59, 55]. This physiological shift, in combination with drought stressed host trees, has resulted in an insect-related forest mortality event at a continental scale that has been considered a departure from the historical levels of disturbance extent and intensity [13, 36, 57, 4]. Such a large scale of disturbance has ramifications for forest structure and processes in terms of ecosystem health.

A number of recent studies has examined the phenomenon of disturbance impacts on slow regenerating forests and how they can mediate the spatio-temporal interactions between future disturbance events separated by years or even decades [76]. Larger scale catastrophic disturbance events can increase the expected interval for future disturbance, but can also replace healthy heterogeneous stand structures with even-aged stands that are suspect to another catastrophic disturbance. This means that the scale of an insect disturbance can have a proportional "legacy effect" that can influence future ecological health and resource availability. Therefore, information regarding the spatial extent of a disturbance event is important for effective regional land management planning of forests, especially under climate change [21].

A recent outbreak from 2000-2010 of *D.pondersae* in the Greater Yellowstone Ecosystem (GYE) is widely believed to be the largest insect induced mortality event in the historic record [36, 45, 57]. However, there are limited quantifiable data that

provide the severity and scale of previous outbreaks for comparison within the entire region. Numerous cases of *D.ponderosae* forest mortality have been noted in lake sediment records that show *D.ponderosae* being associated with the structure of regional forests since the Holocene era, some 8,000 years ago [11]. In recent history, the earliest written record of *D.ponderosae* disturbance describe an outbreak between 1927-1936 that coincided with period of abnormally high temperatures and drought, resulting in the infection of 1.3 million trees in Yellowstone National Park and adjacent forests [15, 29]. Jarvis and Kulakowski [36] were the first to attempt to reconstruct the historical outbreaks within the Northern Rockies using tree ring data, and found evidence of other previous major events in the 1960s and 1970s by evidence of growth ring increases from nutrient release [62]. Despite all of these research studies, there is still little information of the scale of previous outbreaks for comparison with the current outbreak within the GYE region. A spatial analysis describing quantifiable departure from historical levels of *D.ponderosae* impacts could indicate the potential for a novel forest structure.

D.ponderosae outbreaks occur for a number of reasons. Outbreaks are the result of suitable forest stand conditions and abiotic factors, including temperatures and precipitation, that allow *D.ponderosae* populations numbers to increase beyond background levels. *D.ponderosae* prefer specific hosts of the genus *Pinus*, including *Pinus contorta* and the five-needled pine species, *Pinus albicaulis* [68]. Homogeneous and mature aged forest stands tend to be more susceptible to *D.ponderosae* due to larger diameter trees providing thicker phloem and a more suitable environment for population growth [5, 51, 1]. *D.ponderosae* development rates are highly dependent on temperatures, and can generally develop through each stage of their life cycle faster under warmer conditions [55]. Complete development from egg to adulthood typically takes 2 years (semivoltine); however, under ideal temperature conditions adulthood

can be reached within a single year (univoltine), which allows the potential for synchronization of adult emergence within a short time span (adaptive seasonaility) [6, 43, 7]. Beetle mortality can occur in the winter when temperatures drop below -30 and -40^oC, or when cold snaps occur between fall and spring when beetles are not fully cold hardened [67, 59, 63]. Lack of these cold snaps or absolute low temperature days, amplify beetle numbers in the following season. Therefore, warmer spring/summer conditions can maximize *D.ponderosae* population numbers which can result in mass infestation (working in concert with vectored blue stain fungus, *Grosmannia clavigera*) leading to exhausted host tree defenses, and thus mortality [18, 58]. Finally, mass infestation can further be amplified by low annual precipitation and high temperatures, which can impact tree resin production and reduce their ability to pitch out attacking *D.ponderosae* [57, 19]. Thus, unseasonably warm and dry years can allow greater populations of *D.ponderosae* to emerge and contribute to the success of overpowering tree defenses and lead to outbreak events.

Given the current knowledge base on *D.ponderosae* ecology, opportunities exist to explore these relationships in a predictive model. Machine learning approaches, such as artificial neural networks, have been increasingly used for predictive modeling applications in ecological studies [54, 40, 41, 37]. A major advantage of applying an artificial neural network for predictive ecological modeling is that the algorithm makes no underlying assumption of the data distribution in feature space, thus allowing non-linear relationships that do not follow a parametric statistical model [54]. There is potential to apply neural networks with environmental inputs that are thought to have direct physiological roles in beetle populations and responding tree mortality to predict past outbreak events.

Tracking patterns in forest mortality due to *D.ponderosae*, especially under climate change where additional beetle outbreaks, fire frequency, and drought

patterns are expected to change, can be valuable for managers. This is especially true if current and future disturbances display no previous contemporary analog [13, 77, 8, 66, 60, 20, 14, 22]. If the scale of the recent outbreak within the GYE *Pinus* hosts, was beyond the historic record, then it may be expected that stands will shift towards dominance of *Picea engelmannii* and *Abies lasiocarpa* from previous biocimate envelope modeling research [53, 32]. Therefore, characterizing the recent mortality from a predictive model of the past can not only help identify knowledge gaps in our understanding of ecological drivers of *D.ponderosae* outbreaks, but also be a means of predicting novel future forest structure and disturbance dynamics.

This research attempts to reconstruct historic *D.ponderosae* host tree probabilities of mortality within the GYE using an artificial neural network modeling approach based on mechanistic considerations of *D.ponderosae* outbreak. The goals of this research are:

- (1) to predict host tree risk of beetle mortality from emergence and survivorship through use of a combination of process-based modeling and machine learning-based predictive modeling;
- (2) to hindcast the probability of mortality of host tree forests based on past climate;
- (3) to quantify the difference in magnitude and spatial extent of 2000-2010 outbreak from previous outbreaks.

Methods

Overview

To summarize the analysis we go through the following procedure (Fig. 4.1): i) develop *D.ponderosae* phenology and winter survival models based on temperature;

ii) calculate aridity based on precipitation and a water balance model; iii) locate *D.ponderosae* host mortality areas and the year of disturbance; iv) build a predictive artificial neural network model for probability of host tree mortality; v) check predictive model accuracy on test dataset; vi) hindcast probability of host mortality and compare spatial extent with 2000-2010 aggregated outbreak.

Region of Analysis

The Greater Yellowstone Ecosystem (GYE) is a mid- to high-latitude area in the Northern Rocky Mountain region, in the northern temperate zone. The study area encompasses 150,700 km^2 with an elevational gradient from 522 - 4,206m that includes 14 surrounding mountain ranges. The general vegetation structure consists of conifers as the dominant forest type composed of lodgepole pine (*Pinus contorta*), sub-alpine fir (*Abies lasiocarpa*), Douglas-fir (*Pseudotsuga menziesii*), quaking aspen (*Populus tremuloides*), whitebark pine (*Pinus albicaulis*), limber pine (*Pinus flexilis*) and Engelmann spruce (*Pinus engelmannii*).

Response Data

Development of the response variables based on both aerial detection surveys and processed remote sensing applications. These data were used to build filters for identifying pixels with information regarding the presence of dead *Pinus*, and the year of mortality detection within the region of analysis (Fig. 4.1 and Supporting Information).

Aerial Detection Survey Dataset

Filter for *D.ponderosae* disturbance Meddens et al. [47] recently converted the USDA Forest Service Aerial Detection Survey (ADS) database to a 1-km resolution grid. These ADS aerial surveys were flown every year and provide a nationwide strategic

assessment and database of the potential hazard for tree mortality due to major forest insects and diseases [74]. This dataset reports the total percent of forest disturbance by individual disturbance agent within each pixel. A binary definition of *Pinus* mortality per pixel of area by *D.ponderosae* was used for the study time period between 2000-2010, where the minimum level of disturbance is equal to or above the value of 1. This acts as an estimate of pixels detected for *D.ponderosae* related change.

National Land Class Database

Filter for conifer forests The National Land Class Database (NLCD) is a national scale classification dataset that provide land cover class at a 30-m resolution [35]. This includes data classifying pixels as deciduous or conifer cover, urban areas, roads, and other land class types. Since this analysis is focused only in regions where host tree species exist for *D.ponderosae*, pixels were selected that were classified as conifers in 2000, but not noted as conifer in 2011 were flagged as a potential disturbance detected for the later remote sensing portion of the methods.

Monitoring Trends in Burn Severity Dataset

Filter for burned forests regions Using Landsat data and the differenced Normalized Burn Ratio (dNBR) algorithm, the USGS Center for Earth Resources Observation and Science (EROS) and USDA-FS Remote Sensing Applications Center created a map called the Monitoring Trends in Burn Severity (MTBS) dataset, of all fires since 1984 greater than 202 ha (500 ac) in the East, and 404 ha (1,000 ac) in the West [27]. The MTBS data indicating burned pixels within the modeling sample period were excluded in order to capture only pixels where the disturbance was exclusively from *D.ponderosae*.

Remote Sensing

Continuous Change Detection and Classification To increase the spatial accuracy for determining beetle disturbed pixels, a recently developed algorithm that utilized satellite imagery was used to verify the date of change occurrence called Continuous Change Detection and Classification (CCDC) algorithm [80]. CCDC is capable of detecting land cover change continuously using a two-step cloud, cloud shadow, and snow masking algorithm to eliminate "noise" from a Landsat 4/5 image [79, 78]. After removal of noise from an image, a dynamic time series model is fit that considers the seasonality and trend of an individual 30m pixel of the different individual Landsat 4/5 bands. Differences were calculated between the fit of three different moving window time series models depending on continuous data density and predicted out-of-window band reflectance/surface temperature values over time [81]:

$$\hat{\rho}(i,x)_{simple} = a_{0,1} + a_{1,i}\cos\left(\frac{2\pi}{T}x\right) + b_{1,i}\sin\left(\frac{2\pi}{T}x\right) + c_{1,i} \tag{4.1}$$

$$\hat{\rho}(i,x)_{advanced} = \hat{\rho}(i,x)_{simple} + a_{2,i}\cos\left(\frac{4\pi}{T}x\right) + b_{2,i}\sin\left(\frac{4\pi}{T}x\right) + c_{1,i} \tag{4.2}$$

$$\hat{\rho}(i,x)_{full} = \hat{\rho}(i,x)_{advanced} + a_{3,i}\cos\left(\frac{6\pi}{T}x\right) + b_{3,i}\sin\left(\frac{6\pi}{T}x\right) + c_{1,i} \tag{4.3}$$

where,

x Julian date

i the ith Landsat Band (i=1,2,3,4,5 and 7)

T number of days per year (T=365.25)

$a_{0,1}$ coefficient for overall value for the ith Landsat Band

$a_{1,i}, b_{1,i}$ coefficients for intra-annual change for the ith Landsat Band

$a_{2,i}, b_{2,i}$ coefficients for intra-annual bimodal change for the ith Landsat Band

$a_{3,i}, b_{3,i}$ coefficients for intra-annual trimodal change for the ith Landsat Band

$c_{1,i}$ coefficient for inter-annual change (slope) for the ith Landsat Band

$\hat{\rho}(i,x)_{simple}$ surface reflectance for the ith Landsat Band at x Julian date from the simple model.

$\hat{\rho}(i,x)_{advanced}$ surface reflectance for the ith Landsat Band at x Julian date from the advanced model.

$\hat{\rho}(i,x)_{full}$ surface reflectance for the ith Landsat Band at x Julian date from the full model.

A user based threshold of reflectance value difference of 1.75 standard deviations was set to determine if a pixel had changed. An iterative process was used where pre-selected known disturbance points were examined under varying thresholds to check the sensitivity of the algorithm for detection and find the best threshold for change detection in the region.

Due to the computational intensiveness of the algorithm, only pixels which met the following three criteria: 1) conifer forested areas, 2) unburned, and 3) potential disturbance indicated by digitized aerial flyover [47]; were then analyzed for change from CCDC. Using this method, pixels identified as potential *D.ponderosae* host mortality for response variable modeling have agreement from both aerial survey and remote sensing data.

Explanatory Data

Explanatory variables were selected and process-based modeled based on the current understanding of factors that influence *Pinus* mortality from *D.ponderosae*.

The major factors captured in these variables include: 1) annual aridity that relates to host tree defense; 2) *D.ponderosae* over-winter survival determined by a developed *D.ponderosae* cold tolerance model; 3) *D.ponderosae* univoltine emergence and synchronized emergence. Due to the lag effect of identification of infested trees changing to red and gray needles lasting one to five years, predictor variables included the data from 1, 2, and 3 years previous to the detectable mortality [39] (Table **??**). These variables were calculated across the entire GYE for application in artificial neural network model fitting and predictions for comparative analysis.

Gridded Climate Climate inputs from the 800m daily TOPOWX and PRISM climate grids for daily and monthly mean temperatures and monthly mean precipitation respectively were recorded for the time period of 1948-2010 [49, 23]. This temporal extent was chosen based on the time periods where data density was at its highest within the region and met the temporal extent range for integration with CCDC. TOPOWX is a derived product that integrates both DEM-based variables and MODIS land skin temperature as predictors of air temperature, and uses interpolation procedures including moving window regression kriging and geographically weighted regression to generate a continuous grid from local station data. Similarly, PRISM interpolates local station data using a climate-elevation regression from digital elevation models where regions are weighted based on physiographic orientation, vertical atmosphere, topographic position, and orographic effectiveness of the terrain. Additionally, since it has been noted that drought influences the ability for trees to defend themselves during periods of beetle outbreaks, potential evapotranspiration (PET) was calculated using a Thornthwaite-based dynamic water balance model

[16, 24]. An aridity index was derived using the equation:

$$\text{Aridity Index} = \frac{\text{MAP}}{\text{MAE}},$$

where MAP = Mean annual precipitation and MAE = Mean annual potential evapotranspiration [75], to apply as a predictor variable in the mortality modeling.

Process-based Modeling

D.ponderosae cold tolerance The *D.ponderosae* cold tolerance model was rewritten for gridded data analysis with parameters specified from the Rnire and Bentz [59] to simulate winter time beetle survival. Over-winter survival has been noted as a major component for assessing of outbreak risk on *P. albicaulis*. *D.ponderosae* has the ability to change its physiology over the course of the winter to three different states to adapt to extreme cold: State 1, a base state where beetles are not cold hardened; State 2, an early winter state where ice-nucleating compounds (polyols) are removed from the gut; State 3, a deep winter cold-hardened state where anti-freeze proteins are produced. The distribution of the population within each of these states was modeled by the equation:

$$X_i = \frac{e^{-(T-\alpha_i)/\beta_i}}{\beta_i(1+e^{[-(T-\alpha_i)/\beta_i]})^2},$$

where i is the state (1, 2, or 3), T is the supercooling temperature (^{o}C), α_i is the mean supercooling point, and β_i is the distrubution's spread. Population survival at each daily time step was determined after calculating the median supercooling point of the entire population that is a linear combination of the median of each distribution multiplied by the proportion of the population in each state. *D.ponderosae* cold tolerance simulations were run incorporating 30 arc-second grid temperatures from

the TOPOWX climate data set. Daily *D.ponderosae* mortality was calculated for an entire year and the over-winter survival was summarized annually for application in the *D.ponderosae* predictive disturbance model.

Process-based Modeling

D.ponderosae adaptive seasonality Temperature is a strong controller of the development rate for *D.ponderosae*. Given this observation, an adaptive seasonality model was developed to simulate *D.ponderosae* life cycles, parameterized by recorded development rates of sampled beetles in laboratory studies [55]. The general framework for the model considers the development rate as the speed of progression through an instar, or life stage, that is dependent on temperature in a predictable fashion. Assuming this development rate is described by the same function throughout a stage, the developmental rate, $r(T)$, at a constant temperature, T, is the inverse of the time required to complete that instar. The developmental index, a_j, or age in stage j (for $j \in 1 \ldots 8$), is then the fraction of the jth instar completed at any particular time by the median individual in the population. This developmental index can be defined by the differential equation

$$\frac{d}{dt}a_j(t) = r[T(t)], \quad \text{where} \quad a_j(t = t_{j-1}) = 0$$

The points of completion for each instar is observable and can be determined numerically by calculating the upper bound of the definite integral for developmental rate set to equal 1,

$$a_j(t) = \int_t^{t_{j-1}} (r_j(T(t))dt), \quad a_j(t = t_j) = 1 \quad \text{(a completed instar)},$$

where numerical increment size is the timestep of one hour. For the application of this analysis, development from the first instar was begun each day for the 365 day calendar year. Date of emergence, Y, was calculated within a three year limit, after which it was assumed that median adult development could not be reached for the thermal conditions [5].

To gain a measure of the synchrony of adult emergence, the sample kurtosis $\hat{k}$ of the distribution of completion dates for a given year was calculated under the equation:

$$\hat{k} = \frac{\sum_{i=1}^{N}[(Y_i - \bar{Y})^4/N]}{s^4},$$

where where $\bar{Y}$ is the mean, s is the standard deviation, and N is the number of simulations reaching completion within the given cell. Kurtosis is a measure of whether the data are heavy-tailed or light-tailed relative to a normal distribution. That is, emergence date sets with high kurtosis tend to have infrequent extreme deviation, and are assumed to have strongly clustered dates suggesting a greater synchronicity of emergence within each cell (Fig. 4.2).

Univoltine emergence (when the time required for development from an egg to adult emergence occurs in a single year) frequency was captured within a cell by calculating the total number of simulated individuals that reach adulthood within a 365 (366 for leap year) day period. Years with greater univoltine individuals would thus have a greater frequency count. These frequencies were normalized by dividing by the number of days in a year to generate values between 0 and 1.

TOPOWX data were used to determine development rates at a 30 arc-second spatial resolution. Interpolation of hourly Δt data was accomplished using a sinusoidal model based with the period adjusted by estimates of day length from

corresponding latitude, day of year, and slope/aspect of the grid cell and the maximum temperature set at the calculated solar noon.

Statistical Modeling

Artificial Neural Network Probability of mortality was modeled using an artificial neural network. An artificial neural network is a biologically inspired multi-layered architecture composed of many networked non-linear transformations on the data that can be efficiently trained in a supervised manner for both classification and regression based problems [42]. In this analysis, a multi-layer feed-forward neural network or multi-layer perceptron model was fit (Fig. 4.3). The architecture of the neural network begins with input data that pass through non-linear transforms (typically a sigmoid) of weights and biases called neurons. These central neurons called hidden layers are arranged in successive layers and may pass to another set of neurons. The information flows unidirectionally, from input layer (predictor data) through the hidden layer(s) to the final output layer (modeled classification). A stochastic gradient descent type backpropagation method was used to adjust the weights and biases given a set of training data, and 'learns' through minimization of the loss function. The artificial neural network was implemented in Python with the Scikit-learn package [12], parameterized with an adaptive movement estimation optimization, learning rate = 0.04, batch size of 200, and two hidden layers with 8 nodes in both layers.

A ratio of 80% training data (n=1560) to 20% testing data (n=312) was used for model fitting and accuracy assessment of the predictive model. A receiver operating characteristic curve was generated as well as a confusion matrix to determine the accuracy of the model [38, 2].

Spatial Autocorrelation Spatial autocorrelation was accounted for by developing an empirical semi-variogram for each predictor variable. The sill, range, and nugget were determined and sample data where distances were below the range, or minimum distance required for covariation to asymptote [28]. Additionally, the global Moran's I [17, 48] was calculated for the residuals with a predictive model fit with and without the explicit spatial terms (x, y in UTM coordinates) as explanatory variables. The values were compared to determine the impact of potential spatial autocorrelation.

Data/Model Integration and Spatial Analysis

After model fitting and accuracy assessment on the testing dataset, the model was applied to a sub-region of the GYE bounded by: 1) conifer habitat as delimited from the national land class database, and 2) bioclimate niche results for *Pinus albicaulis* and *Pinus contorta* from previous species distribution modeling work in the GYE [16, 53]. In this way, predictions of *D.ponderosae* are limited within the regions where it is possible for their host species to exist. Since outbreaks of *D.ponderosae* last for 3-7 year intervals [36, 5, 68], and the goal in the study was to have a comparable interval to the 2000-2010 outbreak, probability of *D.ponderosae* induced host mortality were aggregated in 10 year intervals. All pixel-level annual probabilities were standardized to unit deviations as follows:

$$z_{ij} = \frac{\widehat{y_{ij}} - \bar{y}_{ij}}{s_{ij}}, \quad \text{for pixel } i, j$$

from the 1951-2010 analysis period. A full temporal period (1951-2010) mean Z-score was calculated at each individual pixel. A 2.5 standard deviations from the mean Z-score was set as the threshold to identify outbreak conditions, since it would represent a year where that pixel had a probability of *D.ponderosae* host mortality that was greater than 95% of the mean of all other years for that pixel (See Supporting

Information). Differences in Z-scores for previous outbreak decades were mapped to visualize the distribution of *D.ponderosae* host mortality spatially across the landscape, to further validate the threshold level that most closely represented aerial detection surveys.

Results

Model results

The artificial neural network model accuracy assessment results from the 20% testing dataset reported an Area Under Curve (AUC) of 0.73 (Fig. 4.4) [10]. This suggests the model provided a fair estimate of accurately predicting host tree mortality from *D.ponderosae* based on the given explanatory variables. Consideration of the confusion matrix with a threshold probability set at 0.54, where specificity (true positive rate) and sensitivity (true negative rate) are maximized, an approximately even level of specificity (0.713) and sensitivity (0.732) were found from the model fit (Fig. 4.5). Given the AUC score and the error level in both Type I and Type II error, the predictor variables provide a reasonable ability to determine *D.ponderosae* host mortality in the region, although additional variables could improve the model. Spatial autocorrelation at a distance of 800m in the residuals determined a Moran's I value of 0.071, with explicit spatial explanatory variables, and 0.073, without spatial explanatory variables. This suggests that the spatial terms do not noticeably change predicted probabilities.

Spatial analysis

Region wide predicted *D.ponderosae* host mortality estimate a 51% mean probability within the GYE with a standard deviation of 21% across all years. Spectrogram analysis of the hindcasted annual host mortality probability suggests

that there were two distinct periods where high frequencies of 95% probability of mortality pixels occurred in 1963 and 2000, and a minor event in 1985 (Fig. 4.6). Other years of high frequency probabilities above the regional 51% mean were 1956, 1960, 1969, 1974, 1980, 1983, 1990, 1992, 1998, and all years from 2000-2010 except 2008.

Decadal aggregated Z-scores of modeled *D.ponderosae* host mortality probabilities indicate higher than normal outbreak risk through the 1960-1969 decade and 2000-2010 decade. These results corroborate evidence of past outbreaks within Yellowstone National Park in the 1960s, 1980s, and the recent outbreak of 2000-2010 [62, 36, 44, 45, 13, 61]. The spatial magnitude of the past outbreak risk, estimates the recent 2000-2010 to represents some 49% of the *D.ponderosae* host area within the GYE (Fig. 4.8). This estimated total outbreak level is supported by MacFarlane et al. [45] finding of 46% of total small-catchment-level mortality having severe levels of mortality. This strengthens the assumption of a 2.5 standard deviation Z-score threshold versus other lower Z-score thresholds, since a lower Z-score threshold would estimate a larger scale of probable severe mortality (Fig. 4.7). The 49% area of host mortality magnitude was more than twice the area from the previous 1960-1969 estimated outbreak (23%). Lower level outbreaks were also estimated within the 1951-1960, 1980-1990, and 1990-2000 decades, with approximately 10% of the total host area showing higher than historically typical *D.ponderosae* host mortality probabilities (Fig. 4.9a). Spatial comparison of the 1960-1969 versus the 2000-2010 *D.ponderosae* probability of outbreak (Fig. 4.10) estimate large differences in probability of host mortality (60%) in the highest elevation regions. Mean elevation rose from 2615m to 2787m and a 300m increase in the upper 97.5 percentile elevation levels (Fig. 4.9b) (Table 4.2). In lower elevation zones, the probability of host mortality declined by up to 22%.

Discussion

The goals of this research were to (1) to predict host tree risk of beetle mortality from emergence and survivorship through use of a combination of process-based modeling and machine learning based predictive modeling, (2) to hindcast the probability of mortality of host tree forests based on past climate, (3) to quantify the difference in magnitude and spatial extent of 2000-2010 outbreak from previous outbreaks.

Research Goal 1: It is well documented that *D.ponderosae* disturbance on host conifer tree species is driven by a number of factors associated with abiotic conditions [13, 34, 9, 43, 65]. The predictive artificial neural network model fitted with process-based modeling outputs as explanatory variables displayed a fair ability to discriminate host tree mortality across the GYE within the testing dataset correctly ($\sim$70%) within the 2000-2010 time period. It should be noted that much of the data were culled to maintain Euclidean distances of 800m between sample points to reduce spatial autocorrelation and be comparable to the grain resolution of the climate data. Accuracy could be improved with finer scale abiotic variables, thus increasing the sampling data to train the predictive model. An autoregressive model that includes the spatial and temporal arrangements of previous outbreak would also be beneficial by influencing the modeled risk probabilities of pixels surrounding regions already disturbed [13, 3, 5].

Research Goal 2: Host tree mortality from *D.ponderosae* typically occurs 1 to 2 years after a successful attack and outbreaks generally last 6 to 10 years [64]. Due to this uncertainty of actual tree death and subsequent visual response, predictions of host mortality probability were summarized in decadal bins. Modeled hindcasts within the GYE region presented two distinct high risk periods in 1960-1969 and 2000-

2010, where more than 20% of the regional total host tree area had anomalous levels of mortality probability. A lower intensity outbreak was also noted from hindcasts in 1980-1989. Regional aerial mortality maps for the entire GYE are not available to verify the past 1960-1969 and 1980-1989 periods, but studies across the continental range of the Rocky Mountains spanning to Western Canada show that these decadal periods corroborate previous recorded outbreaks [46, 36]. During those decades, the warm and dry conditions were consistent for those regions associated to the sub-continental effects of the Pacific Decadal Oscillation phase, potentially leading to the *D.ponderosae* continent wide synchrony [46, 69, 73]. This provides credibility to the hindcasts for scale and intensity comparisons.

Research Goal 3: This study provides evidence to support claims that the recent 2000-2010 *D.ponderosae* outbreak was unprecedented in scale and intensity since 1951. Spatial plots of the modeled outbreak probabilities suggest that the 2000-2010 outbreak was not only more expansive in terms of total host species area, but also represented elevations that historically were considered out of the range of *D.ponderosae* adult emergence due to cold temperature limitations for adult emergence and overwinter survival [45]. This agrees with Bentz et al. [9] research demonstrating a shift in thermal suitability for univoltine development in >2400m elevations which designate the mean elevation for *Pinus albicaulis*. This elevational expansion of host mortality pixels resulted in a doubling of total area with anomalous levels of risk. Climate analysis from Sepulveda et al. [71] provides further support for this trend, by finding increases in regional winter and summer temperatures in the last three decades. Time series of the standardized explanatory variable values for the GYE since 1997-2010 exhibited a uniquely consistent period of overwinter survival, univoltine emergence, and aridity that agree with ecological understanding of *D.ponderosae* mass population and susceptible hosts.

Conclusion

Changes in climate within the GYE since 1980s have let to concerns regarding how to manage the system for novel conditions [71, 15, 50]. The mass mortality event of *P. albicaulis* under the recent outbreak creates concern that the system has not only reached novel conditions climatically, but has the potential to become a new forest structure. The recent *D.ponderosae* disturbance event was of a scale and severity novel to our current historic records, and could leave a legacy effect of even-aged homogeneity and altered species composition. Piekielek et al. [53] recently developed bioclimate envelope models suggesting range expansion of *P.contorta* and *P.menziesii* under warmer climate change at RCP 4.5 and 8.5. This mortality event potentially implicates the release of resources for these species not only in their current habitat, but into the sub-alpine regions previously dominated by *P.albicaulis*. *P.albicaulis* may shift upwards in elevation, but it remains to be seen if this shift will escape the thermal range of *D.ponderosae* [30, 16]. If so, this and future events would impact nutrient and water availability within the system.

D.ponderosae mortality events differ from fire or logging disturbances by altering forest functionality without immediately affecting forest leaf area or stem density [26]. This can leave an elevated nitrogen pool for 30 years after outbreak due to needle fall [31]. Reduced leaf area may also result in increases in the amount of solar radiation and precipitation reaching the soil surface [56, 26, 52, 36]. Fire intensity under post-insect disturbance may not change much due to fire severity being primarily driven by weather and topography [33, 70, 72]. Under warmer climate in the next 30 years, it is possible that the shade tolerant species, *Abies lasiocarpa* will replace and dominate the previous *P.albicaulis* habitat.

This historic outbreak signals the need for a new management considerations under climate change that are focused on maintaining heterogeneous forest stand demographic and structure. Forest structures with mixed age-class distributions have greater resilience to catastrophic outbreaks, since even-aged mature stands are the preferred host for *D.ponderosae* [25]. Left unmitigated, regrowth of large scale homogeneous forest may result in a low frequency/high severity disturbance regime such as the predicted fire behavior into the next century discussed in [77]. Future research integrating process-based models of *D.ponderosae* phenology and cold tolerance into dynamic global and regional vegetation simulations for predicting disturbance could provide more information for management of resilient forests under climate change.

Supporting Information

Psuedo-code of filtering for of response data.

```
conifer_code = 42
##NLCD code for conifer pixels
'''
From: https://www.mrlc.gov/nlcd11_leg.php
CODE 42: Evergreen Forest - areas dominated by trees
generally greater than 5 meters tall,
and greater than 20% of total vegetation
cover. More than 75% of the tree
species maintain their leaves all year.
Canopy is never without green foliage.
'''
```

```
conifer2001 = where(NLCD_2001 == 42)
conifer2011 = where(NLCD_2011 == 42)
ads_beetle = where(ADS == True)
unburned = where(MTBS == False)
host_sdm = where(PIAL==True and PICO==True)

potential_beetle_pixels = where(conifer2001
                            and not(conifer2011)
                            and ads_beetle
                            and unburned and host_sdm)

ccdc_out = ccdc_implementation(potential_beetle_pixels)
                        ##outputs the year of change detected

training_beetle_pixels = where(ccdc_out.change_year ==
                            potential_beetle_pixels.year)
training_absence_pixels = where(conifer2001
                            and conifer2011
                            and not(ads_beetle)
                            and unburned and host_sdm)
```

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Tables and Figures

Code	Predictor Variable
arid2	Aridity index two years prior disturbance detection year
arid1	Aridity index one year prior disturbance detection year
uvolt2	Univoltine index two years prior disturbance detection year
uvolt1	Univoltine index one years prior disturbance detection year
surv3	Annual percentage of population survival three years prior disturbance detection year
surv2	Annual percentage of population survival two years prior disturbance detection year
surv1	Annual percentage of population survival one year prior disturbance detection year
emer2	Kurtosis of emergence two years prior disturbance detection year
emer1	Kurtosis of emergence one year prior disturbance detection year

Table 4.1: Summary explanatory variables to train artificial neural network.

	1951-1959	1960-1969	1970-1979	1980-1989	1990-1999	2000-2010
Percent host area	12	23	2	14	10	49
Total mortality risk area (km^2)	4667	9206	717	5464	4026	19793
Mean elevation (m)	2515	2615	2548	2569	2767	2787
Lower 2.5% elevation (m)	2108	2189	2126	2154	2190	2209
Upper 97.5% elevation (m)	3145	3061	2893	3071	3365	3395

Table 4.2: Summary table of 10-year estimated *D.ponderosae* outbreaks in GYE.

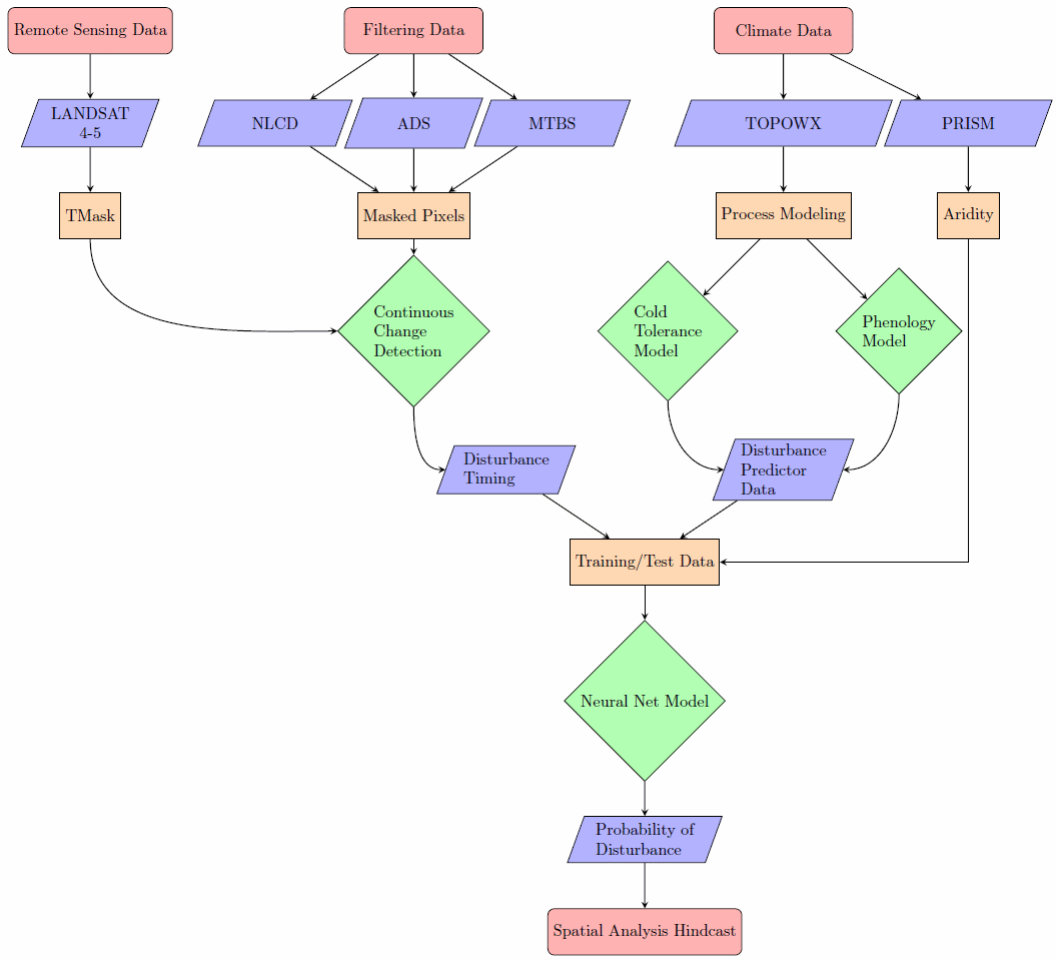

Figure 4.1: Flowchart of data processing and integration into predictive model for hindcasting *D.ponderosae* host mortality

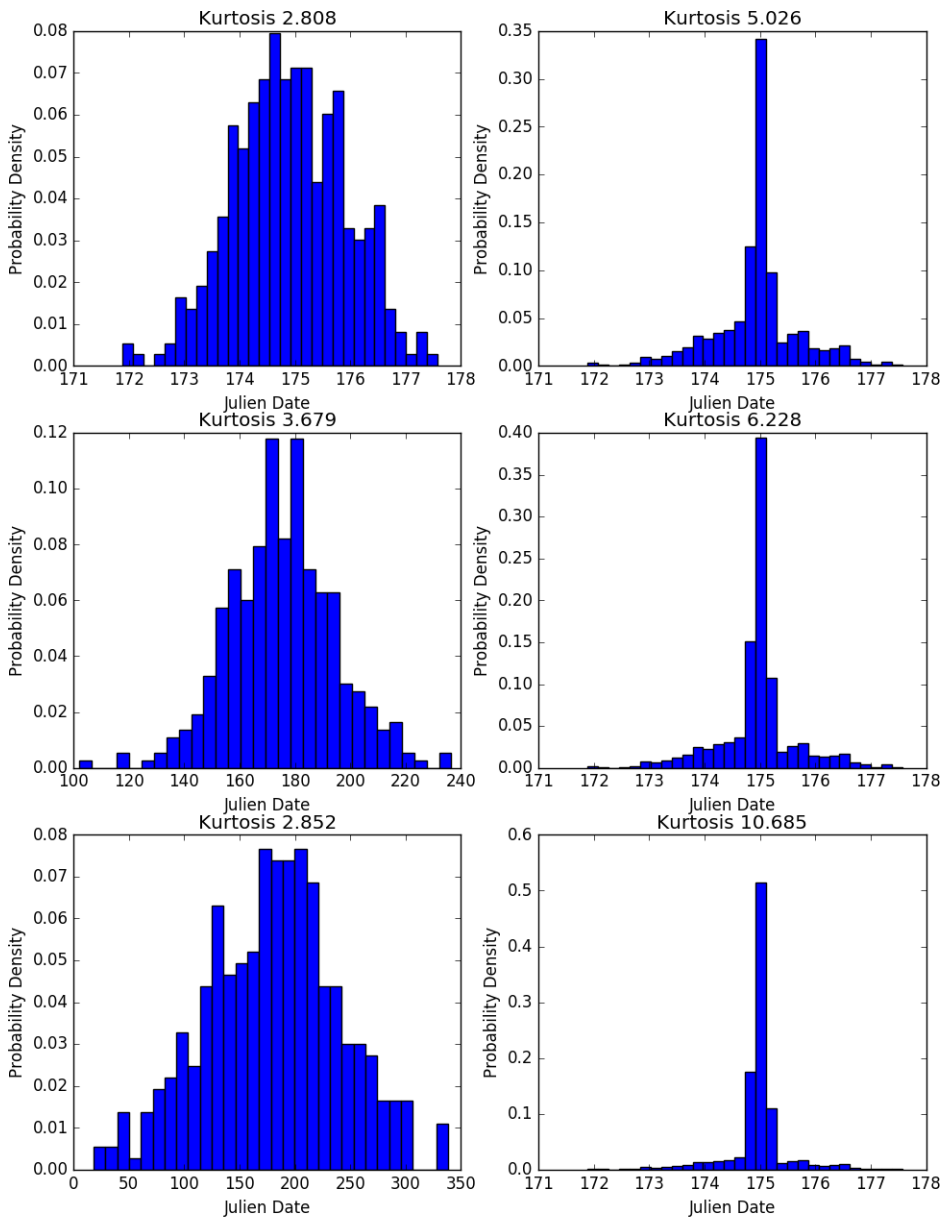

Figure 4.2: Example of various kurtosis values from a normal distribution as a measure to account for increased synchrony of adult emergence of *D.ponderosae* for a year.

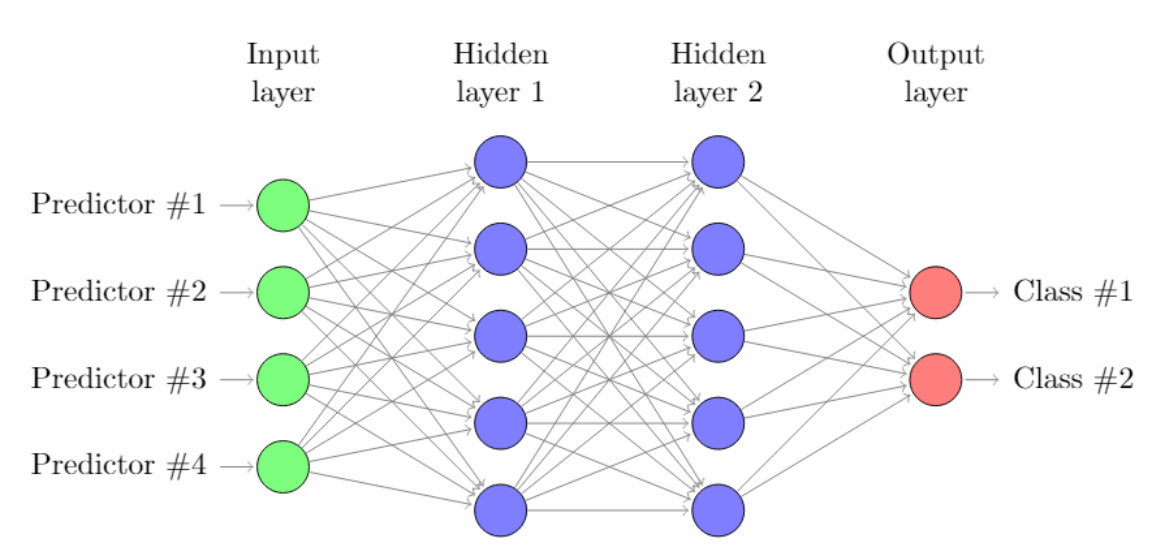

Figure 4.3: Example diagram of a multi-layer feed-forward artificial neural network used to fit probability of *D.ponderosae* host mortality in the GYE. A stochastic gradient descent type backpropagation method (ADAM) was used with two hidden layers with eight nodes each

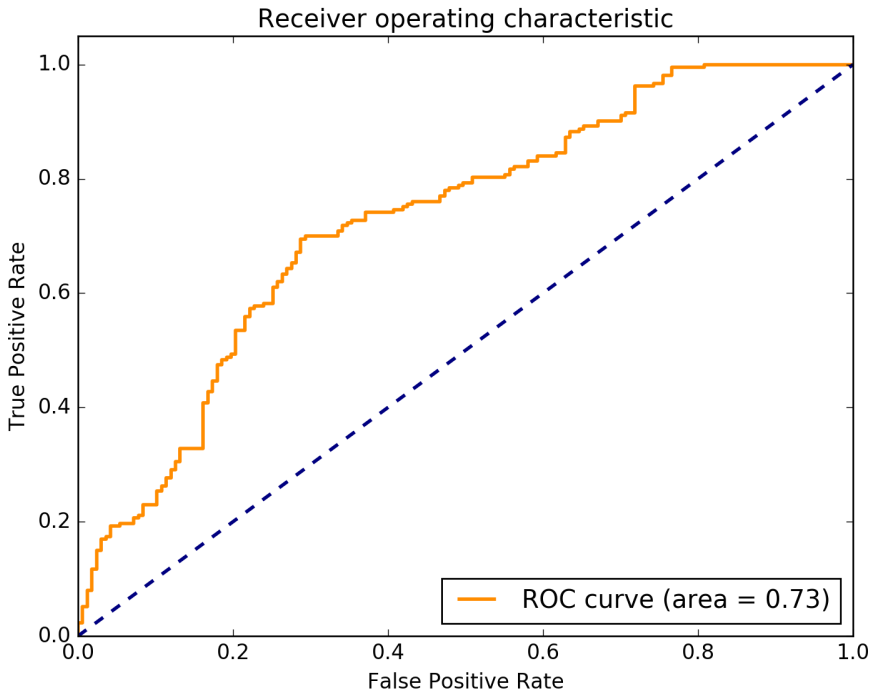

Figure 4.4: Receiver operator characteristic curve from artificial neural network. Area under curve (AUC) value of 0.73 suggests that model has a fair level of accuracy for prediction of presence and absence of *D.ponderosae* host mortality

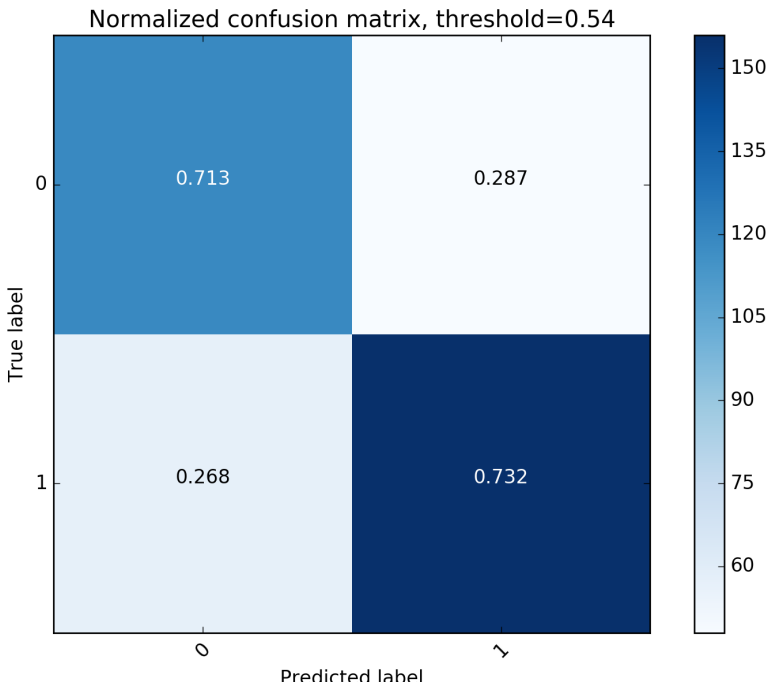

Figure 4.5: Confusion matrix from testing data for artificial neural network fit set at a 0.54 threshold. Model displays balance with 71.3% true negative rate and 73.2% true positive rate for classification of *D.ponderosae* host tree mortality

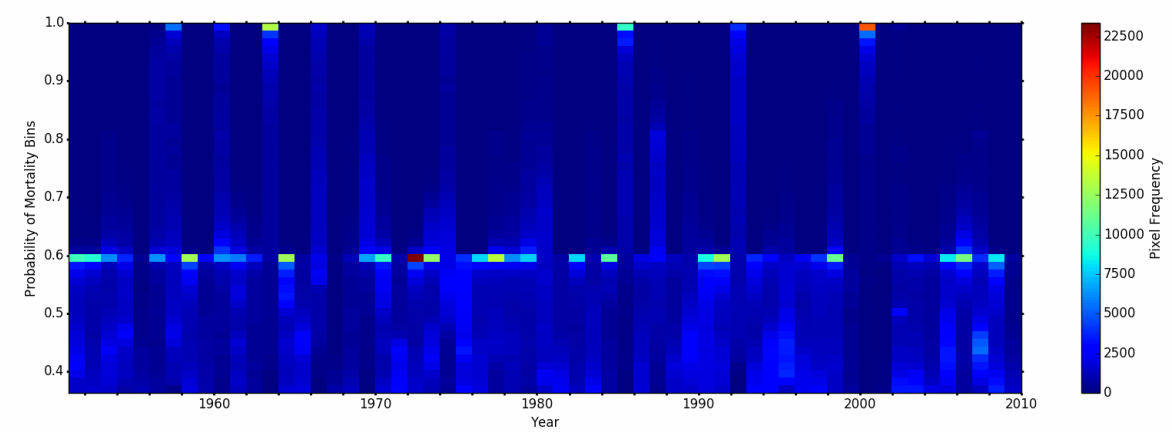

Figure 4.6: Annual spectrogram analysis of probability of *D.ponderosae* host tree mortality indicate high frequencies of > 90% probabilities beginning at 1963 and 2000, indicative of a potential outbreak

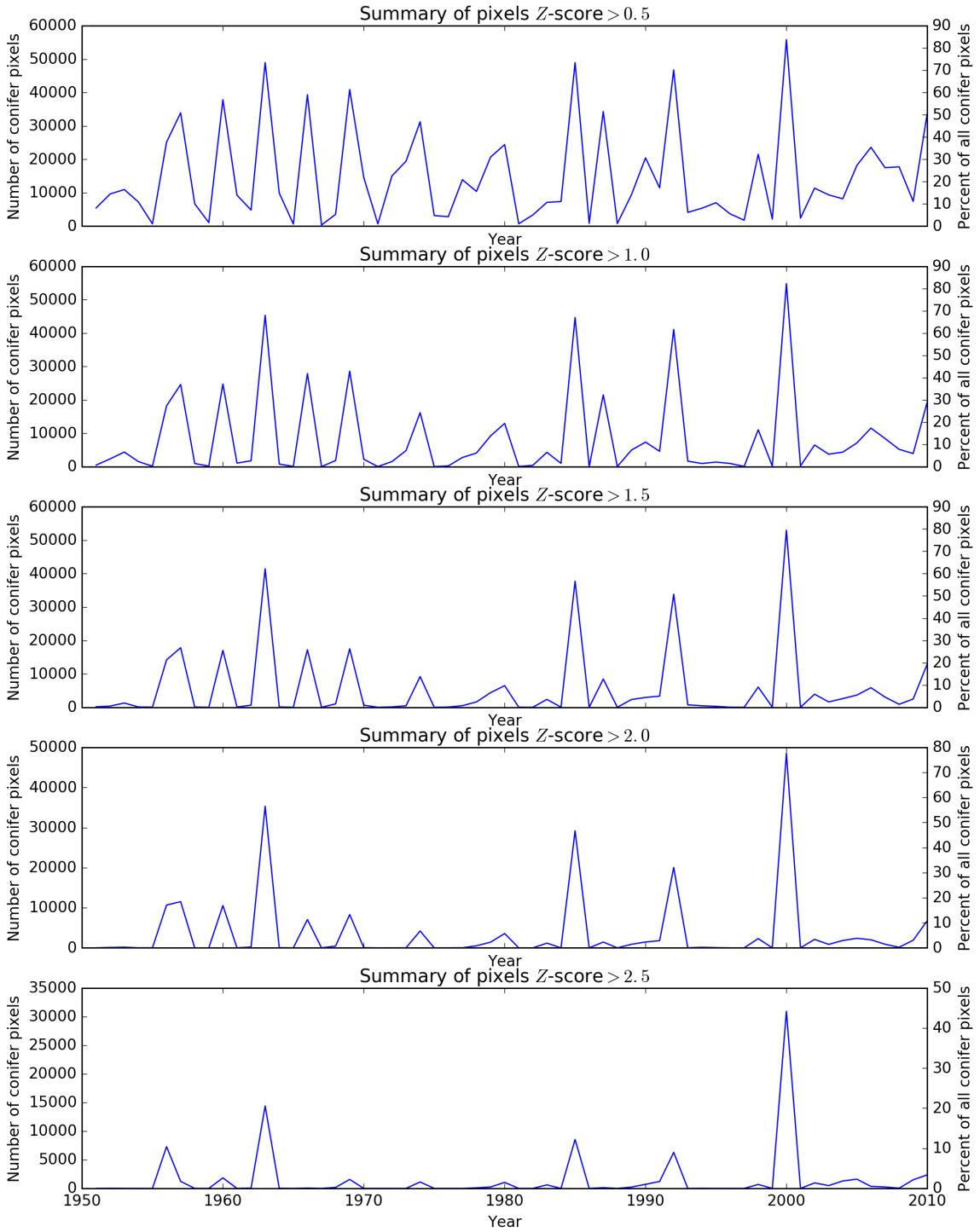

Figure 4.7: Comparison of total host conifer mortality estimates at varying Z-score thresholds suggest that a 2.5 standard threshold is the most similar to the empirical severe mortality levels for 46% of small catchments in the GYE from MacFarlane et al. [45]

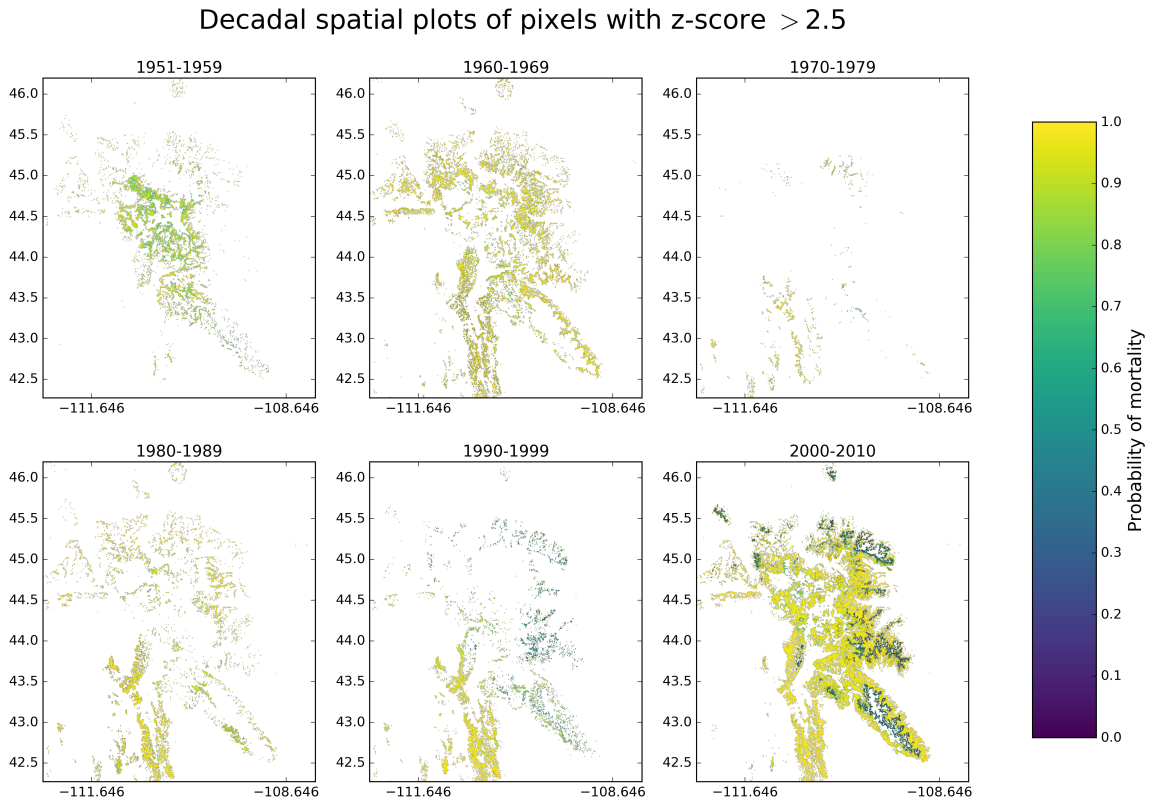

Figure 4.8: Decadal spatially explicit maps of *D.ponderosae* probability of host tree mortality for pixels with a >2.5 deviations from the mean probability

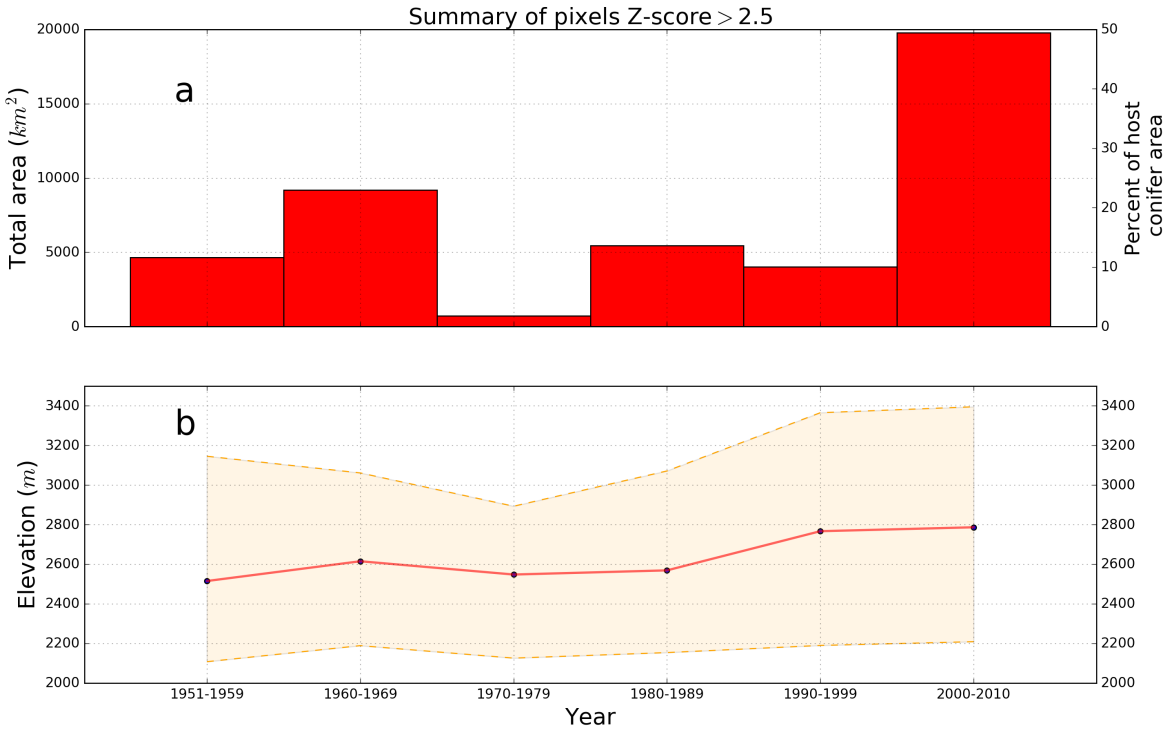

Figure 4.9: Aggregated decadal comparisons of pixels with a >2.5 deviations from the mean probability for *D.ponderosae* host tree mortality. a) Aggregated decadal pixels totals suggest two major outbreaks occurred in the GYE in 1960-1969 and 2000-2010, with the latter outbreak occurring within 49% of all host tree pixels. b) Mean elevation from decadal pixels (red line) indicate steady increase from 2515m to 2717m across host conifer area and increased lower and upper bounds of the 95% interval (orange region)

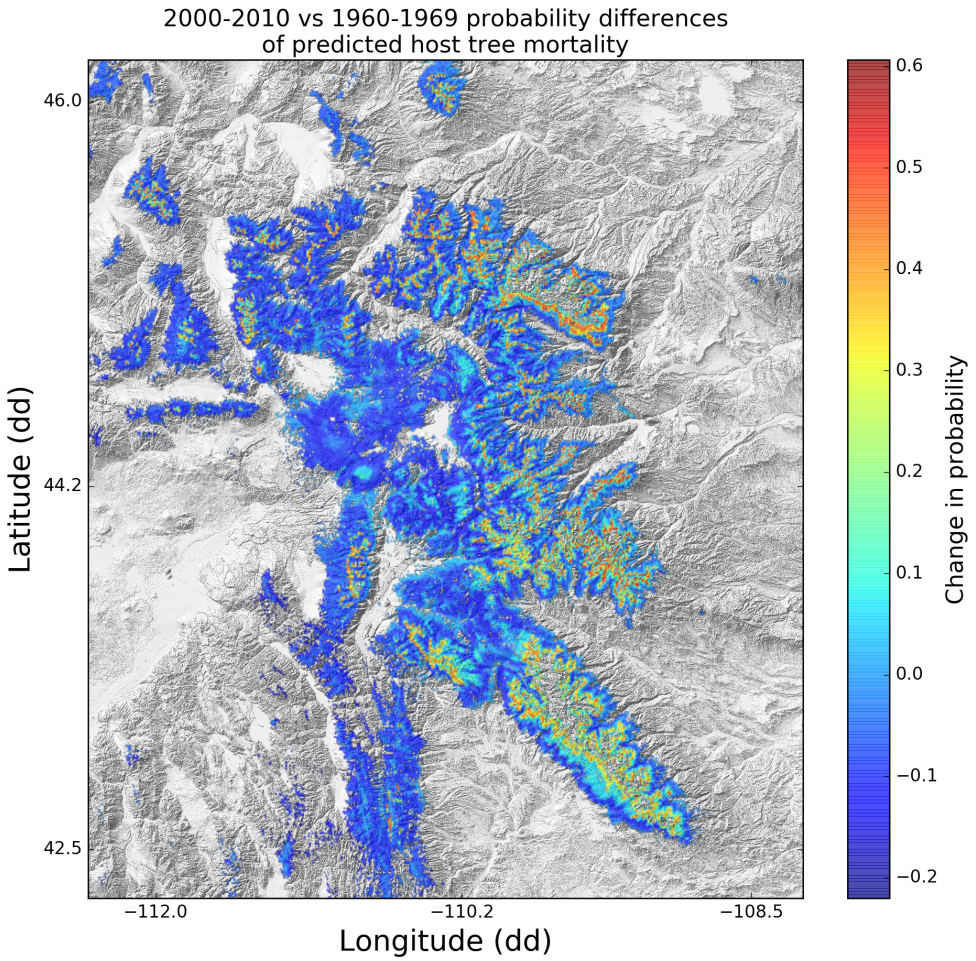

Figure 4.10: Spatially explicit map comparing 1960-1969 and 2000-2010 *D.ponderosae* host tree mortality probabilities in the GYE. Largest probability changes were found in the high elevation regions of the Beartooth and Wind River Range, corresponding to *P. albicaulis* habitat

CONCLUSIONS

Climate in the GYE has seen a notable change in the last 30 years with a 1-2 ^{o}C increase that is consistent with the rest of the US [5]. Notably, snowpack has been reducing and winter minimum temperatures have increased since the 1980s [11, 12]. These changes mean potentially profound changes to the ecosystem in terms of forest structure and disturbance regimes, especially for the higher elevation habitat of *P.albicaulis*. As such, management for the future climate must consider multiple methods including; active restoration involving thinning, burning, and planting to ensure heterogeneity and resilience of *P.albicaulis* ecosystems.

My research projected climate into 2100 under all representative concentration pathway scenarios resulting in reduced suitable climate space for *P.albicaulis* from the present, with upper estimates up to a 61-99% habitat loss. I also found a relationship with maximum summer temperatures, April snowpack, and vapor pressure deficit and suitable bioclimate space for *P.albicaulis*. Given the expectation of less snowpack and warmer summer temperatures, it seems consistent with climate projections that suitable available space would be reduced looking forward. Other research using simulation models have found similar results with a reduction of total basal area for *P.albicaulis* across the region [6]. However, there is also indication that the species will be able to persist under some specific GCM projections due to variations of species performance at a sub-regional scale, micro-climate effects, and disturbance/biotic interactions [8].

My research has indicated that *D.ponderosae* has shifted its distribution to a mean elevations above 2750m and expanded a total risk area in the GYE that is more than double any previous outbreak in the historic record since 1951. The 2000-2010 total anomalous outbreak area was modeled to be 10000 km^2 greater than the

last outbreak in 1960-1969. Given these findings and understanding of the biotic and abiotic relationship with *P.albicaulis* suitable habitat, it may be expect that this recent mortality would result in increases in nutrient, sunlight, and water availability. [14, 2, 13, 7]. Fire intensity may not change directly related to *D.ponderosae* mortality, but could increase under warmer and drier conditions [18, 4, 16, 17]. Potential new disturbance regimes could allow a species composition shift towards *Abies lasiocarpa* to replace the previously dominate P.albicaulis habitat.

Mitigation may be necessary to prevent the functional extinction of *P.albicaulis* in expectation of climate change. This research has provided another source of agreement on the potential ecosystem impacts related to climate change within the GYE region. Rehfeldt et al. used bioclimate envelope models to predict loss of *P.albicaulis* suitable habitat in the next 100 years [15] and Buotte et al., found that *D.ponderosae* suitable climate would become more and more prevalent in nearly all of the current habitat for *P.albicaulis* [1]. These results, compounded with predictions of warm and drier conditions that weaken tree defenses, mean management actions for *P.albicaulis* may need to be active to ensure the species' proliferation.

This research recommends the maintenance of a heterogeneous forest structure to allow for resilience to respond to unforeseeable changes. Rates of global climate change are expected to exceed the ability of many species to migrate to new, climatically favorable locations [9]. Continued research on whitepine blister rust resistant seedlings may be explored within different topographies and soils throughout the region's future suitable core climate zones [3]. *P.albicaulis* may require assisted migration to reach new climatically suitable locations, however such interventions are controversial since studies of effects on assisting species to novel locations are limited, and restrictions may exist within federal jurisdictions (i.e. wilderness areas) [10]. Therefore, it is recommended that thinning of shade-tolerant competitors and

prescribed burning be the major management action to allow *P.albicaulis* to persist on the landscape and maintain a mosaic stand structure that is less prone to extreme disturbance [8].

It is difficult to predict where and when local scale could become climatically suitable for a given species. The future climate is still uncertain, but newer models under development will likely improve spatial resolution, temporal accuracy, and better represent the system. The studies of this dissertation will inevitably be reproduced with more realistic datasets and more robust modeling techniques. As our technology improves and gets more sophisticated, it is likely that sub-meter resolution estimates of potential tree and disturbance agent distribution will eventually be modeled and with it, more useful estimates of species composition change. In the mean time, it is hoped that this research serves as the best available information to assist in management actions that can be taken now to preserve the species from future extreme climate events.

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