University of Alberta

Identifying western North American tree populations vulnerable to drought under observed and projected climate change

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A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Forestry, University of Alberta, Edmonton, Alberta

and

Master of Science in Forest Sciences, University of Freiburg, Germany

Fall 2021

Abstract

Global climate change has impacted forest health and productivity, especially in high latitude regions of the world where the warming signal is strongest. While many climate change impacts are indirect through biotic interactions involving pests, diseases, and competition, one highly visible direct climate impact is dieback and mortality caused by drought periods in moisture-limited ecosystems.

This thesis investigates observed and projected change using a climate moisture index (CMI) specifically developed to map forest-grassland transitions due to moisture-limitations for western North America. CMI values above zero indicate a positive annual evapotranspiration balance (in units of mm precipitation) that supports forested ecosystems. Negative values indicate water deficits with an expectation that forested ecosystems would not be supported.

This research project investigates how the zero-CMI isopleth for the latest 30-year climate normal period (1991-2020) has shifted relative to the historic climate normal period (1961-1990), which often serves as reference, representing climate conditions before a significant anthropogenic warming signal. Similarly, shifts of the zero-CMI isopleth under future climate projections were evaluated, asking what proportion of tree species populations may no longer be supported by a positive annual evapotranspiration balance.

The research identifies populations from the 24 most common western North American forest tree species that experience the lowest CMI values within each species range, using a western North American forest inventory database with 55,700 plot locations. The lowest 2.5th percentile of CMI values within each species were used as a proxy for each species' drought tolerance to evaluate which tree populations may potentially be vulnerable to drought under observed and projected climate change.

About half of the 24 species that were evaluated had 5% or more of their occurrence records were located in areas with CMI value <0, potentially vulnerable to drought conditions. Five species had 25% of their populations exposed to drought, and for two species *Pinus edilus* and *Pinus ponderosa* half of the occurrence records were located within areas with negative CMI values. Climate change projections suggest that water deficits will disproportionately increase for the species and populations that are already in vulnerable positions, whereas other species and populations are not predicted to be affected strongly by decreases in water availability.

The most notable drought-related dieback and mortality in western North America was observed for three tree species over the last three decades: *Pinus edilus*, *Populus tremuloides*, and *Pinus ponderosa*. To test the realism of the CMI-based drought vulnerability assessment, observed geographic patterns of dieback were compared to changes in CMI between the 1961-1990 reference period and the recent 1991-2020 average.

Observed impacts largely conformed to expectations for populations of *Pinus edilus*, *Populus tremuloides,* and *Pinus ponderosa* where dieback was observed. However, there were also important counter examples. Widespread dieback of *Populus tremuloides* in Canada were not associated with directional trends in CMI values, but were instead caused by extreme drought events that could not be associated with directional climate change.

In conclusion, the annual evapotranspiration balance at forest-grassland transitions may pose a significant threat to forest health and productivity across western North America, while inferred drought threats for species and populations that have range boundaries within forested ecosystems do not appear to increase under climate change projections. Observed climate change impacts over the last decade correspond closely to expectations from a CMI-based vulnerability assessment.

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1. Introduction

Tree growth and survival are strongly linked to their climatic environments (Khaine & Woo, 2015). Because plant species are specialized to a set of environmental and climatic conditions, species occur within broader or narrower geographic ranges that coincide with suitable conditions to which they are adapted (Grace, 1987). As climatic conditions change, plant species, including trees are faced with conditions they may no longer be adapted to. The effects of this incompatibility can manifest itself either as direct climate impact, or indirectly through biotic factors such as changes in competitive advantages relative to other species or through vulnerability to pests and diseases. Direct effects leading to dieback and increased mortality can be caused by severe and prolonged drought and warming (Allen et al., 2010). Additionally, indirect effects through biotic interactions include insect infestations, invasive species competition or diseases (Seidl et al., 2017). Other indirect impacts are observed through regenerative or adaptive capacity due to competitive advantages or disadvantages relative to other forest tree species (Morin et al., 2018; Zhang et al., 2018; Oboite et al., 2020). As a result, the composition, distribution, and health of forests are gradually altered. Although these effects have been studied in the literature, individual tree species respond to changing climate differently (McDowell et al., 2008). Thus, identification of individual species' tolerances to direct and indirect climate change impacts can be valuable to evaluate their vulnerability.

Among direct climate impacts, changes in the hydrological balance of forest ecosystems may be the most important driver of changes to species distributions under observed and predicted climate change. Disruptions to the hydrological cycle include decreases in snowfall, earlier spring melt and runoff, as well as drought events (Stewert et al., 2005; Vicente-Serrano et al., 2020). Because drought is caused by decreased precipitation and subsequent loss of soil moisture and increased atmospheric evaporation, there are direct physiological effects seen by trees in response to water stress. Physiological adaptations like stomatal responses, decreased carbon uptake, and xylem transformation are all triggered by reduced water availability (Choat et al., 2018; Brodribb & Cochard, 2009). When tree species experience water stress they have an adaptive ability to limit water intake through stomatal changes, thus also decreasing the uptake of CO_2 needed for photosynthesis. During prolonged and severe droughts, soil moisture decreases causing photosynthetic decline by affected vegetation (Reich et al., 2018). Van Mantgem (2009) found the influence of warming on the hydrological regimes of western North America to lead to an increase in water deficits and prolonged summer droughts and thus are attributed as the major cause of mortality among all genera of trees in the study. Reduced growth caused by climatic events like prolonged drought have also been studied (for example, Chen et al., 2017; Hogg & Michaelian et al., 2017; Huang and Anderegg, 2012). Additionally, drought and its association with soil moisture loss was linked to forest mortality in Southern California (Goulden & Bales, 2019). Furthermore, different populations within wide ranging species have varying physiological adaptive capacities to drought, leading to drought related declines not only at the most exposed populations, usually the southern, low elevation fringe of species distributions (Montwe et al., 2016).

There are also cases where changing climatic conditions contribute indirectly to mortality, dieback and declines in species regeneration. In areas throughout western North America, infestations of bark beetles and defoliators have been linked to changes in regional climate (Anderegg et al., 2015, Woods et al., 2010). Although historically, these kinds of disturbances are quite common in forests and contribute to the natural progression of forest succession, the magnitude and severity of these disturbances are increasing. For instance, from 1989-2004, more than a million hectares of forest were killed by a spruce beetle outbreak in Alaska (Berg et al., 2006). In British Columbia, more than 10 million hectares of Pinus contorta have been killed by mountain pine beetle by 2006 (Kurz et al., 2008). Rising temperatures, longer growing seasons, and decreased precipitation all played a role in these events. Similarly, drought events and biotic factors can interact. In the western United States increases in bark beetles and wood borers after drought periods have been observed (Kolb et al., 2016). An experimental study found that artificial drought stress made adult *Pinus edulis* susceptible to bark beetle attacks and subsequent mortality (Gaylord et al., 2013). However, the relationship between drought, trees, and insect or fungal pathogens is variable. Some evidence suggests that geographic location, insect type, and primary versus secondary fungal pathogens influence the response of trees (Kolb et al., 2016). Because some biotic pathogens thrive in moist environments while others are more successful in already stressed or moisture deficit environments, the predictive ability to determine the indirect drought impacts on trees could be difficult.

With changes in evapotranspirative demand being potentially key drivers of climate change impact on forests, a focus on systematically evaluating changes to the hydrological balance of tree populations appears justified. One way we can examine hydrological changes occurring at continental or subcontinental scale is using moisture deficit indices. Some commonly used indices include the Palmer drought severity index (PDSI), drought area index (DAI), rainfall anomaly index (RAI), standardized precipitation index (SPI), and the crop moisture index, (Keyantash & Dracup 2002). These indices range from having agricultural to meteorological specific uses. This study will use Hogg's (1997) climate moisture index (CMI), which has been specifically designed to track the forest-grassland transition. The index is estimated as the difference of precipitation and potential evapotranspiration and is calculated based on monthly values summarized over the course of a year. CMI values above zero indicate a positive annual evapotranspiration balance that supports forested ecosystems (in units of mm precipitation). Negative values indicate water deficits with an expectation that forested ecosystems would not be supported. In this study we focus on how the zero-CMI isopleth for the latest 30-year climate normal period (1991-2020) has shifted relative to the historic climate normal period (1961-1990), which often serves as reference representing climate conditions before a significant anthropogenic warming signal. Similarly, shifts of the zero-CMI isopleth under future climate projections were evaluated, asking what proportion of forest tree populations may no longer be supported by a positive annual evapotranspiration balance.

Because different species may have different drought tolerances, this analysis will be carried out at the species level, with forest inventory plot data representing populations of each species throughout its range. The main objective is to identify which tree populations may be vulnerable to dieback or mortality under observed and projected climate change with a focus on a single climatic parameter, the evapotranspiration balance represented by the CMI metric. The specific objectives are (1) to determine individual species' climatic niche space based on the reference climate conditions for the period 1961-1990 and species presences in 55,700 plot locations across western Canada and the United States; (2) identify changes in the proportion of each species populations that are potentially exposed to drought under observed and projected climate change; (3) validate if inferred drought vulnerability under observed climate change has lead to observed climate change impacts for three tree species (*Pinus edilus*, *Populus tremuloides*, and

Pinus ponderosa) that have suffered major drought related dieback and mortality in western North America.

2. Literature Review

To aid the assessment of what could be a tree population vulnerable to drought, an overview of climate change, plant tolerances, drought effects on forests, and how we measure drought are reviewed. There have been decades of research dedicated to climate change, observed changes and future projections have been studied (Houghton, 1990; IPCC, 2014). Similarly, plant tolerances and the discussion of physiological responses of stress from temperature, precipitation or evaporation provide a comprehensive but straightforward foundation to how plants are likely to respond to these climatic stresses. The effects of drought on forests in western North America is also discussed alongside how drought is measured and what drought index this study incorporates.

2.1. Observed and projected climate change for western North America

The first *Intergovernmental Panel on Climate Change* (IPCC) assessment on climate change (Houghton, 1990) correlated the greenhouse effect with rising global. The report links human activities and the rise of carbon dioxide, methane, nitrous oxide and chlorofluorocarbon emissions further increases the greenhouse effect. The increase of greenhouse gases has led to increases in global average temperature. According to the last Assessment Report 5 (AR5) (IPCC, 2014), a 0.85-degree Celsius increase in global temperature has occurred since 1880. In other IPCC reports, observations in North America attributed with very high confidence in correlation with climate change is affecting glaciers, snow, ice, permafrost, rivers, lakes, floods, droughts, and marine ecosystems (IPCC, 2014).

The intensification of the hydrological cycle resulting from climate change effects increases global temperature, cloudiness, and frequency of extreme climate events (IPCC, 2014). A study showing the increase in cloud cover and the cloud albedo adds more emphasis on the evidence that corroborates the changes in atmospheric composition due to an increase in anthropogenic activities with the current state of climate change (Norris, 2016). In 2007, Smol and Douglas concluded a 24-year monitoring survey of ponds on Cape Herschel in Nunavut, Canada (Smol, 2007). The study was monitoring the conductance of ponds in the region as a measure of precipitation and evaporation. By the end of the study, most of the ponds being monitored had significantly lower levels or had dried up completely. The authors associate this change in water levels to an increase in regional temperatures, resulting in increased evapotranspiration of the ponds and the length of ice-free conditions.

There are also many predictions about how the current climate change is progressing and where it will take us in the future. The IPCC has different scenarios that follow various emission levels, and the resulting climate change is likely to occur based on these emission scenarios (Zhang et al., 2007). The emission scenarios vary because of humans' adaptive capacity to change or alter greenhouse gas emissions resulting in RCP 2.6 or 4.5 scenarios. However, if business as usual dominates, the RCP 8.5 scenario is likely to unfold. Business as usual refers to a lack of action from people to reduce greenhouse gas emissions (Zhang et al., 2007). This paper will focus on RCP 4.5 and 8.5 scenarios.

Many of the predictions include an increase in global temperature, variation in precipitation, and a loss of biodiversity. The loss of biodiversity is a consequence of the changes happening to the climate. The changing climate has initiated atypical phenological responses from various plants and animals. These responses result in spring events happening sooner and fall events happening later, including migratory birds arrival, budburst, flowering, leaf fall, migratory bird departure and hibernation timing (Parmesan & Yohe, 2003). A meta-analysis found a phenological mean shift by 2.3 days per decade in spring timing for over 170 species, including herbs, shrubs, trees, birds and butterflies. In the same study, 62% of species included in the analysis were revealing signs of early spring showing, and that 87% of the findings were in agreement with climate change predictions (Parmesan & Yohe , 2003). Other future implications of projected climate change affecting biodiversity in western North America include shifts in tree ranges and distribution, declines in alpine species like Cinereus and mountain shrew, and a decline in the reproductive capacity of 6 female bats (Shafer et al., 2001; Langdon & Lawler, 2015; Adams, 2010).

As a result of changing climatic conditions, a shift in species ranges has been detected. Through demographic studies where the location of seedlings compared to the location of mature trees has been used to detect potential latitudinal shifts of species (Hanberry & Hansen, 2015). However, a species ability to migrate into more favourable climatic environments can be challenging to prove based on the frequency of assisted migration through ornamental planting or animal dispersal (Hanberry & Hansen, 2015). Furthermore, the sensitivity of a species to changing conditions can also affect its ability to migrate. Mainly, species sensitive to climate extremes will reside in particular regions, making migration outside this region difficult (Germain & Lutz, 2020).

2.2. Plant tolerances

Temperature influences the physiological processes of trees, including photosynthesis, respiration and cell growth, and how trees respond to seasonal fluxes (Burns 1990). The temperature during the growing season affects the growth rate of trees, which is a mechanism of the biochemical processes of photosynthesis. A review paper by Way and Oren (2010) synthesized the catalogue of research on how tree growth responds to changes in temperature. They found that boreal tree species, which operate below their temperature optimum, respond positively to growth at higher temperatures, but that tropical trees, who operate at their temperature optimum, do not respond to increased growth at higher temperatures. Other studies have found similar results pointing to a positive correlation between temperature and tree growth (Boisvenue, C. & Running, S. W., 2006, Gamache & Payette 2004, Myneni, R. B. et al., 1997, Lucht et al., 2002). These findings have attributed increased growth from higher temperatures to an increase in the duration of the growing season and earlier spring budburst. However, increased growth is limited to the extent of the temperature increase, with a 1-2 degree increase making the most significant difference in growth. As temperature increases beyond 1-2 degrees, the effect can begin to negatively affect tree growth with temperature increases growing to 3-4 degrees (D’Orangeville et al., 2018). Because the effects of temperature vary depending on the degree of the temperature increase, species, or latitude, temperature changes should be considered in conjunction with other climatic factors.

Precipitation can have a much lesser effect on plant traits, including plant height, leaf area, and photosynthesis than temperature (Moles et al., 2014). Because precipitation only tells part of the story in terms of water availability, it can be a poor measurement to assess plant traits (Griffin-Nolan et al., 2018). However, what is essential about precipitation is the amount of water made available to the plants. Factors like surface run-off, snowmelt, and evapotranspiration all affect soil moisture and play a role in plant water availability. Precipitation in the form of rain, snow, and fog all act as inputs of water into the soil made available to plants through their roots. The wilting point of soil is the amount of soil moisture that is no longer accessible to plants, whereas the field capacity is associated with the amount of water in the soil available for plants (Burns, 1990). These two concepts are important as plants that experience moisture deficits beyond the wilting point cannot recover (Burns, 1990). As described by Ciais (2005), rainfall deficit can lead to increases in evapotranspiration and soil dryness and thus can affect a drop in gross primary production. Although the precipitation regime for western North America is very diverse, plants tend to respond to variability in precipitation events rather than precipitation amount (Gu et al., 2016).

2.3. Climate change and drought effects on plants

Drought has long been a climatic disturbance faced by forested landscapes. However, during increases in temperature, drought events are becoming more severe and frequent. The following terms all describe the same new types of droughts characterized by recent rises in temperature: "global-change-type-drought," "hot droughts," and "hotter droughts" (Allen et al., 2015; Breshears et al., 2005; Overpeck & Udall, 2010). Global change type droughts was referred to by Breshears (2005) and is characterized by an increase in severity and frequency of droughts associated with warming temperatures from anthropogenic climate change. Hot and hotter droughts coined by Allen et al. (2015) and Overpeck & Udall (2010) refer to the compounding impacts of hot temperatures on an already severe drought.

When drought conditions occur, there are several physiological responses from trees that lead to mortality and dieback. Trees can face the risk of mortality due to drought through xylem cavitation (Hogg et al., 2008). Under severe stress from lack of water, the xylem vessels become damaged through embolism by uptaking air bubbles, and trees lose their ability to uptake water (Tyree & Sperry, 1988). Xylem cavitation can frequently occur in aspen and popular trees and will often present itself as crown dieback as the xylem vessels farthest from the roots will become affected first (Frey et al., 2004). *Zimmermann's hypothesis* is a theory that explains the variability of hydraulic conductivity throughout a tree, with the most significant conductance at the top of the tree and towards the ends of branches to ensure water reaches the leaves (Zimmermann, 1978). This hypothesis proposes that the leaf-specific conductivity (LSC) in peripheral branches is much less than in dominant branches (Tyree & Sperry, 1988). The physiological ability of a tree to draw water from its roots and move that water against gravity towards the top branches while prioritizing what branches receive the most water is a mechanism built to combat drought stress. However, despite a tree's ability to sacrifice less valuable branches in times of hydraulic stress and xylem malfunction, this direct cause of mortality during drought is still of concern.

Another mechanism of mortality in drought-stricken regions is carbon starvation, where droughts are not severe enough to cause xylem cavitation but prolongs enough to disrupt photosynthesis and, thus, critically foiling the trees' carbon reserves (McDowell et al., 2008). In carbon starvation, stomata dysfunction occurs to overcome xylem cavitation and vessel embolism, and as a result, photosynthesis decreases (Adams et al., 2009). The depletion of carbohydrate reserves results from a lack of water available to the roots. To prevent more water loss through transpiration, stomatal closure occurs, resulting in lack of water but also a loss of CO2 from the soil (Adams et al., 2009). However, there is also speculation of carbon starvation as a mechanism of tree mortality. The counter argument to carbon starvation is based on a lack of evidence to show a reduction in stored carbon at the time of tree death (Sala, 2009).

Despite not having a comprehensive understanding of tree mortality (Güneralp & Gertner, 2007), drought can play an influencing role in the death of a tree. Following a severe drought in 2001-2002 in western Canada, tree measurements were collected from plots in Manitoba, Saskatchewan, and Alberta to study the effects of severe water stress on Populus tremuloides. It found that the stress caused by drought conditions was the major contributing factor to widespread Aspen dieback and mortality in the study region (Hogg, 2008). Additionally, studies on the same species in the Canadian Rocky mountains found that despite trees having been affected by secondary mortality agents like pathogens and insects, 20% of the dead trees had no signs of these secondary agents, leading to a significant driver between drought and Aspen mortality (Anderegg, 2015). Another study in Texas following drought found little evidence of insects, leading researchers to believe a strong influence of drought on Pinus mortality (Anderegg, 2015).

A secondary or indirect effect of drought on tree mortality is the increase in insect infestations. A significant correlation was found between drought and Pinus edulis trees attacked by pinon beetles while conducting a drought-induced experiment (Gaylord et al., 2013). The same study found higher mortality rates in the trees affected by water restrictions and that 92% of dead P.edulis trees had evidence of beetle infestation (Gaylod et al., 2013). Although these are indirect effects, the effects hotter droughts have on forests can make trees' defence mechanisms weak, thus compromising their ability to combat insect infestation (Millar & Stephenson, 2015).

2.4. Drought types and indices

Just as there are many different types of drought, there are also many ways to measure drought. Indices are created to measure drought characteristics, often specific to the type of drought or application of drought research. Drought indices incorporate data from one or more indicators like precipitation, relative humidity, or temperature to categorize droughts into a single numerical value (Zargar et al., 2011). For example, drought defined in a meteorological way describes drought events in terms of a lack of precipitation and therefore uses data that accounts for the amount of precipitation for a given period (Mishra & Singh, 2010; Yevjevich, 1967). Furthermore, meteorological drought indices are location-specific due to the connection between climate and geographic influences (Quiring, 2009). In addition to the meteorological drought, there is also agricultural and hydrological drought, defined by a measure of soil moisture deficiency and reduced flow in watersheds, respectively (Zargar et al., 2011). Because of the variation in drought definitions, a diverse group of indices is used appropriately for each specific drought.

A review of drought indices from the United States includes 13 indices. Munger's, Kincer's, Marcovitch's, Blumenstock's, Antecedent Precipitation Index, Moisture Adequacy Index, Palmer's Index, Crop Moisture Index, Keetch-Byram Drought Index, Surface Water Supply Index, Standardized Precipitation Index, Vegetation Condition Index, and Drought Monitor (Heim, 2002). In the 1960's, Palmer (1965; 1968) developed two indices that are among the most widely used drought indices in the United States (Ji & Peters, 2003). The Palmer Drought Severity Index (PDSI) uses hydrological variables like precipitation, evapotranspiration and soil moisture to calculate spatial and temporal drought severity (Alley, 1984). Because this index utilizes direct water balance variables, it is thought of as an easy-to-use approach. However, over time PDSI has been modified and improved to account for its overestimation of drought based on its use of simplified estimates of potential evaporation (Sheffield et al., 2012).

There are many other indices that can be used to measure and account for drought than the ones listed above, it is generally up to the index user and its application to choose the appropriate indices. There are also different classes of indices including meteorological, hydrological, soil moisture, remotely sensed, and modelled (WMO, 2016). Of these indices, some of the variables used to provide quantitative and qualitative measurements include available water content, crop data, evapotranspiration, precipitation, potential evapotranspiration, solar radiation, snowpack, soil type, soil water deficit, temperature, and wind data (WMO, 2016).

Drought indices range from simple, having only one or two variables, to complex multivariable calculations. For example, the Marcovich Index ($=\frac{1}{2}(N/R)^2$), where " N is the total number of two or more consecutive days above 32.2°C (90°F), and R is the total summer rainfall for the same months" (Heim, 2002). However, drought indices can become increasingly more complicated by adding multiple variables accounting for soil moisture, aridity, humidity, potential evapotranspiration, run-off potential, coefficients, constants, and inclusion of different time scales and algorithms.

These measurements are used to assign threshold values to species in order to be able to predict and further research plant responses to drought. However, based on the variability in indices to choose from, the effectiveness of thresholds can also vary. In agricultural studies of different crops, the effectiveness of drought indices depends on the variety of crops. For instance, the Marcovich Index was developed to study the Bean beetle in the eastern portion of the United States (Heim, 2002). The CMI index offers effective forecasts of forest coverage in the Prairie provinces (Hogg & Bernier, 2005). However, the complexity and specificity of drought indices make it challenging to rank them. There are many limitations to indices if the algorithms used to create them are too specific. For example, the Palmer drought severity index (PDSI) algorithm uses Thornthwaite's method to calculate potential evapotranspiration, which only uses monthly temperature data, even though PET can be calculated more accurately using the Penman-Montieth equation from FAO (Quiring, 2009). A review of drought indices used in the United States made a note of 7 indices, their strengths, weaknesses, and a qualitative ranking based on robustness, traceability, transparency, sophistication, extendibility, and dimensionality (Quiring, 2009). Although some indices scored better than others, the paper's final suggestion was to use a multi-index approach based on the implicit variability of the index’s studies.

CMI is the drought index used in this study. It is derived from Hogg (1997) and focuses on the relationship between forested landscapes and the atmosphere and how moisture can predict the spatial distribution of forest cover. The index uses a simple formula, where the annual precipitation (P) gets subtracted from the mean annual potential evapotranspiration (PET). To estimate PET, the Penman-Monteith equation is used. This estimate of PET allows for accurate estimation of evapotranspiration by calculating radiative energy balance coupled with aerodynamic theory (McNaughton, 1984). The parameters for the Penman-Monteith equation can also be adjusted, allowing for location-specific use of the CMI index (Hogg, 1997). For use in this study, CMI is an appropriate fit because it works for large spatial scales without the use of agricultural metrics. CMI aims to connect forested ecosystems with climate to show where forest distribution occurs (Hoggs, 1994). Hoggs’ study (1994) found the zero isoline representing where precipitation equals the annual potential evapotranspiration corresponds significantly to the southern boundary of the Canadian boreal zone. Because forests are confined to regions where precipitation is greater than potential evapotranspiration (Hoggs, 1994), the CMI index is a poignant metric to use when looking at directional climate change impacts.

3. Methods

3.1. Plot data

The study relies on a compilation of 55,743 forest inventory plots of species occurrence for 24 western North American tree species, compiled by Roberts and Hamann (2012). This data coverage includes all major forest biomes west of the 100 degree longitude. It includes the coastal forests of the pacific northwest, represented by Pacific silver fir (*Abies amabilis*), Noble fir (*Abies procera*), Bigleaf maple (*Acer macrophyllum*), Red alder (*Alnus rubra*), Incense cedar (*Calocedrus decurrens*), Alaska yellow cedar (*Chamaecyparis nootkatensis*), Sitka spruce (*Picea sitchensis*), Douglas fir (*Pseudotsuga menziesii*), Coast redwood (*Sequoia sempervirens*), Western redwood (*Thuja plicata*), and Western hemlock (*Tsuga heterophylla*); the interior region spanning British Columbia, Alberta and southward along the Rocky Mountains towards Colorado represented by Subalpine fir (*Abies lasiocarpa*), White birch (*Betula papyrifera*), Western larch (*Larix occidentalis*), Engelmann spruce (*Picea engelmannii*), Black spruce (*Picea mariana*), Whitebark pine (*Pinus albicaulis*), Lodgepole pine (*Pinus contorta*), Western white pine (*Pinus monticola*), Ponderosa pine (*Pinus ponderosa*), and Mountain hemlock (*Tsuga mertensiana*); the Boreal regions of Northern BC and Alberta, the Northwest Territories and Alaska represented by White spruce (*Picea glauca*); the southern region including New Mexico, Arizona, Texas and the north western tip of Mexico represented by Colorado pine (*Pinus edulis*); as well as Trembling aspen (*Populus tremuloides*), a widespread species spanning a major portion of the study region. These 24 species represent the most common or ecologically most important trees found within the study region.

3.2. Climate data

The data generated for this study utilizes Climate NA V6.4 software, which generates climate data following methodology detailed by Wang et al. (2016). This software generates interpolated data for a wide variety of biological climate variables. Climate NA produces historical data using Parameter-elevation Regressions on Independent Slopes Models (PRISM) based on methodology from Daly et al. (2008) and WorldClim (Hijmans et al., 2005), which provides greater accuracy of climatic conditions in mountainous regions (Hamann et al., 2013). The future predictions are based on the Coupled Model Intercomparison Project phase 5 (CMIP5) of the World Climate Research Programme. All data sets generated for this study used ClimateNA software package (Wang et al., 2016), which is available via http://tinyurl.com/ClimateNA.

The essence of this software is to provide better accuracy of climate predictions in cases where the elevation sensitive climatic conditions can change over a few kilometres. The software incorporates lapse-rate adjustments to each variable and geographic location. These adjustments improve accuracy of grid versus geographic elevation discrepancies. Because the study region is so diverse in elevation, having many mountain ranges and narrow bands of elevation gradients hosting tree species, the scale-free nature of the software is specifically formulated to improve accuracy of climate variables in these areas. ClimateNA produces high-resolution data that accounts for these geographic conditions and provides greater accuracy along elevation gradients, mountainous regions, and rain shadows.

ClimateNA is used to generate climate data for a prewarming-historical timeframe (1961-1990), recent timeframes (1990-2020), and future scenarios based on RCP emission scenarios 4.5 and 8.5 for 2025, 2055, and 2085 timeframes using a subset of the plot dataset previously mentioned. The raster output data represents values for annual climate variables, including mean annual temperature, mean annual precipitation, and Hogg's climatic moisture deficit (CMI). ClimateNA generated raster outputs files for two applications in this study. First, ClimateNA was used to generate a gridded data set to create base maps representing full coverage of climate variable values for CMI, mean annual temperature, and mean annual precipitation at a resolution of 5 km. The second application was to generate projections of CMI values for two scenarios and 3 future timeframe intervals.

3.3. Visualization of climate change for western North America

Gridded raster datasets generated for a current time frame (1991-2020) represent observed changes. Gridded data sets are also compiled for predicting 2020, 2050, and 2080 values for CMI, mean annual temperature (MAT) and mean annual precipitation (MAP). To validate the predictions made by the software, I compare using the observed changes from the 1991-2020 timeframe. This data set from 1991-2020 represents 30 years of actual environmental observations. The gridded data set forms the basis for a 5 km resolution raster grid. This gridded data set is inputted into the ClimateNA software to generate values for climate variables under the past scenario (1961-1990), current scenario (1990-2015), and RCP 4.5 and 8.5 for 2020, 2050, and 2080.

The climate variables used during this comparative analysis are CMI, MAT, and MAP. For each scenario, the difference between the values generated from each climate variable and the values for the past data set (1961-1990) are used to determine the degree of change from the baseline pre-warming conditions. This delta value represents the observed change in climate over time. Using ArcGIS to visualize this change, maps of western North America are created in 5km resolution. These visual aids are an approachable way to validate the climate modelling software and determine similarities and differences between the observed and predicted change in temperature, precipitation, and moisture deficits over time.

CMI is the product of potential evapotranspiration defined by the daily maximum and minimum temperatures subtracted from precipitation (Hogg, 1994). Because CMI is a simple approach using available climate metrics, it is an accepted way to denote geographic ranges of closed-canopy forested landscapes (Hogg et al., 2013). To emphasize and further validate this function, I use the CMI map showing the absolute values from the recent timeframe (1991-2020) and compare it to a remotely sensed tree cover ASC file. The images produced from this comparison analysis will show the CMI isoline, where CMI equals 0 and the potential evapotranspiration is equal to the amount of precipitation. These areas demonstrate a moisture regime suitable for forested ecosystems and should be similar to the map created using only the remotely sensed tree cover.

3.4. Identification of threatened populations

The climate data generated using ClimateNA produces historical values (1961-1990), observed values (1991-2020), and future values for three timeframes under two different emissions scenarios, allows for further investigation of the directional trends associated with CMI. Each species has a range of CMI values depending on geographic distribution and niche climatic tolerance of the species. For each species, the range of CMI values is determined. These values represent the minimum and maximum CMI values for each species, plus the CMI value corresponding to the 1st, 2.5th, 5th, 25th, 50th, 75th, 95th, 97.5th, 99th percentiles between the minimum and maximum values (Table 1).

To find and identify populations of threatened species, CMI values from the past timeframe (1961-1990) are used to compare the CMI values of observed and future timeframes for the same plots. To account for the possibility of trees growing outside of their niche climatic environment, the lowest 2.5 percentile from the historical data set is used as the CMI proxy value. The data is then sorted to identify the plots where each tree species is present (species occurrence = 1) and is less than the historical proxy limit. For each time frame (observed, RCP 4.5 for 2020, 2050, 2080, RCP 8.5 for 2020, 2050, 2080) and for each species, CMI values for each plot where the species is present are compared to the historical CMI proxy value.

In this study, threatened populations are determined by finding when a tree species CMI values from observed or future timeframes are below the historical CMI proxy value. The frequency of species occurrence from the historical data set and the frequency of species occurrence that resides below the historical CMI proxy value from the other time frame is used to calculate the proportion of each species that reside or will reside in a drier climatic environment (Table B). The exploration, sorting and calculating of species occurrence and CMI values was done using R-Studio Version 4.1.1 (RStudio, 2020).

4. Results

4.1. Climatology and tree cover of the study area

The maps for CMI, mean annual precipitation, and mean annual temperature are shown for the 1961-1990 climate normal period (Figure 1). This historical timeframe represents a pre-warming period, where the effects of climate change have minimal effect.

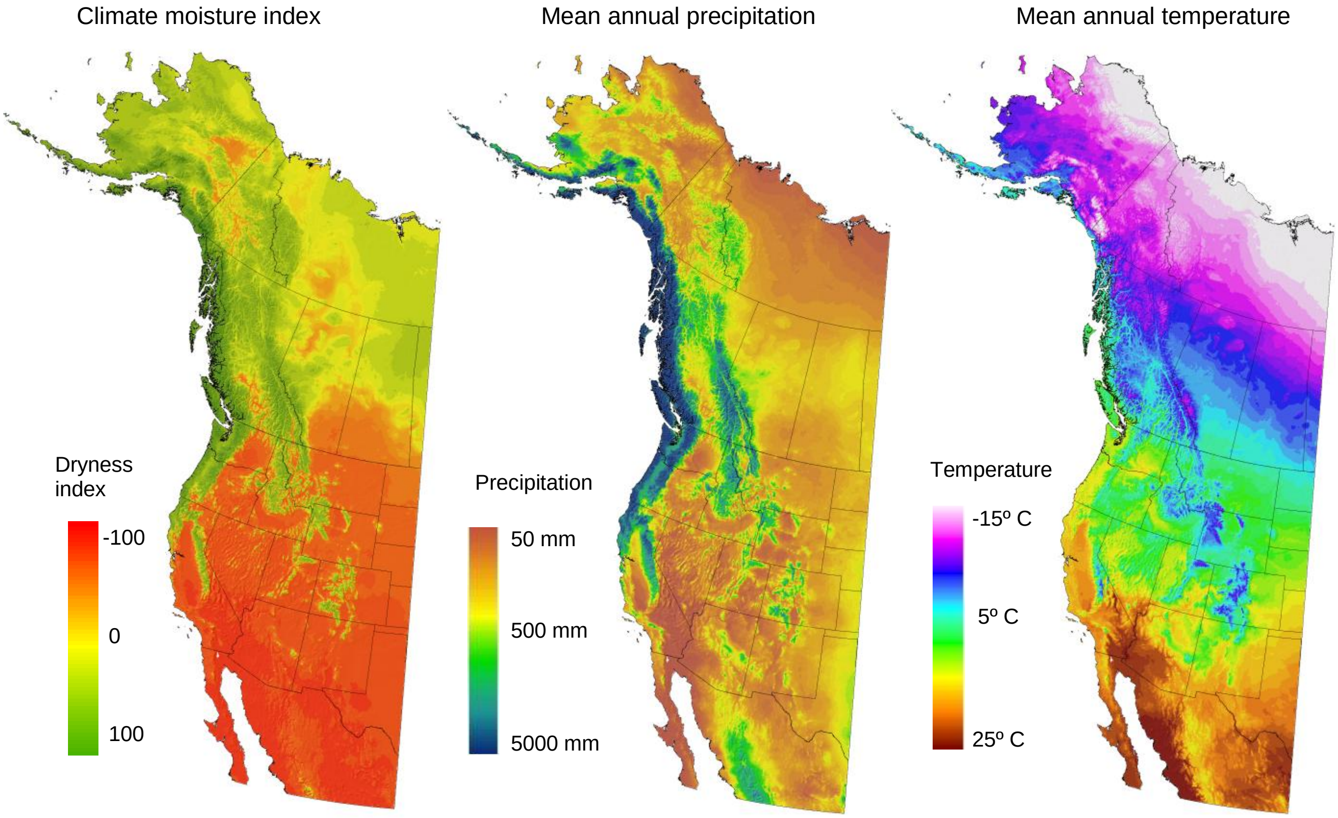


Figure 1. *From left to right, climate normal grids for the 1961-1990 period of Hogg's (1997) climate moisture index, mean annual precipitation and mean annual temperature for the study area.*

The CMI map shows moisture deficits in red and orange, these areas are primarily located in the southern portions of western North America, with some exceptions extending north within the prairie regions of Canada and in the interior of Alaska. Areas of marginal moisture availability primarily exist in non-mountainous regions of the northern extent of western North America, as well as between the boundaries of high moisture deficit and areas of moisture abundance. Moisture abundant zones exist in areas along the coast, in mountainous regions, where annual snowfall contributes to a higher moisture index. Because CMI is influenced by other climatic factors, historical averages for precipitation and temperature are also shown (Figure 1).

The map of mean annual precipitation shows a similar pattern to the CMI map. Mean annual precipitation ranges from approximately 1000 mm in southwestern Alaska and northwestern British Columbia to approximately 50 mm in Death Valley California and southern and northern portions of Baja, California. However, precipitation does not solely govern the values for CMI. Looking at Northern Mexico, where a band of high precipitation extends north, in the same location on the CMI map, a large area is actually moisture deficient. This is why CMI is shown alongside precipitation and temperature. In northern Mexico, where precipitation is high, but CMI is low, the evaporation potential causing drier conditions is driven by the region’s high temperatures.

Conversely, in areas of lower annual temperatures and low precipitation like Alaska, eastern Yukon and the Northwest Territories, moisture availability is stable. The relationship between temperature and precipitation in governing CMI values, reflects temperature’s ability to regulate evapotranspiration.

The comparison using remotely sensed tree cover data next to the CMI map for the observed data set gives a sense of how CMI corresponds to tree cover (Figure 2). Regions where similarities between positive CMI values correspond to forested ecosystems include the prairie border along the southern edge of the Boreal forest in Alberta and Saskatchewan, the coastal forests that extend north from Northern California towards Alaska, and the southern Rocky Mountains that extend from Montana down into Colorado. However, in the most southern regions, including Mexico, Arizona and New Mexico, CMI as a predictor of forest coverage works less well. A similar pattern occurs for the most northern climates. CMI overpredicts forested regions in the mountain ranges of Alaska, Yukon and NWT, as well as the high arctic.

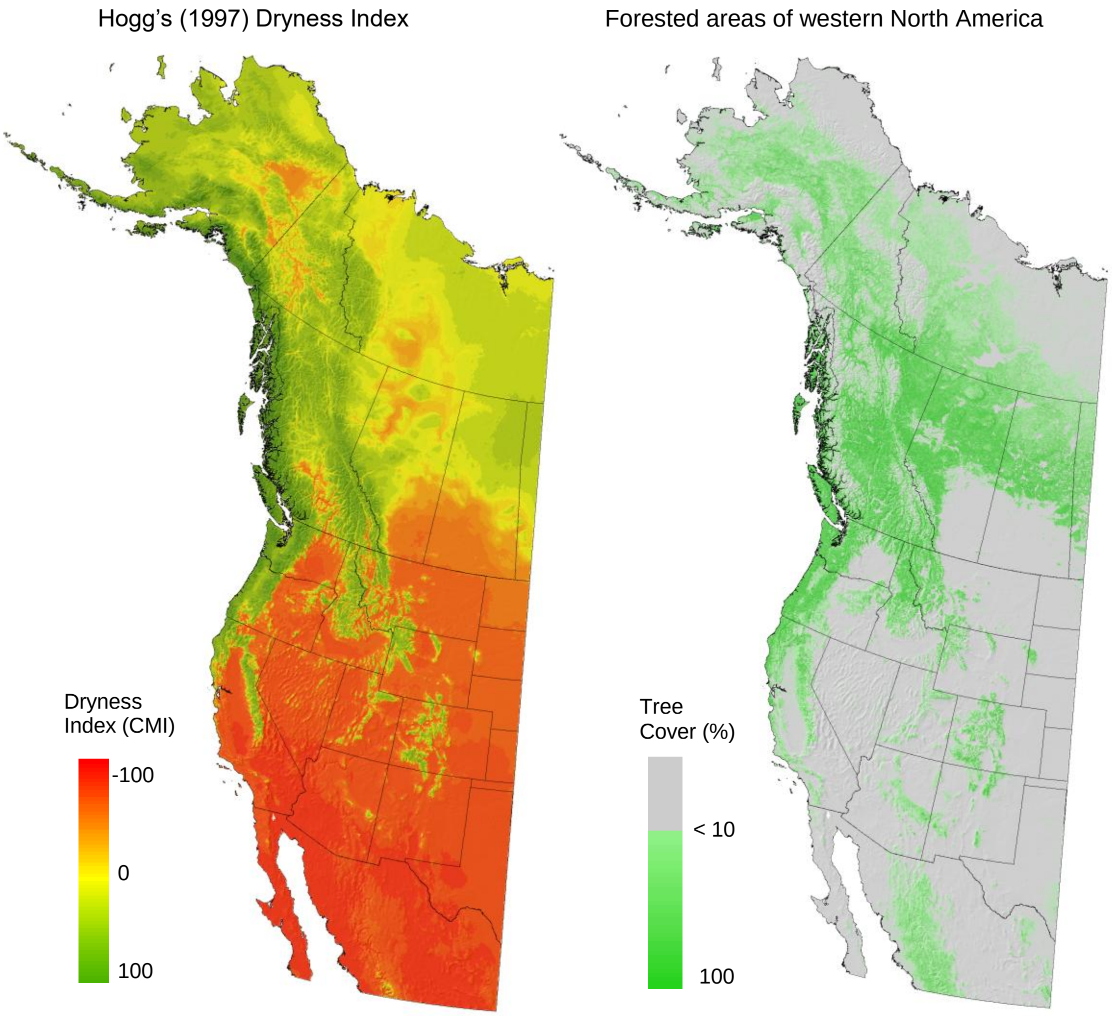


Figure 2. *Correspondence of Hogg's (1997) climate moisture index (left) and remotely sensed tree cover (right, from MODIS vegetation continuous fields) for western North America.*

4.2. Observed climate change

Observed climate change in this study is represented by the difference between the 1961-1990 climate normal period and the subsequent 1991-2020 climate normal. CMI is a metric influenced by other climatic variables, including temperature and precipitation. To understand what is driving changes in CMI, changes in temperature and precipitation must also be considered (Figure 3).

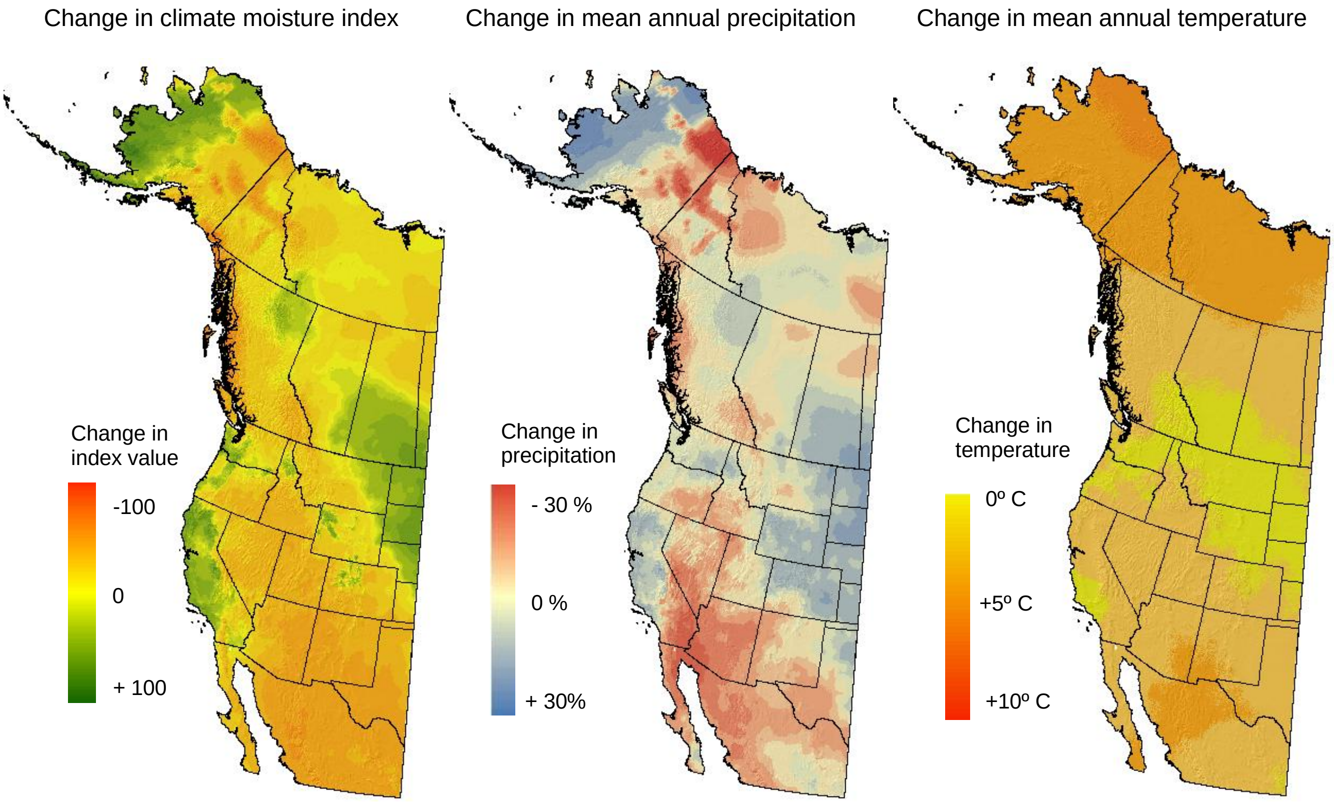


Figure 3. *Maps showing the changes in climatic variables when comparing a historical reference data set (1961-1990 normal) with a recent climate average (1991-2020 normal period). From left to right, changes in Hogg's (1997) climate moisture index, changes in mean annual precipitation and changes in mean annual temperature.*

Temperature across western North America from past levels to averages from the current timeframe (1991-2020) show an overall increase. These increases range from 0.5 degrees to 1-2 degrees. The largest increase in temperature occurs in the south, affecting parts of Northern Mexico, Arizona, New Mexico, and Texas. Additionally, there is large increase in temperature occurring in the North, affecting parts of the Yukon Territory and Alaska. However, there also exists regions where temperature has seen little change, including southern California and through the central interior region of western North America.

Precipitation has seen more variable changes over the two timeframes. Decreases in precipitation as a percentage from historical averages can be seen throughout the southern United States, affecting parts of Northern Mexico, California, Nevada, Arizona, New Mexico, and Texas. These areas have been affected by up to a 30% loss of precipitation from what these regions usually see. Additionally, decreases in precipitation have also affected the coastal regions of British Columbia, the Rocky Mountains bordering British Columbia and Alberta, as well as Northern regions including Alaska, the Yukon, and Northwest Territories. Despite loss of precipitation in some regions of the study area, there are also regions where precipitation has seen an increase from historical averages. These regions include western Alaska, southern Saskatchewan and parts of eastern United States.

When looking at the combined changes of temperature and precipitation, a general pattern emerges to help explain the driving forces behind the changes in CMI. In areas affected by a decrease in precipitation and an increase in temperature, we see a decrease in CMI levels. The decrease in CMI corresponds to a lack of moisture availability indicating the increases in temperature influence the evaporative demand without precipitation to restore the dryness. The regions affected by this pattern include Northern Mexico, Arizona, and New Mexico as well as parts of Alaska and the Yukon Territory. However, precipitation alone can also drive changes in CMI, as seen in areas where little temperature change occurred but precipitation increased there is a positive effect on CMI. This pattern reinforces the impact increases in temperature can have on the evaporative potential of the region.

4.3. Projected climate change

Similar to the maps of observed change, projections for two emission scenarios for the 2030’s, 2050’s, and 2080’s in temperature and precipitation are used to better understand projected changes in CMI. The results for changes in temperature from the past to future timeframes show the northern portion of western North America most affected by increasing temperature (Figure 4). Although all regions of western North America are projected to increase in temperature, the greatest temperature increases reside in the northeastern portion of western North America, affecting parts of the Yukon and the Northwest Territories. The two RCP scenarios follow similar paths and trends. However, what should be noticed is the severity of temperature increases as time progresses under the RCP 8.5 scenario.

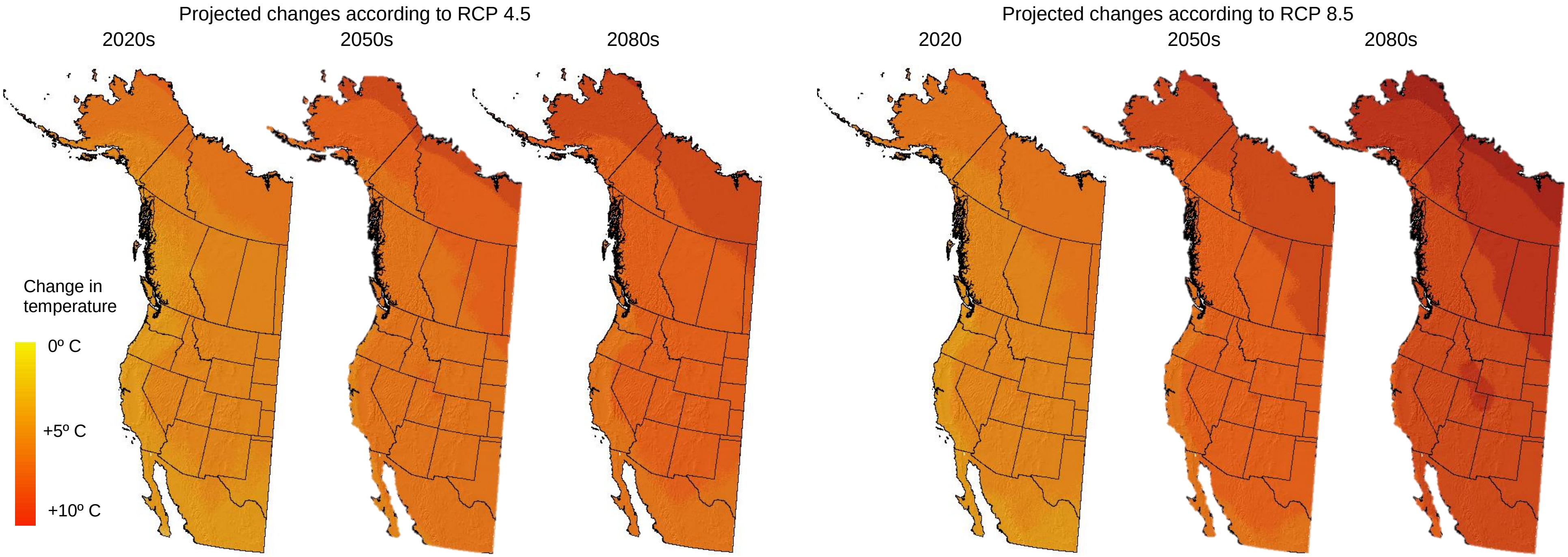


Figure 4. *Projected changes in mean annual temperature for two RCP scenarios (4.5 & 8.5) and three timeframes (2020s, 2050s and 2080s). Changes in precipitation were calculated as a difference from the historical values represented by the 1961-1990 normal period.*

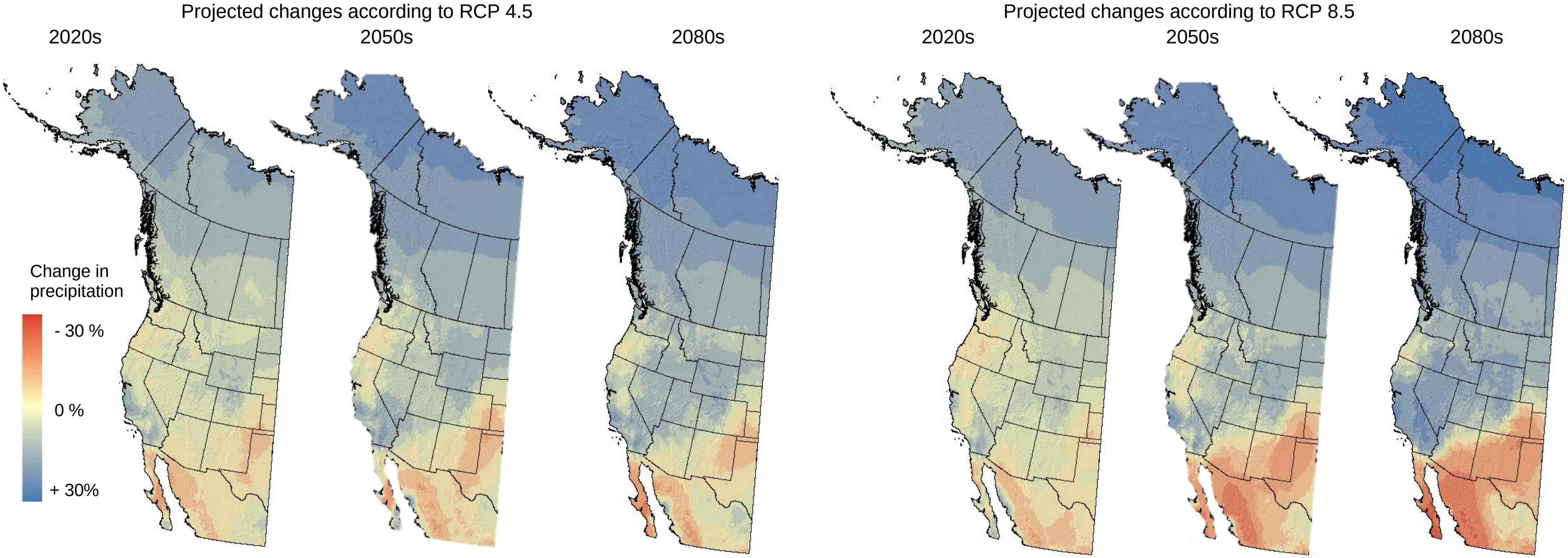


Figure 5. *Projected changes in mean annual precipitation for two RCP scenarios (4.5 & 8.5) and three timeframes (2020s, 2050s and 2080s). Changes in precipitation were calculated as a percentage from the historical values represented by the 1961-1990 normal period.*

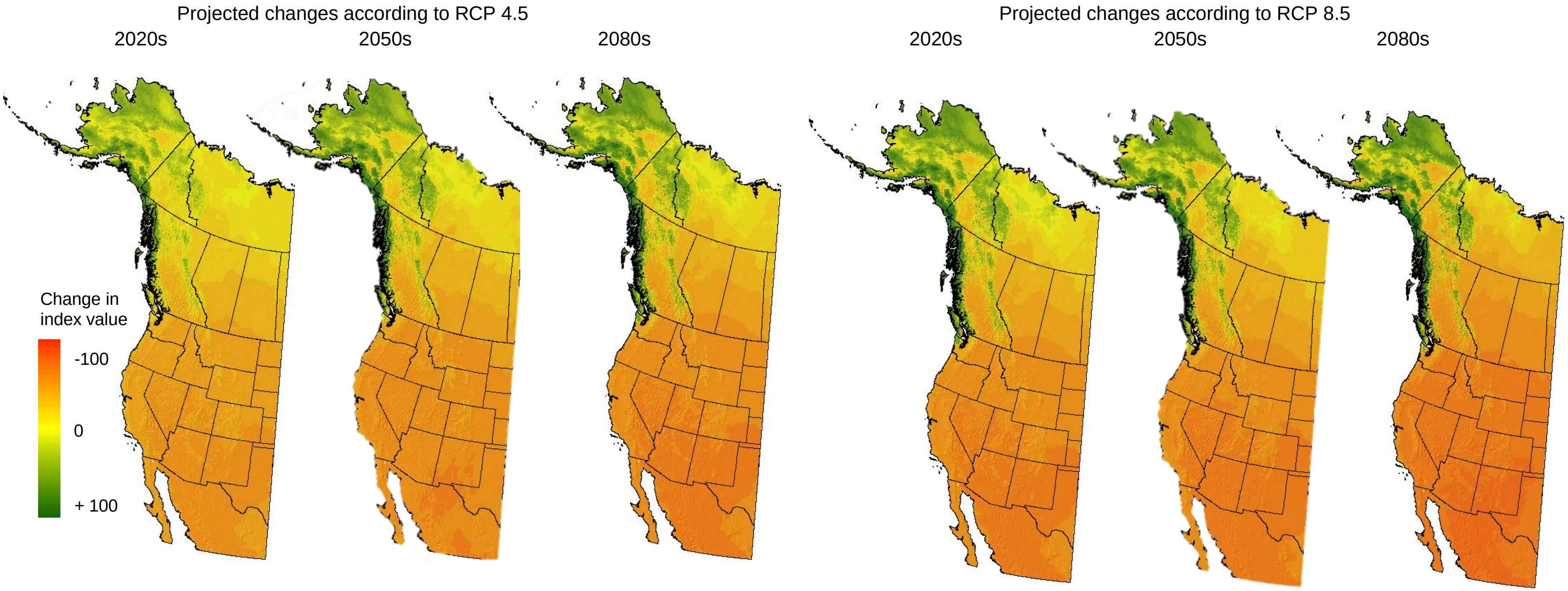


Figure 6. *Projected changes in Hogg's (1997) climate moisture index for two RCP scenarios (4.5 & 8.5) and three timeframes (2020s, 2050s and 2080s). Changes in precipitation were calculated as a difference from the historical values represented by the 1961-1990 normal period.*

The changes projected for precipitation for the 2020, 2050, and 2080's timeframes were calculated as a percentage from the values of the historical data set. There is a general trend of increasing precipitation in the higher latitudinal regions as well as an increase in drier conditions in the southern United States and northern Mexico (Figure 5).

Similar to the comparison of the most recent timeframe (1991-2020) to the historical timeframe, the changes projected to occur for CMI are largely driven by the other climatic variable, temperature and precipitation. There is an intensification of CMI over time for the projected timeframes and scenarios (Figure 6). In the northwestern portion of the study region there is an intensification of increasing moisture availability overtime. Although temperature is predicted to increase in the same region, ultimately affecting the evapotranspiration potential, there is also a predicted increase in precipitation. There is also an indication of increasing severity of moisture loss in the southern portion of the study region, affecting most of the southern United States and Northern Mexico. This portion of the study region is already susceptible to hotter temperatures, in combination with predictions of less precipitation over time, the CMI indicates potential future drought like conditions for all timeframes and scenarios in this region.

4.4. Putative species tolerances

In order to better understand the tolerance levels and climatic niche breadth with respect to climate moisture conditions of each species, I quantified the CMI values for incremental percentiles, including the minimum and maximum values where each species is confirmed to occur (Table 1). CMI values below the 2.5th percentile limit or above the 97.5th percentile are defined in this study as outliers, where tree species are growing in extraordinary conditions, ill-suited for normal growing conditions of the population. What this range of CMI values helps to show is the moisture regime according to the Hogg (1997) Moisture Index for 95% of all species occurrences.

For example, CMI values for Pinus edulis range from -96 to -23. This means that for 95% of where Pinus edulis is present, the CMI levels are at a deficit, pointing to the type of moisture regime this species can tolerate. For P. menziesii, the CMI value range is more extensive, going from -22 to 147, perhaps pointing to greater tolerance of different moisture regimes. Similarly, species like *A. lasiocarpa, B. papyrifera, C. decurrens, L. occidentalis, P. engelmannii, P. glauca, P. mariana,* and *P. tremuloides* all have 95% of their occurrences in a CMI range that is negative on the dry end and over 100 on the moist end. Furthermore, these values point to the geographic region where these species are most often found, like in the case of *C. nootkatensis* or P. sitchensis, where 95% of the species occurrences occur within CMI ranges between 80 and 484, and 113 and 479, respectively, corresponding to the moisture-rich, coastal habitats.

4.5. Potential vulnerable populations

About half of the 24 species that were evaluated had 5% or more populations located in areas with a CMI value <0, potentially vulnerable to drought conditions. Five species had 25% of their populations exposed to drought, and for two species *Pinus edilus* and *Pinus ponderosa* half of the occurrence records were located within areas with negative CMI values. Climate change projections suggest that water deficits will disproportionately increase for the species and populations that are already in vulnerable positions, whereas other species and populations are not predicted be affected by climate change impacts related to drought.

Under the most severe climate scenario, this study identifies *Larix occidentalis*, *Picea glauca, Picea mariana*, *Pinus ponderosa*, and *Pinus edilus* as vulnerable with over 25% of its population located below each species historical CMI limit. Of these species, *Pinus edlius* and *Pinus ponderosa* reside within geographic locations affected by directional climate change including increased temperature and reduced precipitation.

Table 1. *Exposure of 24 western North American tree species to drought conditions, quantified by the percentiles of Hogg's (1997) climate moisture index (CMI) values for sample plots. Tree species are sorted from most to least exposed, based on the average CMI value of the 5th to 95th percentile. In this study populations below the 2.5th percentile value were defined as potentially vulnerable to drought.*

Species	min	1	2.5	5	25	50	75	95	97.5	99	max
Colorado pine (*Pinus edulis*)	-119	-103	-96	-92	-77	-67	-54	-31	-23	-13	20
Ponderosa pine (*Pinus ponderosa*)	-98	-75	-69	-62	-40	-23	-4	44	70	94	270
Trembling aspen (*Populus tremuloides*)	-53	-27	-19	-13	1	9	19	44	55	70	300
White birch (*Betula papyrifera*)	-45	-20	-13	-7	2	10	23	62	81	102	297
White spruce (*Picea glauca*)	-40	-13	-9	-5	4	14	25	55	69	88	190
Black spruce (*Picea mariana*)	-13	-3	-1	2	10	18	27	48	57	73	146
Western larch (*Larix occidentalis*)	-42	-28	-26	-23	-1	15	37	85	108	123	167
Incense cedar (*Calocedrus decurrens*)	-56	-46	-41	-37	-5	24	61	124	167	198	290
Lodgepole pine (*Pinus contorta*)	-51	-19	-11	-4	14	27	48	107	162	291	532
Douglas-fir (*Pseudotsuga menziesii*)	-79	-51	-42	-33	-7	16	61	186	228	280	509
Coast redwood (*Sequoia sempervirens*)	-31	-27	-22	-18	9	32	87	137	147	167	167
Subalpine fir (*Abies lasiocarpa*)	-45	-6	2	8	27	48	78	130	148	169	478
Engelmann spruce (*Picea engelmannii*)	-48	-14	-6	1	32	57	86	129	145	164	213
Whitebark pine (*Pinus albicaulis*)	-32	-8	9	17	41	66	92	135	151	168	294
Western white pine (*Pinus monticola*)	-53	-16	-9	0	37	70	114	224	287	356	380
Bigleaf maple (*Acer macrophyllum*)	-56	-47	-20	-2	49	86	129	213	237	268	278
Western redcedar (*Thuja plicata*)	-40	-14	-5	4	34	91	191	350	387	443	606
Noble fir (*Abies procera*)	4	16	22	45	115	159	197	256	316	341	377
Red alder (*Alnus rubra*)	-41	13	29	46	99	137	213	320	349	379	553
Western hemlock (*Tsuga heterophylla*)	-25	1	11	19	59	128	238	373	410	474	777
Amabilis fir (*Abies amabilis*)	-34	15	28	39	123	198	289	406	449	508	625
Mountain hemlock (*Tsuga mertensiana*)	-28	24	46	61	113	185	279	424	498	577	777
Sitka spruce (*Picea sitchensis*)	15	56	80	98	179	250	313	411	484	534	777
Yellow cedar (*Chamaecyparis nootkatensis*)	19	89	113	122	206	265	339	431	479	533	777

Table 2. *Change in percent of potentially vulnerable populations of 24 western North American tree species based on observed and projected climate change. Potentially vulnerable populations were defined sample plots with Hogg's (1997) climate moisture index value lower than a species-specific 2.5th range percentile (Table 1). Tree species are sorted from highest to lowest percentile of potentially vulnerable populations for the RCP 4.5 scenario for the 2050s.*

Species	Observed	Projection for the 2020s		Projection for the 2050s		Projection for the 2080s	
		RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
Colorado pine (*Pinus edulis*)	3.1	16.5	17.5	39.6	60.0	52.7	84.8
Ponderosa pine (*Pinus ponderosa*)	0.0	7.2	7.2	14.4	24.3	20.8	42.5
Western larch (*Larix occidentalis*)	-0.4	6.8	7.6	12.5	17.8	16.4	34.0
Incense cedar (*Calocedrus decurrens*)	-0.4	7.5	8.2	13.4	17.6	15.5	24.1
Black spruce (*Picea mariana*)	1.1	5.0	5.3	9.9	17.0	15.6	43.5
Douglas-fir (*Pseudotsuga menziesii*)	-0.3	3.4	3.7	7.1	11.1	9.7	21.4
Trembling aspen (*Populus tremuloides*)	0.4	3.9	4.3	7.2	10.3	9.1	23.9
Coast redwood (*Sequoia sempervirens*)	-1.4	1.9	4.2	7.5	9.7	8.6	11.9
Lodgepole pine (*Pinus contorta*)	0.2	3.3	3.6	6.0	8.5	7.7	18.5
Subalpine fir (*Abies lasiocarpa*)	0.3	2.7	3.0	5.4	7.8	6.9	17.1
Whitebark pine (*Pinus albicaulis*)	-0.8	3.4	3.8	5.9	7.7	7.0	13.8
Engelmann spruce (*Picea engelmannii*)	-0.1	3.1	3.3	5.1	7.4	6.4	13.8
White birch (*Betula papyrifera*)	1.0	2.5	2.5	4.9	7.1	6.3	21.6
White spruce (*Picea glauca*)	0.4	1.9	1.9	3.8	6.9	6.3	26.9
Western white pine (*Pinus monticola*)	-0.7	2.4	2.9	4.6	5.9	5.4	12.1
Western redcedar (*Thuja plicata*)	0.7	1.8	2.1	3.9	5.6	4.7	10.9
Western hemlock (*Tsuga heterophylla*)	-1.2	2.0	2.1	3.2	4.4	4.0	7.6
Bigleaf maple (*Acer macrophyllum*)	-0.7	1.6	1.8	2.5	3.2	2.8	7.8
Amabilis fir (*Abies amabilis*)	-1.9	2.1	2.1	2.3	2.7	2.6	3.6
Red alder (*Alnus rubra*)	-1.9	1.0	1.0	1.7	2.5	1.8	4.8
Noble fir (*Abies procera*)	-0.1	2.4	2.4	2.4	2.4	2.4	3.6
Mountain hemlock (*Tsuga mertensiana*)	-2.4	0.8	1.0	1.5	2.3	1.9	4.3
Yellow cedar (*Chamaecyp. nootkatensis*)	-0.5	0.5	0.5	0.9	1.0	0.8	1.2
Sitka spruce (*Picea sitchensis*)	-2.5	0.3	0.3	0.4	0.6	0.4	1.3

4.6. Validation of CMI-based vulnerability inference

The most notable drought-related dieback and mortality in western North America was observed for three tree species over the last three decades: *Pinus edilus*, *Populus tremuloides*, and *Pinus ponderosa*. To test the realism of the CMI-based drought vulnerability assessment, observed geographic patterns of dieback were compared to changes in CMI between the 1961-1990 reference period and the recent 1991-2020 average (Table 3).

During the period 2002-2003, New Mexico experienced a "global-change-type-drought" (Allen et al., 2015). This climactic event was defined by its high temperatures mixed with a prolonged drought and caused widespread *Pinus edulis* die-off (Clifford et al., 2013). They used plot surveys, parameter-elevation regressions on independent slopes model (PRISM) data, and remotely sensed Landsat imagery to determine the locations of *Pinus edulis* mortality (Clifford et al., 2013). Furthermore, this study found a precipitation threshold of 600mm corresponding to either survival of trees or increased mortality depending on whether the plots received more or less than 600mm (Clifford et al., 2013).

A literature search found 8 studies that link drought to *P. tremuloides* mortality, dieback, reduced growth, and tent caterpillar infestations (Hogg et al., 2002; Worrall et al., 2008; Michaelian et al., 2011; Peng et al., 2011; Huang and Anderegg, 2012: Anderegg et al., 2013; Worrall et al., 2013; Chen et al., 2017). The areas of *Populus tremuloides* decline from Worrall et al. focus on wide-scale decline linked to landscape-level crown thinning, dieback and mortality (2013). There are many similarities between the locations of potentially vulnerable *P. tremuloides* from this study and the location of *P. tremuloides* dieback from Worrall, particularly in the southern Rocky Mountain region of the United States. Additionally, mortality of *P. tremuloides* in the southern Rocky Mountains has also been depicted in Huang & Anderegg's work (2012). However, this study shows no evidence to support the aspen decline shown in the Aspen Parkland located in Alberta and Saskatchewan, Canada. Despite this discrepancy, CMI values are strongly associated with *P. tremuloides* mortality (Hogg et al., 2008).

Observed drought impacts for *P. ponderosa* occur primarily in California. Drought events have occurred during the observed timeframe and have been attributed to biotic causes of tree death (Byer & Jin, 2017; Ganey & Vojta, 2011). Ganey and Vojta (2011) found a 74% mortality of ponderosa pine during the 2002-2007 timeframe. This study region is characterized by a recent long-term drought event from 1996-2007. Although the population of *P. ponderosa* from this study was not found to coincide with the findings from Byer and Jin (2017), this study shows how drought has led to increased mortality of P. ponderosa through insect infestations.

4.7. Observed impacts versus CMI-inferred vulnerability

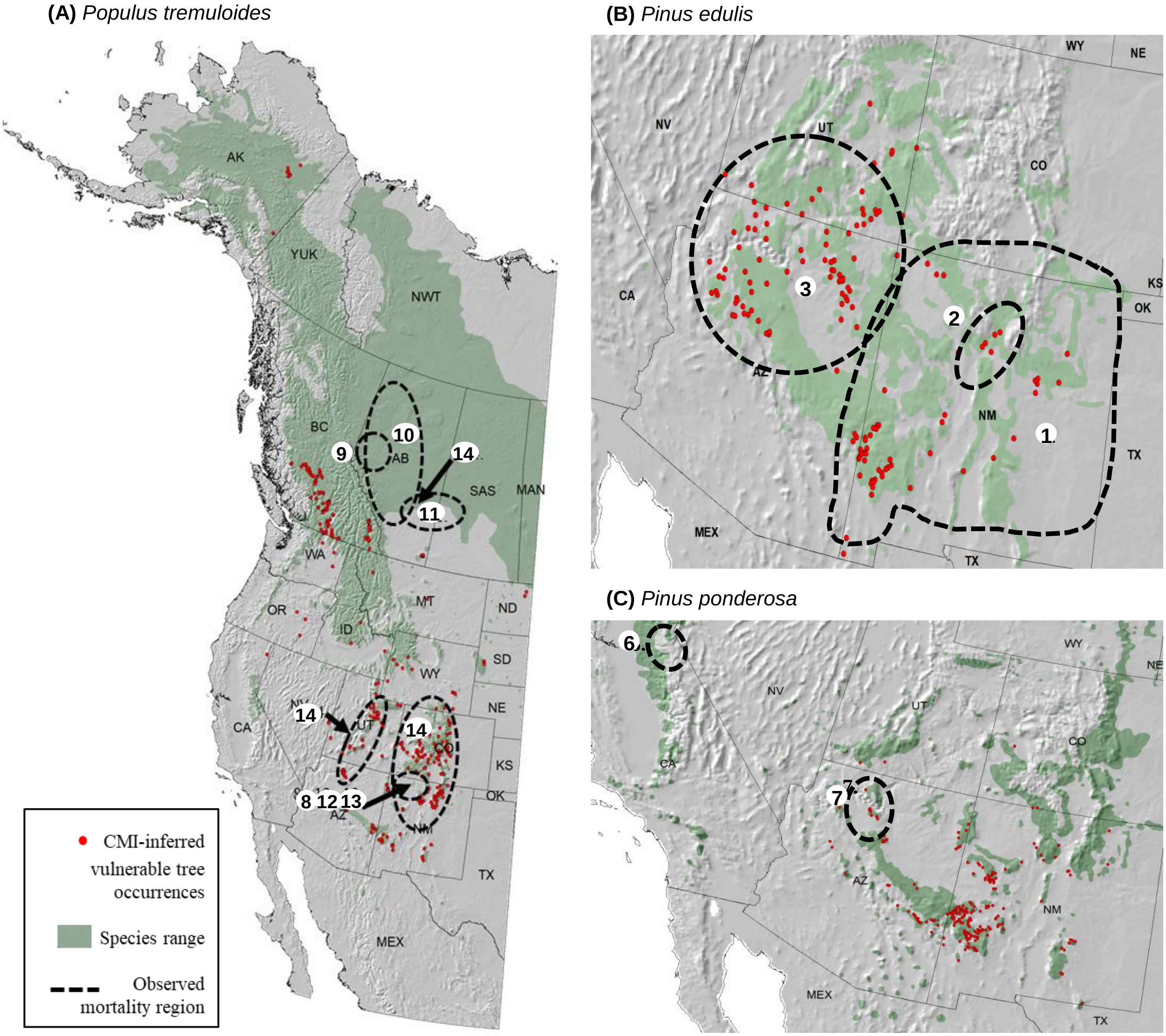
The three most vulnerable species according to the CMI-inferred data from this study, *Pinus edulis*, *Populus tremuloides*, and *Pinus ponderosa* are compared to areas in the study region where mortality and dieback has been observed in the literature. What will emerge from this comparison are the instances where vulnerable trees (red dots) align with the regions of observed dieback (dashed lines) and instances where there are no similarities.

For *Pinus edulis*, the CMI-inferred vulnerable trees correspond strongly with observed instances of P. edulis mortality from the literature (Figure 7B). The connection between results from this study and observed instances of P. edulis mortality in similar geographic areas is strong. There are 4 studies that have identified drought as a contributing factor to P. edulis mortality (Shaw et al., 2005; Breshears et al., 2009; Clifford et al., 2013; Gaylord et al., 2013). These studies match strongly with the trees identified as vulnerable in this study (Figure 7B). Like many tree species, P. edulis mortality can also be linked to indirect mortality agents like bark beetles, with drought being a dominant stressor that predisposes these trees to infestations (Floyd et al., 2009). These similarities correspond to the directional trends of climate change.

Table 3. *References for potentially vulnerable tree species with ID locations shown in Figure 7.*

ID	Citation	Region	Severity Synopsis
Colorado pine (*Pinus edulis*)			
1.	Clifford et al., 2013	NM	Identified a precipitation threshold of 600mm during the drought period, a precipitation: die-off gradient from south to north (increased mortality to the north). Did not find a relationship between die-off and soil water holding capacity. Found 42% of the pine forests within the study region classified as die-off -> 1029km^2
2.	Gaylord et al., 2013	NM	Secondary drought effects lead to insect attacks. Drought predisposes p edulis to insect attacks. Mortality due to insect attacks was higher in water deprived sites. Increased temp. will increase insect populations leading to an increase in infestations.
3.	Shaw et al., 2005	AZ, CO, ID, MT, NV, NM, UT, WY	Agents of mortality of pinyons likely compounding-including drought and insect attack-namely ips beetles, where outbreaks have been previously associated with drought.
4.	Breshears et al., 2009	NM	Smaller less severe droughts preluded the big drought in 2000-2003. Mortality caused by water stress leading to depletion of carbon reserves and creating susceptibility to insect attacks.
5.	Floyd et al., 2009	CO, NM, AZ	Ips beetles primarily responsible for Pinyon mortality. Spanning 3 sites, mortality ranges from 32%-65%. Evidence of ips found on almost ALL dead pinyons.
Ponderosa pine (*Pinus ponderosa*)			
6.	Byer & Jin, 2017	CA	Sierre Nevada drought from 2012-2016 characterized by less than usual precipitation and hotter temperatures. Area covered in study ranges between 5.6 million – 7.9 million acres in 2015 and 2016, respectively. Found approximately 20% mortality. Drought contributed to beetle infestations on Ponderosa dominated forests. Mortality attributed to high forest density and low elevations.
7.	Ganey & Vojta, 2011	AZ	Mortality of Ponderosa present at 98% of sites (1ha/site) from 2002-2007. 74% more mortality during 2002-2007 than during 1997-2002. Mortality not correlated with elevation or density. Mortality linked to insect infestation, brought on by severe drought conditions.

Trembling aspen (*Populus tremuloides*)			
8	Anderegg et al., 2013	CO	Hydraulic changes within a tree can accumulate leading to compounding and irreversible effects, making surviving trees more vulnerable to future drought events. Looking at the drought of 2000-2003.
9	Hogg et al., 2002	AB	Historical study using tree ring analysis to determine the causes of aspen dieback during 1990-1992. Variation in growth is explained by tent caterpillar defoliation, climate moisture index from the previous year, growing degree days, and snow depth.
10	Chen et al., 2017	Western Canada	Droughts effect a reduction in growth of aspen in western Canada. Using standardized precipitation-evapotranspiration index (SPEI) as a spatially temporal index. Discusses that drought maybe a "triggering factor" for reduce growth.
11	Michaelian et al., 2011	AB and SK	Reports on the effects of a massive drought. Moisture the greatest factor when assessing aspen mortality and dieback between 2000-2005. Almost half of the plots surveyed had > 35% mortality, and 6 plots had >80%.
12	Huang and Anderegg, 2012	CO	60 sites were selected to determine study region above ground biomass loss and how that contributes to C emissions. Found 30% of plots experienced greater than 50% canopy dieback, 57.9% were affected by aspen mortality, and of the estimated above ground biomass 55.3% was effected. 2.7 Tg of C emission from the above ground biomass loss, equals to roughly 36.5% of Colorado's total C emissions.
13	Worrall et al., 2008	CO	Increased mortality from 2002/2003 to 2006, by 24-51%. High elevation and steep slopes had less mortality. Southern and western aspects had higher mortality. Mortality agents were canker, bark beetles, and borers. Regeneration is poor resulting in a long-term loss of aspen forests distinct from natural aspen successional changes.
14	Worrall et al., 2013		Developed a bioclimatic model to show very unsuitable climate before periods of decline. Tent caterpillars and stem damage also contributed to periods of decline. However, drought was a significant factor in this period of decline, climate model shows these aspen forests are not suited to increased temperature and aridity, which predicts a widespread loss of aspen habitat in the future.
15	Peng et al., 2011	Canadian Boreal	High latitude study of boreal forest decline. Increase in mortality by 4.7% per year from 1963-2008. Western boreal seen more severe mortality rates than the east.



(A) *Populus tremuloides*

(B) *Pinus edulis*

(C) *Pinus ponderosa*

Figure 7. *Species ranges, CMI inferred vulnerable populations, and observed mortality regions based on a literature review, with numbers on the map referring to publications listed in Table 3. Note that not all publications in the table included maps allowing a location reference in this figure.*

For *Populus tremuloides* (Figure 7A), there are regions where observed dieback and mortality from the literature corresponds to vulnerable trees from data in this study primarily in Colorado, Utah, and New Mexcio. However, observed regions of mortality and dieback exist in Alberta and Saskatchewan, but the CMI-inferred vulnerable tree species from this study do not correspond. These inconsistencies show the directional trend of climate change associated with the southern regions and suggest the northern areas of dieback could be related to a one-time drought event.

For *Pinus ponderosa* (Figure 7C), only one study was found to corroborate drought induced tree mortality in a similar region to the CMI-inferred vulnerable trees identified in this study (Byer and Jin, 2017). However, *Pinus ponderosa* range in the southern states exists in a climatically vulnerable area, with predictions of increased temperature and loss of precipitation. This suggests the resilience associated with physiological factors present in *Pinus ponderosa* (Anderegg & Hillerislambers, 2016). However, the extent and duration of these resiliency factors is unknown.

5. Discussion

5.1. Vulnerability projections

For future projections, the 2050’s time frame under the most severe scenario is used to account for possible underestimations of consequences associated with growing changes to forest composition, distribution, and health (Allen, 2015). A vulnerability ranking of high, moderate, and low has been developed based on the findings of this research alongside the findings of other studies (Table 4). Of particular concern are the species found in this study with a high proportion of threatened populations with distributions concentrated within small geographic boundaries. However, not all species listed as high on the vulnerability score are limited to a geographically small range. These insights into future projections of vulnerable tree species in western North America are not limited to the species projected to have the most sizeable proportion of vulnerability (Table 2); they must also correspond to similarities in the literature.

Table 4. *Assessment of species vulnerability to future drought. Scored as high, moderate, or low based on findings from this study.*

Highly vulnerable	Moderately vulnerable	Low vulnerability
Pinus edulis	*Picea mariana*	*Picea sitchensis*
Pinus ponderosa	*Abies lasiocarpa*	*Acer macrophyllum*
Populus tremuloides	*Picea glauca*	*Alnus rubra*
	Pinus monticola	*Abies amabilis*
	Pseudotsuga menziesii	*Tsuga mertensiana*
	Picea engelmannii	*Chamaecyparis nootkatensis*
	Pinus contorta	*Sequoia sempervirens*
	Tsuga heterophylla	*Larix occidentalis*
	Thuja plicata	*Betula papyrifera*
	Calocedrus decurrens	*Abies procera*
	Pinus albicaulis	

5.2. Highly vulnerable species

The species that made it into the high vulnerability score rank include *P. edulis, P. ponderosa,* and *P. tremuloides*. This rank is a qualitative assessment of vulnerability based on the results of this study and inputs from other studies. *P. edulis* is of great concern with 60% of the plots from this study falling below the CMI threshold by the 2050s under the most severe emission scenario. Furthermore, the niche geographic boundary of P. edulis residing primarily in Utah, Colorado, Arizona, and New Mexico is also of concern (Figure 7B). Because the distribution of *P. edulis* range is limited to these specific states, the possibility of species migration to more suitable habitat could be limited or not possible. This species ability to resist bark beetle infestation and manage hydraulic reserves during non-drought events will be critical to this species survival (Clifford et al., 2013; Allen et al., 2010). Furthermore, conservation efforts should be directed at the northern edge of the range, where under the severe scenario, some areas are still unaffected by the CMI threshold.

However, even species with a wide range distribution are included in the high vulnerability score. *P. tremuloides* is one of the most widespread tree species in North America (Huang & Anderegg, 2012). However, as we have seen in this study, up to 10% of the plots face vulnerable moisture conditions within the severe emission scenario for the 2050s. A concentration of vulnerability is seen in Colorado and southern BC (Figure 7A). As Worral et al. (2008; 2013) pointed out, a global-change type drought drove mortality of P. tremuloides in Colorado. The southern interior of British Columbia has also experienced severe drought conditions in 1998 and 2003 (Woods et al., 2010). Future projections of increased temperature and decreased precipitation in P. tremuloides western North American range make this species extremely vulnerable to future mortality. Future *P. tremuloides* vulnerability will also be influenced by climate-driven insect and pathogen agents, which adds more difficulty in predicting severity, spatial, and a temporal extent (Woods et al., 2010).

Other species listed as high on the vulnerability score include P. ponderosa. Similar to the observed trends of mortality of P. ponderosa in Arizona from the recent time frame, the projections of future vulnerability are mostly concentrated in the same region (Figure 7C). Ganey & Vajta (2011) note that future climate in the southern range of P. ponderosa is expected to increase in temperature and aridity, causing increased vulnerability to a species already at its limit of a hot and dry climate. Under the most severe scenario for the 2050's, this study finds that 24% of the plots with P. ponderosa present will reside below the predefined CMI threshold.

5.3. Moderately vulnerable species

Species given a moderate vulnerability score have moderate proportions of their populations as vulnerable defined by the CMI-inferred vulnerability (Table 2) and share moderate indications of vulnerability from the literature. In addition to moderate levels of vulnerability, many of these species have variable responses to drought and are influenced by insect attacks, pathogens, and spatial variation.

Of the moderate species, *P. mariana*, *P. menziesii*, and *P. glauca* have been studied to show reduced growth during drought-like climatic conditions. While reduced growth is certainly a concern for future forests in terms of biomass for production or carbon sequestration, it should also stand outside of the species vulnerable to die-back or mortality. Using Landsat imagery in Alaska, P. mariana brownness has been detected and affiliated with decreased vegetative growth and productivity (Baird et al., 2012). In addition to decreases in *P. mariana* greenness in Alaska, Girardin et al. (2016) found that increasing temperature contributes to the decline of productivity. However, they also point out that variable responses can occur depending on site-specific characteristics. Similarly, a tree ring analysis of *P. glauca* from Alaska found reduced radial growth with increasing temperatures (Barber et al., 2000). While few studies have addressed the mortality of *P. menziesii*, Restaino et al. (2016) pointed to the limited growth of P. menziesii seedlings during periods of atmospheric and soil moisture deficits.

Furthermore, Case & Lawyer (2016) came up with a vulnerability score that assessed species' vulnerability based on their sensitivity, exposure, and adaptive capacity. The species listed as moderate in that study align well with the findings of vulnerability in this study. They are *P. monticola* and *T. plicata*. Furthermore, an assessment of climate driven forest health found that after drought events in 1998 and 2007, mortality and increased stress have been seen in the driest zones of BC coastline for *T. plicata* (Woods et al., 2010).

The variability of drought onset with vulnerability to mortality for *A. lasiocarpa* and *P. engelmanni* has been researched (Bigler et al., 2007). This study discusses increased mortality for *P. engelmanni* seen up to 1 and 5 years after late and early season drought onset, respectively. For *A. lasiocarpa*, Bigler et al. (2007) finds increased mortality up to 2 years after a late-season drought but considers early-season drought onset to be the strongest associated with increased mortality up to 11 years after the drought year. Based on the lag effects seen from Bigler's study, these two species fit well in the moderate category. In addition to the study of lag effects, A. lasiocarpa mortality in interior British Columbia has been attributed with bark beetle infestations, an indirect effect on mortality (Woods et al., 2010).

T. heterophylla is considered for the moderate drought vulnerability score based on the concentration of threatened populations from this study connected with a known drought event in the southeast of British Columbia and a western hemlock looper outbreak. This type of insect infestation has been associated with periods of soil moisture deficits during June, warmer temperatures, and drier conditions during the growing season (McCloskey et al., 2009; Woods et al., 2010). With projections of increased temperature and decreased precipitation expected to occur in British Columbia's southern interior, the likelihood of future hemlock looper outbreaks is expected, especially in the driest zones (Figure 22) (Woods et al., 2010).

P. albicaulis is a high elevation species and is listed as threatened by the United States Fish and Wildlife Service (USFWS, 2011). Based on a study looking at the vulnerability of tree species in western North America, Whitebark pine was listed as one of the most vulnerable species based on its high sensitivity and low adaptive capacity (Case & Lawyer, 2016). However, the major agent of mortality for this species is the mountain pine beetle. Historically, this species was safeguarded from the spread of mountain pine beetle by the colder temperatures associated with its high elevation habitat (Buotte et al., 2017). However, recent studies have found an increase in mortality correlated with increased temperature and drought events (Buotte et al., 2017; Millar et al., 2012). Millar et al. (2012) used climatic water deficit (CWD) as a drought indicator, they found a mean mortality rate of 70% across their study sites (Figure 11). While mortality was linked to mountain pine beetle infestations, it was also strongly associated with a regional drought from 2006-2010 (Millar et al., 2012). Further reduction in precipitation will likely exacerbate the population and trigger continued insect infestations (Buotte et al., 2017).

For *P. contorta*, although there is widespread mortality throughout its range, this mortality is only slightly linked to drought events. Like other species in this study, the mountain pine beetle is a popular source of mortality predisposed by drought conditions. However, in the case of P. contorta there is a gap in the literature connecting mortality events with drought. This complex issue highlights lag mortality and the difficulty in determining the effects of drought, especially when mortality from bark beetles continues beyond the point of drought influence (Anderegg et al., 2015). Furthermore, in certain cases after the onset of early and late season drought, P. contorta was found to have no drought related mortality (Bigler et al., 2007).

The final species for the moderate category has limited insights from the literature pointing to any vulnerability due to drought conditions. However, *Calocedrus decurrens* was found to have 17% of its population below the predefined CMI threshold by the 2050s under the most severe scenario. More research is likely needed to better understand this species tolerance to moisture deficits.

5.4. Species with low vulnerability

The selection of species given a low score for the future vulnerability has higher adaptive capacity to drought conditions, resides in areas less likely to be affected by future drought conditions, or lacks being studied in the literature. Of these species, many are lacking in the scientific literature including *P. sitchensis*, *A. rubra*, and *A. procera* , *B. papyrifera*, *C. nootkatensis, T. mertensiana, A. amabilis, A macrophyllum*, and *S. sempervirens*. Additionally, under the most severe scenario for the 2050s, only 0.6% of *P. sitchensis* and 2.5% A. rubra populations were below the predefined CMI threshold, respectively.

S. sempervirens had a higher proportion of their population threatened for the same scenario at 9.7%. However, because of the lack of studies in the literature to corroborate this finding, perhaps this species has a high adaptive capacity to drought. Furthermore, considering the limited range of this species and proximity to the ocean, drought-like conditions could be compensated by fog and moisture coming off the coastline.

Although 17% of *L. occidentals* was below the CMI threshold, this species is still listed as having a low vulnerability. L. occidentals was listed as low on the severity score by Case and Lawyer (2016), pointing to this species high adaptive capacity. Furthermore, temperature and summer precipitation were not well-suited predictors for range suitability in a British Columbian study (Rehfeldt et al., 2006). Another finding to support a low vulnerability score for L. occidentals is an assessment of weather on seedling growth by Chen & Nelson (2020). They found that although number of days with precipitation can be a predictor of root collar diameter growth, weather variables were not a great predictor for first- or second-year seedling mortality.

6. Conclusion

About half of the 24 species that were evaluated had 5% or more populations located in areas with a CMI value <0, potentially vulnerable to drought conditions. Five species had 25% of their populations exposed to drought, and for two species *Pinus edilus* and *Pinus ponderosa* half of the occurrence records were located within areas with negative CMI values. Climate change projections suggest that water deficits will disproportionately increase for the species and populations that are already in vulnerable positions, whereas other species and populations are not predicted to be affected strongly by decreases in water availability.

Observed impacts conformed to inferences drawn from the changes in available moisture for populations of *Pinus edilus*, *Populus tremuloides*, and *Pinus ponderosa* where dieback was observed. However, there were also important counter examples: widespread dieback of *Populus tremuloides* in Canada were not associated with directional trends in CMI values but were instead caused by extreme drought events that could not be associated with directional climate change.

In conclusion, the annual evapotranspiration balance at forest-grassland transitions may pose a significant threat to forest health and productivity across western North America, while inferred drought threats for species and populations that have range boundaries within forested ecosystems do not appear to increase under climate change projections. Observed climate change impacts over the last decade correspond closely to this inference, drawn from a CMI-based vulnerability assessment.

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