

**Biophysical and Climate Analysis of the Mountain Pine Beetle (*Dendroctonus ponderosae*)
Infestations in the Crown of the Continent, 1962 to 2014**

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ACADEMIC ABSTRACT

Mountain pine beetles (*Dendroctonus ponderosae*) are native insects that have decimated millions of hectares of mature pine (Pinaceae) forests in western North America. The purpose of this study is to investigate biophysical and climatic correlates of Mountain Pine Beetle (MPB) insect outbreaks in the Crown of the Continent Ecosystem (CCE) from 1962 to 2014 using Aerial Detection Survey (ADS) and climate data. Specific objectives were: 1) to develop statistical models to determine how selected biophysical correlates (slope, aspect, elevation, and latitude) and 2) to understand how local and global climate variables relate to the extent of the MPB infestations in the CCE, and 3) to contextualize the results of the models with historical climate data. Overall, the major findings of this study are: 1) despite its limitations, the ADS data seems suitable for analysis of beetle damage with respect to climate and topographic factors, on a regional scale, 2) there appears to be a link between local biophysical factors and winter precipitation and TPA within the CCE, and 3) a combination of a negative-phase PDO and La Niña is important in forecasting a decline in MPB spread, during a given year. This study is the first, to our knowledge, to explore spatio-temporal patterns of MPB outbreaks using biophysical factors, and both local and global climate variables, over a fifty-year timespan in the CCE. In the future, additional geospatial analyses may enable a landscape assessment of factors contributing to variability of MPB infestation and damage as this insect continues to spread.

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PUBLIC ABSTRACT

Mountain pine beetles (*Dendroctonus ponderosae*) are a native insect that has decimated millions of hectares of mature pine forests in western North America. The purpose of this study was to investigate, using GIS-derived variables, biophysical and climatic factors that have influenced past mountain pine beetle insect outbreaks, as evident by beetle-induced tree mortality in the Crown of the Continent Ecosystem (CCE) from 1962 to 2014. Specific objectives of this study were to determine how selected biophysical variables (slope, aspect, elevation, and latitude), regional climate variables (temperature, precipitation, and drought) and global climate oscillations (ENSO, PDO, NAO, AO, and PNA) relate to bark beetle infestations in the Crown of the Continent Ecosystem from 1962 through 2014, as measured by aerial survey-recorded tree mortality. We sought to contextualize the results of the statistical models with historical data to further understand the relationship between increases and decreases of tree mortality by comparing these trends to geopotential height and sea-surface temperatures that may influence CCE climate. Our work revealed first, that while the aerial survey data has important limitations, overall it is a useful dataset for analyzing historical spatio-temporal patterns of insect infestations. Second, there appears to be a link between local biophysical factors, such as latitude, elevation, and winter precipitation (as opposed to global climate factors) and tree mortality within the CCE. Local climate analysis revealed the importance of winter precipitation to be the biggest influence of MPB decrease or increase along with lower geopotential heights during a decline in MPB spread over the CCE. Finally, a combination of a negative PDO and El Niño was important in forecasting a decline in MPB spread, as shown by damage, during a given year. This is the first study to use aerial survey data in a geospatial analysis incorporating biophysical variables for the US portion of the Crown of the Continent Ecosystem. Additionally, this study is unique to explore the potential relationship between global teleconnections and regional climate in the CCE area, and the spatio-temporal extent of mountain pine beetle infestations.

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Chapter 1: Introduction and Objectives

Mountain pine beetles (*Dendroctonus ponderosae*) are the most destructive biotic agent of mature pine (Pinaceae) forests in western North America (Safranyik and Carroll, 2007; Safranyik et al., 2010). Over the past century, the mountain pine beetle infestation has reached epidemic levels four to five times in northwestern North America (Safranyik et al., 2004; Taylor and Carroll, 2003; Aukema et al., 2006). Exotic species are frequent culprits of extensive damage and mortality in North American forests (e.g., Ellison et al. 2005). Bark beetles, however, are native and yet have caused the mortality of billions of coniferous trees from Mexico to Alaska (Kurz et al., 2008; Bentz et al., 2010). In fact, the current infestation of bark beetles in North America is the most severe and largest in history (Bentz et al., 2009; 2010). Aukema et al. (2006) notes that an estimated 1.84 million ha of mature pine forests in western Canada have been lost due to the MPB in the 1980s; and again in 1999 – 2005 western Canada suffered a loss of an estimated of 7.1 million ha. Ramifications of this widespread mortality include huge economic losses, and substantial change in forest composition from dense coniferous stands to a mix of herbs, shrubs, and grasses on the forest floor (Raffa et al., 2008).



Figure 1: Bark Beetle Damage in North America have decimated North American Forests. Photo Credit: John Frank, taken at Glacier Lakes Ecosystems Experimental Site, Wyoming

Contributing to the extent of the bark beetles' success is a myriad of biotic strategies and shifting abiotic factors. For example, bark beetles are extremely resilient to climate. Further, their defenses, including their ability to migrate, (Bentz et al., 2010; Cudmore et al., 2010; Safranyik et al., 2010; Cullingham et al., 2011), and accelerated life-cycle (Raffa et al., 2008; Jenkins et al., 2012), have proven to be much greater than previously understood (Bentz and Schen-Langenheim, 2007; Bentz et al., 2010). These strategies are also impacted by climate. For example, large scale models show an increasing northward spread into the extreme northern latitudes of Canada and Alaska (Bentz et al., 2010) due to a continuously warming climate that exacerbates outbreaks (Bale et al., 2002; Raffa et al., 2008; Bentz, 2010; Hicke et al., 2012). Recent work by Six (2016) has reported northward pine beetle expansion of pine beetle into British Columbia and Alberta, where, in these new territories, the beetle is exotic and may spread as it encounters new species (Six 2016).

Warm air and dry conditions may trigger outbreaks by stressing tree vigor and decreasing the development time of mountain pine beetles (Raffa et al., 2008; Jenkins et al., 2012). Thus, a challenge for research and management is predicting bark beetle outbreaks due to changes in weather and climate (Creeden et al., 2014). Such a task may be assisted by broad scale spatio-temporal approaches to enable a more thorough understanding of factors that relate to the spread of invasions.

The purpose of this study is to investigate biophysical and climatic correlates of MPB insect outbreaks, as evident by beetle-induced tree mortality in the northern Rocky Mountains of northern Montana between the years 1962 to 2014 using U.S. Forest Service insect and disease aerial detection surveys (ADS) and climate data provided from National Centers for Environmental Information (NCEI).

The specific objectives of this study are to:

1. Develop annual statistical models to determine how selected biophysical correlates (slope, aspect, elevation, and latitude) relate to the extent of the bark beetle infestations in the Crown of the Continent Ecosystem from 1962 through 2014.
2. Develop models to understand how trends in climate variables, (including atmospheric composites of regional air temperature, precipitation and drought, and

global climate oscillations) relate to the extent of bark beetle infestations in the Crown of the Continent Ecosystem from 1962 through 2014.

3. Contextualize selected severe bark beetle outbreak cycles using historical climate data to further understand the relationship between increases and decreases of MPB spread and historical climate conditions.

Research has shown that climate is the primary factor in determining the spread of bark beetles, but studies that incorporate data over a long spatial and temporal region are rare. Given the inherent relationship between topography and environmental variables (e.g., air temperature and precipitation) (Basist et al., 1994) and ecological processes such as wildfire (Bisrat, 2010; Hicke et al., 2012; Hicke et al., 2013) a spatio-temporal examination of bark beetle damage and its relationship to topographic and climatic variables should be worthwhile because it enables the assessment of relationships between beetle outbreaks, across local (i.e. topography) and regional (i.e. climate) factors.

Further, studying spatio-temporal patterns of MPB mortality over a relatively small region (the CCE), but over a long time period (1962-2013) using a GIS will enable an understanding of mountain pine beetle outbreaks in this region from a historical context. and to some degree, whether the factors contributing to historical outbreaks differ from present day outbreaks (Williams et al., 2002; Seidl et al., 2009; Bentz et al., 2010; Cudmore et al., 2010; Temperli et al., 2013).

Chapter 2: Background

Overview

A study that examines the potential relationships between climate, topography and pine beetle necessitates understanding of the conditions that both foster and constrain MPB spread. Thus, this literature review will include key concepts such as the life cycle of mountain pine beetle, its relationship to climate and global climate oscillations, and the potential role of topography in the spread of the beetle.

2.1 Life Cycle of the MPB and its Relation to Climate

The life cycle of the native mountain pine beetle (among other species of bark beetles) generally consists of 1) adults landing on a tree, 2) adults boring into the phloem of that tree, 3) mating, and 4) creating galleries to lay eggs. When the larvae hatch they feed on the phloem tissue and develop into adults (Raffa et al., 2008). The majority of the MPB's life-cycle is spent as larvae feeding on the phloem, which eventually kills the host pine tree during the spring season before emergence (Amman and Cole, 1983; Amman et al., 1990; Furniss, 1997; Logan and Powell, 2001; and Hicke et al., 2006). Unlike most phytophagous insects, the MPB must kill its host in order to successfully reproduce (Logan and Powell 2001).

The mountain pine beetle can successfully attack, mate, and breed in 22 species of the genus *Pinus*, along with 4 pines non-native to North America (Furniss and Schenk, 1969; Smith et al., 1981; Amman and Cole, 1983; Safranyik et al., 2010). The lodgepole pine (*Pinus contorta*) is the primary host of the MPB (Wood, 1963; Furniss and Schenk, 1969; Amman and Cole, 1983; Logan and Powell, 2001; Aukema et al., 2006; Aukema et al., 2008; Safranyik et al., 2010), but another major host species is ponderosa pine (*Pinus ponderosa*; Logan and Powell, 2001; Bentz et al., 2010).

Even high elevation mountain pines such as whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*) (Bentz et al., 2010) are susceptible to MPB attack Logan and Bentz (1999). Whitebark pine (*Pinus albicaulis*) grows at high elevations in western United States into southern

Canada, including the CCE (Keane 1989; Keane 1993). Whitebark pine comprises approximately 10-15% of the forests of the Northern Rockies in Montana, Idaho, and Wyoming and is found in the alpine timberlines and the upper subalpine forests along with the MBP's primary host, lodgepole pine (*Pinus contorta*, Keane 1989). Logan et al. (2010) found that the high elevation whitebark pine has been increasingly susceptible to MPB attacks in the Greater Yellowstone Ecosystem. In Grand Teton National Park, Wyoming, for example, whitebark pine MPB-caused mortality was also observed at alpine treeline in stands also impacted by blister rust (Resler, 2015, personal observation).

In order for the MPB to successfully reproduce, it has to overcome the defenses of the tree and eventually kill the host tree (Raffa and Berryman, 1983; Raffa and Berryman, 1987; Amman et al., 1990; Raffa and Smalley, 1995; Nebeker et al., 1993; Logan and Powell 2001). The beetles attack collectively by using aggregation pheromones to help coordinate the attack (Safranyik et al., 1975; Raffa and Berryman 1983; Raffa and Smalley 1995; Aukema, et al., 2006; Aukema et al., 2008). The attack and oviposit occur during late summer during the months of July through August (Safranyik et al., 2010; Hicke et al., 2006).

A host tree's defense system includes production of a highly viscous residue when the beetles bore into the bark of the tree (Nebeker et al., 1993). The visible popcorn-shaped masses of dried resin are called "pitch tubes," which indicate the location that the MPB have tried to attack the tree (Nebeker et al., 1993; Aukema et al., 2006). Disturbances caused by climatic factors can dramatically affect the available resin for MPB defenses including moisture availability. Drought can reduce available resin, which why drought is a concern for increased host tree susceptibility for MPB attacks (Safranyik et al., 1975; Raffa and Berryman, 1983; Nebeker et al., 1993; Aukema et al., 2006; Safranyik et al., 2010; Lusebrink et al., 2011; Chapman et al., 2012).

A second defense mechanism by host trees is known as a secondary resinosis (Reid et al., 1967; Nebeker et al., 1993), also referred to as a wound response. This defense consists of localized drying of the tissue and/or tissue necrosis (toxic chemicals) (Nebeker et al., 1993). This technique works by chemically and physically fighting the invading organisms by making itself less edible and less susceptible to fungal growth caused by the MPB by reducing water, soluble sugars, amino nitrogen, carbohydrates, and triglyceride fatty acids (Richmond et al.,

1970; Miller and Berryman, 1985; Barras and Hodges, 1969; Nebecker et al., 1993). Another technique in the induced defense system is resin secretion by the damaged tissues surrounding the wound (Franceschi et al., 2005; Raffa et al., 2005; Keeling and Bohlmann 2006). Trees that lack the performed defense system such as conifers in the genera *Abies*, *Tsuga*, *Cedrus*, and *Pseudolarix* (Cates and Alexander, 1982) rely mainly on the induced defense system (Nebecker et al., 1993). The induced defense system is more common than the performed defense system (resin), but when it comes to the rapid mass attack of the MPB, it has a minor role especially in the *Pinus* hosts (Cates and Alexander, 1982; Nebecker et al., 1993).

Mountain pine beetles typically prefer to attack large mature trees mainly due to the thicker bark that helps defend the larvae from natural predators and low temperatures. These trees also have more phloem tissue than younger trees that provide more nutrition for developing larvae (Amman, 1969; Shrimpton and Thomson, 1985; Safranyik and Carroll, 2007; Safranyik et al., 2010).

Once the mountain pine beetles bore past the bark and into the phloem tissue where vertical galleries, or tunnels, are chewed by the adult beetles where they oviposit (Aukema et al., 2006). The eggs are laid in niches in the vertical galleries and after eclosion, the larvae feed on the phloem tissue in the galleries circumferentially during development through four instars.

The late-instar stage is most susceptible to climate factors, when larvae must withstand the potentially fatal low temperatures during the winter (Bentz and Mullins 1999, Reid 1962, Aukema et al., 2006). In an experimental study, Bentz and Mullins (1999) collected beetles of different instars from 4 sites and subjected the larvae to different temperatures to study cold tolerance of MPB development stages. The temperatures were reduced by $\sim 1.5^{\circ}\text{C}$ per minute and when the formation of an ice lattice in insect tissue was observed, the supercooling point of the individual instar had been reached. The supercooling point refers to the temperature that ice crystals begin to form in the tissue (Lee, 1989) and represents a lethal temperature threshold for those insects that cannot survive tissue freezing (Bentz and Mullens, 1999). In a warming climate, higher elevations and latitudes will have greater wintertime temperatures that will reduce larvae mortality (Bentz et al., 2010).

Bentz and Mullins (1999) studied beetle flight, host colonization, and brood emergence monitoring. The results of the test had a 4°C difference in the supercooling point for two test

years: 1992-1993 had a supercooling point at -34°C and 1994-1995 had a supercooling point of -29.9°C (Bentz and Mullins 1999). The tests successfully supported the claims by Reid (1963), Reid and Gates (1970) and Amman (1973) that the threshold of MPB survival is at -30°C . Thus, a temperature threshold of -30°C has been set as the lower limit of survival in MPB populations (Reid, 1963; Reid and Gates, 1970; Amman, 1973; Bentz and Mullins, 1999).

Mountain pine beetles are able to survive extreme temperatures due to a cold-hardening process that functions to the supercooling point (Hamilton et al., 1985; Lee, 1989; Lee and Denlinger, 1991; and Bentz and Mullins 1999). The larvae typically overwinter during the third or fourth instar stages and then continue to mature in the spring when pupation occurs in early summer before adult emergence in late July or early August, and then begins to colonize a host tree and oviposit (Bentz, et al. 1991).

2.2 Spatial Patterns of Outbreaks

Aukema et al. (2006) and Myers (1998) suggest that long-term analysis can reveal whether the pine beetles' eruptions are predominately periodic, or if they are intermittent as is suggested by Werner and Holsten (1983), Bakke (1989), Eisenhart and Veblen (2000), and Alfaro et al. (2003). Aukema et al. (2006) suggested that spatial patterns can help provide insight on how outbreaks develop by analyzing MPB eruptions that may have originated from an epicenter or from multiple simultaneous eruptions that coalesced. The same study also mentioned that knowledge of the temporal and spatial patterns should offer some insight into the outbreak processes of mountain pine beetles. The spread of MBP is affected by many factors such as known predators, pathogens, resource availability, habitat heterogeneity, climate, and dispersal (Aukema et al., 2008). All trees infected by the MPB in a particular area do not necessarily become infested; the distribution of the MPB is best described as innocuous, which means that only that damaged, decadent, suppressed, or distressed trees are typically infected (Safranyik et al., 2010).

Research centered on climate change has attributed the growth of bark beetle infestations to increasing temperatures and drought (Raffa et al., 2008; Seidl et al., 2009; Bentz et al., 2010; Sherriff et al., 2011). Past outbreaks have been associated with warm and dry summers (Crosby

and Curtis 1970; Werner and Holsten 1983). Drought conditions are also a major influence on outbreaks (Christiansen et al., 1987; Hart et al., 2013). Drought can enhance the susceptibility of tree infestation and aggregation of the infestation (Raffa et al., 2008); in conjunction with a warming climate, the mortality of the larvae during the winter months is reduced (Raffa et al., 2008 and Bentz et al., 2010). The wintering of the larvae is the most critical stage for the MPB's survival in its life cycle which will affect the future infestation of new host species once the larvae develop into adults (Bentz and Mullins, 1999; Aukema et al., 2008). A warming climate is also associated with accelerated reproduction time (Kurz et al., 2008) and developmental cycle (Raffa et al., 2008; Jenkins et al., 2012).

Precipitation (or lack thereof) is an important factor along with temperature when considering MPB infestation, especially in higher drought conditions (Hadley, 1994; Raffa et al., 2008; Bentz et al., 2010; and Chapman et al., 2012). Additionally, it has been found that temperature is the most important climatic factor contributing to MPB spread, as it affects insect biology including flight and colonization, and larval development and survival (Aukema et al., 2008).

2.3 Global Climate Oscillations and influences on local climate.

Depending on the current phase, whether negative or positive-phase, global teleconnections such as the El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) can influence variations in temperature and precipitation in the winter (Shabbar and Khandekar, 1996; Shabbar et al., 1997; Mantua et al, 1997; Mantua and Hare, 2002), which is the time the MPB is most susceptible to mortality risks (Raffa et al., 2008; and Bentz et al., 2010; and Meyn et al., 2010). Whereas the phases of the ENSO lasts for 6-18 months, the PDO phases can persist for 20-30 years. Schoennagel et al., 2005 found that positive phase PDO can influence strength in the relationship between climate oscillations and fire occurrences in the subalpine forests in this region; this study will explore the same relationship with MPB outbreaks and spread.

Stahl et al., (2006) stated that MPB mortality is reduced in a neutral or positive phase PDO; however, a contradictory observation in 1984 and 1985 showed that positive winter PDO

had caused a decline in MPB outbreak, by an onset of mortality-induced cold temperatures in the autumn of those years. MBP spread is decreased with a negative phase PDO, which is conducive to cooler and wetter conditions than positive phase PDO, which yields warmer and drier conditions. Warm and dry conditions can reduce mortality of MPB during development (Schoennagel et al., 2005; Raffa et al., 2008; Jenkins et al., 2012). This study will test to see which phase of PDO and which climate condition influences MPB spread.

The Pacific North American (PNA) Oscillation correlates strongly with precipitation and temperature in the northern Rocky Mountains. A positive PNA is indicative of a strong Aleutian low, which can influence more ridging patterns of the polar jetstream in the western United States, advecting warmer and drier air. Negative PNA, creates a zonal pattern in the jetstream and a relatively large negative PNA can influence more troughing patterns in the western United States which can yield decrease in temperature and more precipitation (Mock 1996).

Combinations of certain El Niño Southern Oscillation (ENSO) and teleconnections indices (e.g. ENSO, Pacific Decadal Oscillation (PDO), Pacific North American (PNA), Arctic Oscillation (AO), North American Oscillation (NAO), Southern Oscillation Index (SOI), and specific Niño phases) could explain outbreak patterns by analyzing the influence over western Montana.

2.4 Topographical influences on MPB spread

Topography influences a range of abiotic conditions by moderating meso- and microclimates over a range of spatial scales (Barry 1992). Topography affects environmental controls at local to regional spatial scales, including (but not limited to) wind exposure, local soil moisture, freeze-thaw processes, snow accumulation, and temperature (Johnson & Billings, 1962; Oke, 1978). Some research has found connections between the impacts of bark beetles and topographic factors. For example, Hadley (1994) found that tree mortality due to bark beetles was the highest on northern facing slopes and lowest on southern facing slopes in northern Colorado due to several factors (i.e., older host age, higher density, bigger basal area, and less moisture). Further, bark beetle infestations are also connected to the distribution and properties of host species, which also vary according to topographic factors.

Other factors such as crown or basal damage from recent wildfires can increase the susceptibility of the host tree to be infested by bark beetles (McHugh et al., 2003; Jenkins et al., 2008). Schoennagel (2012) even suggested that bark beetles can increase the risk of wildfires once the hosts have been killed due to decreased moisture in dead trees and increased forest ground litter and fuel from dead trees. Climate change, specifically rising temperatures, may be responsible for increasing the frequency of fires and bark beetles in North America, especially since the start of the 21st century. This effect of a warming climate could exacerbate the fire-beetle cycle (Bentz et al, 2010).

Climate change studies have concluded that MPB range is increasing on a latitudinal and elevational scale due to a warming climate. Bentz et al., (2010) notes that the geographic spread of bark beetles on a regional scale is limited by climate and not host availability, which suggests the likelihood for northern expansion. Global mean annual global temperatures are expected to increase, particularly at higher latitudes and elevations, where host trees in these areas are becoming increasingly more susceptible to MPB attack. Also, more extreme weather events and greater frequency and duration of droughts (e.g., more stress on host tree vigor) is expected to accompany with the increase in mean annual global temperatures (Seager et al., 2007; Solomon 2007; Bentz et al., 2010). Bark beetles spread is a function of a direct effect on temperature and as temperatures increase, the host susceptibility in northern latitudes is becoming more favorable (Bentz et al., 2010; Cudmore et al., 2010; Safranyik et al, 2010; Cullingham et al., 2011).

Chapter 3: Study Area

I focused my analysis within the U.S. portion of the Crown of the Continent Ecosystem (CCE). The CCE is a mountainous ecosystem in the U.S. and Canadian Rocky Mountains with complex terrain and variable climate. It encompasses approximately 72,000 km² (Prato and Fagre, 2007), 60% of which is in the United States (Waldt, 2004). The ecosystem extends from the southern end of the Bob Marshall Wilderness in the Blackfoot Valley in northwestern Montana, USA (~ 46.5° N) northward into southwestern Alberta and southeastern British Columbia (~ 49° N) and is bounded on the north by the Highwood River in Alberta (Quinn et al., 2002; Pate, 2009). The west is bounded by the Rocky Mountain Trench and the east is bounded by the prairie foothills to the eastern mountain front (Pate, 2009). This area includes vast expanses of relatively intact ecosystems, including Glacier National Park and Flathead National Forest. Bark beetles and other defoliators have affected forest stand health within this region by increasing risk for wildfires (Bisrat, 2010; Hicke et al., 2012; and Hicke et al., 2013), decreasing biodiversity (Bentz et al., 2010), and altering forest function (Hicke et al., 2013). The U.S. portion of the CCE (~47,200 km²) is comprised of 80% federal and state public land, including Glacier National Park (GNP), lands managed by the USDA Forest Service (including designated wilderness and National Forests), the Bureau of Indian Affairs, and Montana State Forests.

Topographic complexity and relief, which ranges from ~1000 m on the Blackfoot Indian Reservation to 3194 m on Mount Cleveland in Glacier National Park, contribute to the CCE's extensive and intact native biodiversity (Quinn and Broberg, 2007). Prairies and foothill vegetation along the eastern Rocky Mountain front transition into a patchwork of montane mixed deciduous and coniferous forests at higher elevations, eventually to be replaced by subalpine and alpine plant species at the higher elevations. This ecological diversity translates to habitat for 65 mammals native to the CCE, a grizzly bear and wolf recovery area, North America's most diverse ungulate species composition, and elusive species such as the wolverine, which require large areas of undisturbed core habitat (Long, 2002). The CCE is extremely diverse at many biological levels, including high genetic, species, community and habitat diversity (Broberg, 2012) and "supports over 1,000 native plants, 70 mammals, and 260 species of birds" (CCEEC). The region includes a broad range of ecosystems, from low-elevation valleys, to watersheds and

floodplains, to extreme alpine summits. The CCE is heavily protected by cooperating organizations from federal to state levels, and is known to have “not suffered a known animal extinction in the past 200 years” (Broberg, 2012).

Biodiversity is diminishing in the CCE due a culmination of bark beetles and other biological disturbances. Whitebark pine for example, are succumbing due to mortality by MBP and white pine blister rust, caused by the invasive pathogen *Cronatrium ribicola*. Fire suppression is also detrimental to fire-dependent stands species turnover in these forests is characterized in some places by a replacement of pine with subalpine fir (*Abies lasiocarpa*). Fire suppression allows the subalpine fir to flourish and prevent fire-adapted species such as whitebark pine and other pine species with serotinous cones from replenishing the population. Fire suppression has been detrimental to forest health and has made it easier for MPB to infest its host and spread without the risk of fire-induced mortality (Keane and Key 2010; Taylor et al., 2006).

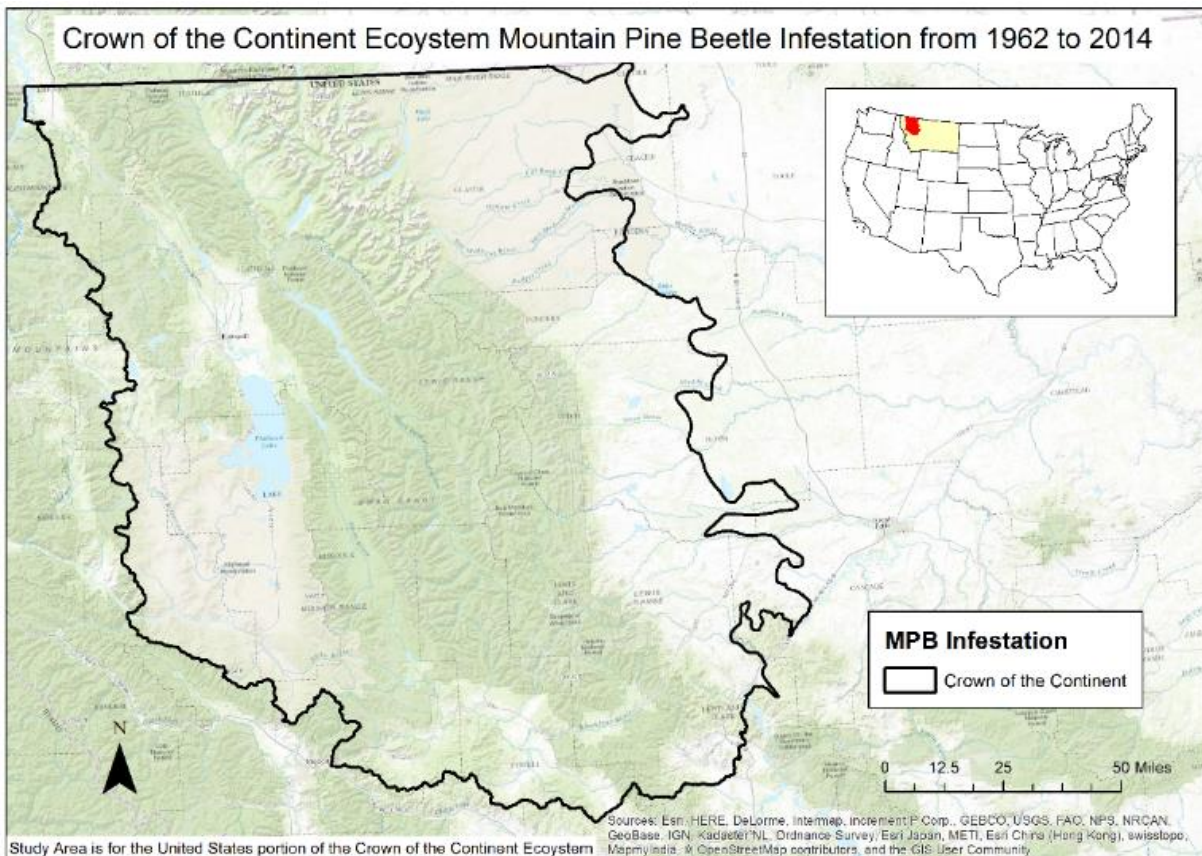


Figure 2: Mountain Pine Beetle infestation in the U.S. portion of the Crown of the Continent Ecosystem from 1962 to 2014 mapped by decade. Data were analyzed on a yearly basis.

Chapter 4: Data and Methods

4.1: Aerial Detection Surveys, Geographic Information System (GIS) Data

For this study, I estimated spatio-temporal spread of MBP within the U.S. portion of the CCE by focusing on MBP damage as estimated from Forest Service insect and disease aerial detection surveys (ADS) in GIS format. I obtained the data via CD directly from the Missoula Field Office in Montana for 1962-2014. Aerial surveying is a type of remote sensing that involves manually documenting (through sketchmapping) forest change from a fixed-wing aircraft on a map. The primary type of change detected is tree mortality, which may result from a myriad of disturbances such as bark beetles, defoliators, fire, and tree diseases. Aerial surveys are conducted by the USDA Forest Service annually in cooperation with other programs, such as the U.S. Department of Interior's Bureau of Land Management, the U.S. Environmental Protection Agency, the USDA Natural Resources Conservation Service, Forest Health Management, and several universities (Johnson and Wittwer 2008). Since tree mortality caused by bark beetles can occur rapidly (USDA 2015), data collection on an annual basis is well suited for the study of this particular system.

One advantage of the aerial survey data for forest health assessment is its availability in a georeferenced format for use in a Geographic Information System (GIS). The aerial survey GIS data are compiled from aerial survey sketchmaps of killed trees and then converted to GIS shapefiles through digitization. (Johnson, n.d.; Meddens 2012). The GIS attributes table of each polygon of the ADS includes year, perimeter and area, magnitude, severity, host tree species, damage causal agent, symptoms, and an estimate of number of trees affected. ADS-reported tree mortality and causal agents are verified by ground surveys, so that the final maps generated are a culmination of both ground surveys and aerial surveys.

An additional advantage of ADS is that the collection, analysis, ground verification, and digital conversion have strict quality assurance requirements (McConnell et al., 2000). The process of tree mortality sketchmapping are governed by strict requirements established by the Forest Health Protection program to ensure consistency and quality control. First, the maps used during the survey must be at a scale of 1:100,000 or larger for the continental U.S. Furthermore, they need to display a standard projection and coordinate system, and have a minimum of four

points suitable for registration points when converting paper to digital format. If the map is digitized, the sketchmap is taped to a digitizing table and the map is traced with a digitizing mouse to create the polygons. The data attributes are either coded in a feature table in ArcInfo v.10.3.1 (ESRI 2015) or in an Oracle database system to create polygons of tree mortality. The quality assurance/quality control process ensures that the conversion of the sketchmap data into GIS data maintains the accuracy of the original sketchmaps (Aerial Survey GIS Handbook 3-4).

MPB damage results in tree discoloration from green to yellow to red before the host tree's death, which usually occurs within 1 or 2 years after initial infestation. For tree mortality associated with MPB, only standing dead trees that have died since the last survey can be mapped by aerial survey. The assessment is estimated by the number of dead trees by acre (TPA) and is calculated by recording the percent mortality within a polygon or by counting the number of dead trees in a polygon and then converted later to dead trees per acre. Data in each polygon's attribute table are categorized to show the year of survey, unique survey identifier, damage type code, defoliation severity and pattern codes, dead trees per acre, number of dead trees, damage causal agent code, host tree species code, forest type codes, acres, and comments. Tree discoloration is characterized by foliage color other than green. If it is guaranteed that the tree will result in death within 1 or 2 years, it will be classified as mortality rather than discoloration ("Aerial Survey Standards").

One potential limitation of data used in this thesis is that the GIS data prior to 1999 do not have a "fly/no fly layer" and therefore cannot be verified as being surveyed from both the ground and air (Sontag, Scott M – U.S. Forest Service, personal communication; "Aerial Survey Standards"). The fly/no fly is a supplemental polygon provided with the data that indicates if the area was surveyed by aircraft and on the ground. Trees that show mortality in areas outside of the fly layer were verified by ground only. All survey data are accompanied by a fly/no fly (FNF) layer and coded as such. The FNF layers are best used as damage location indicators rather than overall forest health monitoring. Another limitation of the survey data is that a few endemic populations of pine beetle may not kill enough trees to become visually apparent from the air, but ground-truthing and ranking severity levels of an outbreak error help reduce observation errors (Aukema et al., 2006).

4.2 Objective 1 Data: Topographic Data and Analysis

All data preparation and geospatial analyses were conducted using ArcGIS v.10.3.1. For the purpose of meeting Objective 1, Digital Elevation Models (DEM) raster images were downloaded from the USGS National Map site (<http://viewer.nationalmap.gov/basic/>) at a 1/3 arc second (or 10 meter) resolution. DEMs, are effective tools for deriving surrogates of field-collected environmental variables, such as slope and moisture (Brown, 1994) and solar radiation (Guisan et al., 1998) in models of mountain landscapes (del Barrio et al., 1997; Bader and Ruijten, 2008). Four separate digital elevation models ranging from 46° to 49° N and 112° to 117° W were mosaicked into a new raster and then clipped to the study area.

Raster layers for aspect and slope (°) were derived from the DEMs using the Spatial Analyst Tools in ArcMap v.10.3.1. Other studies have determined aspect to be important in MPB tree mortality (Hadley 1994). Aspect and slope angle are also of interest because of variations of temperature, precipitation, wind, solar radiation, soil moisture, and snow accumulation, all of which may impact the MBP life cycle. The aspect raster layer was reclassified to values of 1 through 9, (flat = 1, N = 2, NE = 3, E = 4, SE = 5, S = 6, SW = 7, W = 8, and NW = 9). North (2) was chosen as the reference category to test against the other aspects to track MPB spread. For the purpose of assessing potential latitudinal changes in MPB spread over time, I created 24, 0.1° latitudinal zones from 46.6° to 49.0° N; others have suggested bark beetles are expanding northward due to rising temperatures in high latitudes and elevation in regards to the CCE (Bentz et al., 2010).

Table 1: Descriptive Statistics for Biophysical Variables.

Biophysical Variables used in Stepwise Multiple Linear Regression Model		
<i>Biophysical Variable</i>	Range	Mean ± SD
Elevation (meters)	742 - 3192	1417.32 ± 19.90
Slope (in degrees)	1 - 83.9	15.98 ± 5.06
Latitude Zones*	1 - 24	12.16 ± 0.01
Aspect**	1 - 9	5.21 ± 1.27

*24 Zones divided up into 0.1° increments ranging from 46.6° to 49.0° N.

**Aggregated into 9 categories: flat = 1, N = 2, NE = 3, E = 4, SE = 5, S = 6, SW = 7, W = 8, and NW = 9

Zonal Statistics in ArcGIS was used to summarize annual statistics for raster images (ESRI 2015) for elevation, slope, aspect, and latitudinal zones for each TPA polygon; these zonal statistics were then joined to the TPA polygon data so that each polygon's attribute table contained topographic summary data. Descriptive statistics for each variable are provided in Table 1.

4.2.1 Biophysical models (Objective 1)

For the purpose of exploring the relationship between the selected biophysical predictor variables (elevation, aspect, slope and latitude) and the response variable (yearly TPA) from 1962-2014, a series of stepwise multiple linear regression models were generated in JMP v. 12.0.1. Stepwise multiple linear regression combines the concepts of both forward selection and backward elimination variable selection (Liao et al., 2007). All variables included in the final models were significant at $\alpha = 0.05$.

4.3 Objective 2 Data: Climate

4.3.1 Local Climate (Climate Divisional Data)

Climate Divisional Data are a historical dataset (1895-2013) for the contiguous U.S. that uses temperature and precipitation averages from reported cooperative station daily observations. There are 344 climate divisions within the contiguous U.S. that assess large-scale climatic features or anomalies within a large period of time (Guttman and Quayle, 1996). The advantage of using a coarse scale dataset over a finer resolution (such as PRISM datasets) (Daly et al., 2002; PRISM Climate Group), was to gain an understanding of broad-scale climate trends for the region of interest and to determine how they relate to global rather than micro-climate influences.

In support of Objective 2, I extracted the following climate variables from the Climate Divisional dataset: precipitation (PCP), temperature average (TAVG), minimum temperature (TMIN), maximum temperature (TMAX), Palmer Drought Severity Index (PDSI), and Standard

Precipitation Index (SP01; for one-month only). The local Climate Divisional Data obtained were for the Western Division of Montana. Even though the CCE encompasses three different climate divisions, the majority of the area and MPB infestation are best represented in the western division.

Average, minimum, and maximum temperature values were obtained to test the significance of the MPB-temperature relationship. Precipitation and Standard Precipitation (one-month index only) indices in conjunction with Palmer Drought Severity Index were obtained to study the MBP-drought relationship. The dataset was acquired from National Centers for Environmental Information (NCEI).

To assess seasonal effects of temperature and precipitation on MPB infestation, the climate divisional data were aggregated from mean monthly values to seasonal aggregations, based on variable means, to analyze seasonal influences on MPB spread: Spring (March, April, and May); Summer (June, July, and August); Fall (September, October, and November); and Winter (December of the previous year, January and February).

4.3.2 Global Climate Teleconnection Influences

In order to study the global teleconnection's influence on western Montana's climate (Temperature and Precipitation), global climate teleconnections such as El Niño-Southern Oscillation (ENSO) phases and other atmospheric oscillations (Pacific Decadal Oscillation (PDO), Pacific North American Pattern (PNA), Arctic Oscillation (AO), North American Oscillation (NAO), Southern Oscillation Index (SOI), Niño₁₊₂, Niño₃, Niño₄, and Niño_{3,4}) tabular data were obtained from the Climate Prediction Center and National Oceanic Atmospheric Administration's Earth System Research Laboratory Physical Sciences Division websites. These phase indices were aggregated from month to season to match the data style of the ENSO phases in three month averages. Both the climate divisional data and the global teleconnections were given previous year, two-year, three-year, four-year, five-year, and ten-year lags to test for prolonged statistical relevance of each of the climate variables. Descriptive statistics of local and Global climate variables to be used in subsequent analysis are reported in Table 2.

4.3.3 Exploratory Climate Analysis

Exploratory analysis of the relationships between the climate variables (Table 2) and TPA were assessed using a series of independent, two-sample t-tests using JMP v. 12.0.1. In particular, we were interested in assessing statistically significant differences between low and high TPA years for each climate variable. The purpose of this test is to determine if we can reject the null hypothesis ($\alpha = 0.05$) that there are no differences in individual climate variables in the low and high categories. Since preceding climate factors would be most important in determining MPB damage, climate data from the year prior to outbreaks of interest were used for the two-sample t-tests (Safranyik et al., 1974; Aukema et al., 2006). TPA values were sorted in ascending order and divided into two even categories: low and high spread years. These two groups contain the values for each climate variable, which are divided up in high or low MPB spread and then averaged. Each individual climate variable was analyzed separately; however, results were grouped by each season and climate type (local or global teleconnection).

Table 2: Descriptive Statistics for Climate Variables used for this study.

Local Climate and Global Teleconnection Variables			
<i>Climate Divisional Data</i>	Abbreviation	Range	Mean \pm SD
Minimum Value of Minimum Temperature*	Min_TMIN	-20.8 - 7.0	-4.1 \pm 2.0
Maximum Value of Maximum Temperature*	Max_TMAX	-2.78 - 30.1	15.0 \pm 1.9
Mean Value of Average Temperature*	Avg_TAVG	-10 - 16.8	4.7 \pm 1.3
Mean Value of Minimum Temperature*	Avg_TMIN	-14.4 - 8.17	-1.1 \pm 1.3
Mean Value of Maximum Temperature*	Avg_TMAX	-5.5 - 25.9	10.5 \pm 1.5
Mean Value of Precipitation	Avg_PCP	0.7 - 6.0	2.6 \pm 0.3
Mean Value of Palmer Drought Severity Index**	Avg_PDSI	-4.1 - 4.2	0.0 \pm 1.4
Mean Value of Standardized PCP Index of 1-Month	Avg_SP01	-1.8 - 1.6	0.0 \pm 0.3
<i>Teleconnection (Index values)</i>	Abbreviation	Range	Mean \pm SD
Southern Oscillation Index	SOI	-0.94 - 0.85	0.036 \pm 0.386
El Niño Southern Oscillation Index	ENSO	-1.157 - 1.009	0.040 \pm 0.458
Niño Eastern Region	Niño 3	-1.503 - 1.370	0.031 \pm 0.610
Niño Western Region	Niño 4	-1.816 - 1.631	0.013 \pm 0.734
Niño Peruvian Coastal Region	Niño 1+2	-1.932 - 1.843	0.009 \pm 0.798
Niño Middle Region	Niño 3.4	-1.780 - 2.703	0.014 \pm 0.831
Pacific Decadal Oscillation	PDO	-2.183 - 2.083	0.219 \pm 0.923
North Atlantic Oscillation	NAO	-0.975 - 1.200	-0.002 \pm 0.510
Pacific/North American Oscillation	PNA	-0.917 - 1.765	0.017 \pm 0.576
Arctic Oscillation	AO	-1.019 - 0.809	0.042 \pm 0.421

* Temperature Variables in °C

** Winter has the highest variation of PDSI (-4.1 to 4.2)

4.3.4 Stepwise Multiple Linear Regression Model (Climate)

We used a stepwise multiple regression model to assess the relationship between the response variable (TPA) and 1) average temperature and precipitation for all four seasons and all years combined; and 2) seasonal NAO, AO, PNA, ENSO, and PDO for all years combined. The variables used in the two climate models were chosen to avoid multicollinearity. I was unable to perform analysis on a yearly basis in our climate/TPA assessment because we lacked the necessary climate data at the polygon level.

4.4 Objective 3: Geopotential Height and Sea-Surface Temperature Anomalies – Data and Analysis

Geopotential Height and Sea-Surface Temperature anomalies may help to understand how certain atmospheric factors (e.g., movement of polar air masses due to air pressure strength and location) correlate with increases or decreases in the MPB spread. Studying climate phenomena, such as air temperature and geopotential height, may help explain MBP fluctuations. Both Geopotential Height Anomaly and Sea-Surface Temperature Anomaly maps were created from NOAA's Earth System Research Laboratory website using NCEP/NCAR data (<http://www.esrl.noaa.gov/psd/data/timeseries/>) during either high or low MPB caused-damage year(s).

Further, teleconnections have been shown to influence the polar jet stream patterns. Understanding polar jet stream patterns are important in tracking seasonal or yearly weather trends in western Montana in regards to temperature patterns and precipitation amounts that can influence MPB outbreaks and spread. Specifically, temperature is important for the development and survivability of the MPB, while precipitation and drought often affect the stress on the host tree's vigor (Raffa et al., 2008; Seidl et al., 2009; Bentz et al., 2010; Sherriff et al., 2011). Thus, both of these variables may impact the spatial pattern of trees killed by MPB.

Here, we examined large-scale climate teleconnections to understand the relationships between MPB damage and regional climate variables. El Niño-Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO), Pacific North American Pattern (PNA), Arctic Oscillation (AO), and North American Oscillation (NAO) can influence the pattern of the polar jet stream,

which in turn can affect temperature and precipitation in the western United States. Maps of Geopotential Height Anomalies at the mid-atmosphere level (500hPa) and sea-surface temperature anomalies in the Tropical Pacific and North Pacific were generated to help visualize the phases of each teleconnection during high and low TPA years.

4.4.1 Global Climate Teleconnections

To meet Objective 3, a qualitative assessment of Geopotential Height Anomalies (500 hPa) was undertaken to interpret the different phases of NAO, AO, and PNA in the northern hemisphere; sea-surface temperature anomalies were also assessed to interpret the different phases of ENSO (Tropical Pacific) and PDO (North Pacific). The intent of this assessment was to corroborate the results of the statistical analysis conducted for Objective 2.

TPA was subtracted from the prior year and the difference was analyzed into two segments: decreasing and increasing TPA (Figure 3). Dividing the data in this manner allowed me to analyze large scale atmospheric influences that may have attributed to increases or decreases in MPB infestation.

First, Geopotential Height Anomalies at the 500 hPa level and Tropical Pacific Sea-Surface Temperature Anomalies for decreasing and increasing TPA years were used to generate maps for the following categories: Winter (December – February), and Spring (March – May), Summer (June – August), and Fall (September – November). These categories were chosen to assess the relevance of climate in critical infestation and life cycle stages, as documented in the literature (Raffa et al., 2008 and Bentz et al., 2010).

PNA phases are analyzed based on height anomalies over the western and eastern U.S. During a positive-phase PNA, higher heights are found over the western U.S. and below average heights exist over eastern U.S., resulting in warmer temperatures over the western U.S. Negative-phase PNA are simply the inverse of a positive-phase PNA.

ENSO and PDO are sea-surface temperature anomalies that can have a major influence on temperature and precipitation in North America. ENSO phases (El Niño and La Niña) and the different sections of ENSO include Niño₁₊₂, Niño₃, Niño₄, and Niño_{3,4}, are sea-surface

temperature anomalies for the Tropical Pacific Region. Sea-Surface Temperature Anomaly maps were generated for the Tropical Pacific Region to visually assess the different ENSO phases and its individual sections (e.g., Niño₁₊₂, Niño₃, Niño₄, and Niño_{3,4}) in relation to MPB fluctuations. Due to the decadal nature of the PDO phases, box and whisker plot of the high and low TPA years was constructed to assess the PDO's potential influence on MPB outbreaks.

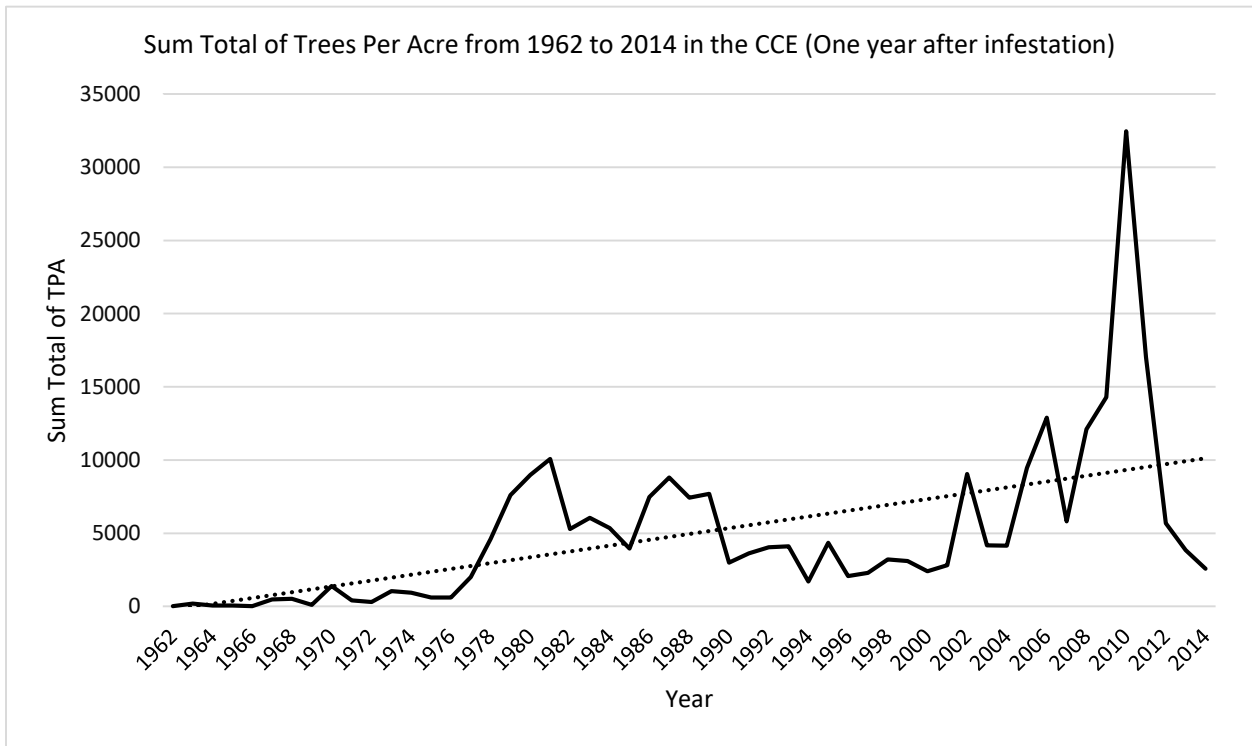


Figure 3: MPB spread from 1962 to 2014. Any years that have an increase or decrease were categorized into increasing and decreasing years of TPA.

Chapter 5: Results

5.1 Biophysical Analysis

5.1.1 Relationships between biophysical variables and Mountain Pine Beetle Damage (TPA)

Estimated coefficients and standardized betas of only those variables that were statistically significant for estimating TPA on a yearly basis are provided in Tables 3 and 4. Positive estimates indicate a positive association with TPA; negative estimates indicate that as the given variable increases, TPA decreases. Standardized coefficient estimates (Std. Beta), are reported to allow comparison of the magnitude of the coefficients for variables with different units. Standardized coefficients are interpreted in such a way that for each one standard deviation increase in the predictor variable, TPA increases by the standardized estimate.

Although the Adjusted R^2 values were relatively low (ranging from 0.002 to 0.364), biophysical factors did contribute to explaining variation in TPA for most years. At least one biophysical predictor variable contributed to explaining TPA in the regression models for 42/53 total years. Of these years with at least one significant variable, latitude was the most frequently significant (33/53 years) followed by elevation (28/53 years). Slope and aspect each contributed to explaining TPA 16 out of 53 total years. Throughout the study period, the overall trend was a positive relationship between TPA and elevation (Figure 4). For the first half of the study period (through 1993), latitude had a positive relationship with TPA, and was overall more important for explaining TPA than other variables examined, as measured by the standardized betas (Table 3). However, after 1993 the strongest positive relationship with TPA was with elevation (Table 3). For the majority of the study period, the relationship between the distribution of TPA and slope angle was negative, as evident by negative coefficients (Table 3), meaning that most MPB damage was associated with gentler topography when elevation and latitude increased; however, during 1992 to 2002, MPB moved southward, but to higher elevation and steeper slopes.

Northwest, southeast, and flat terrain had the most positive coefficients (Table 4), which indicate that these aspects had more TPA than the northern aspect (Figures 7). Although southern and southwestern aspects are associated with warmer temperatures in this region, TPA had negative association with these aspects.

Visualizations generated by graphing the standardized beta for elevation, slope, and latitude are provided in Figures 4 and 5, respectively, Figure 4 visualizes results of Table 3 by graphing the standardized beta. Figure 5 visualizes the results of Table 4 by using the standardized beta of aspect. Areas of dead trees resulting from Mountain Pine Beetle, recorded as dead trees per acre (TPA) for each polygon is shown temporally in decadal intervals to visualize the spread of damage (Figure 6).

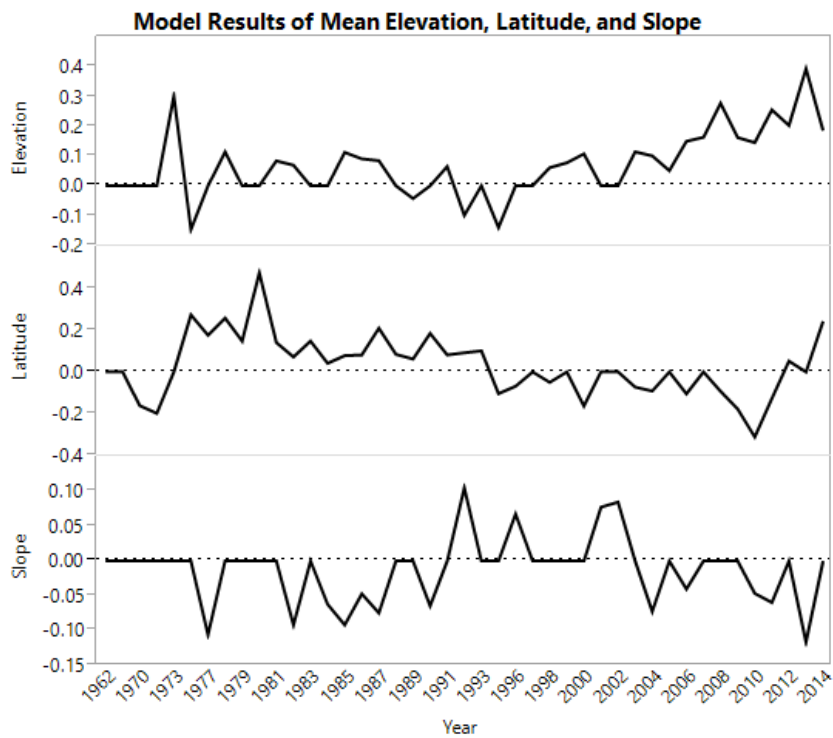


Figure 4: Results from Multiple Linear Regression Model - Biophysical Variables in Graphed by the Standardized Beta. 41/53 Years had Significant Explanatory Variables.

Table 3: Results from Yearly Stepwise Multilinear Regression Models – Coefficient Estimate and Standardized Beta for Elevation, Slope, and Latitude

Topography Stepwise Regression Model Results (<i>Excluding Aspect</i>)								
Year	Coefficient Estimate			Standardized Beta			R ²	Adj. R ²
	Elevation	Latitude	Slope	Elevation	Latitude	Slope		
1970		-0.330			-0.162		0.026	0.023
1971		-0.081			-0.199		0.160	0.114
1973	0.012			0.300			0.090	0.086
1976	-0.002	0.150		-0.147	0.274		0.109	0.100
1977		0.165	-0.088		0.176	-0.106	0.073	0.051
1978	0.007	0.845		0.113	0.258		0.087	0.083
1979		0.535			0.148		0.013	0.012
1980		0.476			0.476		0.034	0.033
1981	0.005	0.512		0.084	0.141		0.034	0.033
1982	0.003	0.173	-0.119	0.069	0.072	-0.092	0.022	0.014
1983		0.165			0.148		0.029	0.024
1984		0.037	-0.026		0.041	-0.062	0.006	0.005
1985	0.001	0.037	-0.026	0.112	0.078	-0.092	0.023	0.018
1986	0.001	0.044	-0.013	0.091	0.082	-0.047	0.017	0.013
1987	0.002	0.290	-0.062	0.084	0.210	-0.075	0.055	0.051
1988		0.040			0.084		0.007	0.007
1989	-0.001	0.036		-0.043	0.062		0.005	0.005
1990		0.056	-0.012		0.185	-0.065	0.054	0.046
1991	0.000	0.025		0.065	0.082		0.029	0.023
1992	-0.001	0.035	0.023	-0.099	0.092	0.105	0.021	0.019
1993		0.039			0.101		0.010	0.010
1995	-0.002	-0.052		-0.140	-0.104		0.052	0.046
1996		-0.024	0.015		-0.069	0.068	0.009	0.007
1997	0.001			0.001			0.004	0.003
1998	0.001	-0.050		0.061	-0.050		0.015	0.013
1999	0.001			0.077			0.006	0.005
2000	0.001	-0.069		0.107	-0.163		0.041	0.039
2001			0.021			0.078	0.006	0.005
2002			0.038			0.085	0.007	0.007
2003	0.001	-0.032		0.114	-0.073		0.034	0.029
2004	0.001	-0.036	-0.019	0.101	-0.092	-0.073	0.026	0.020
2005	0.001			0.051			0.003	0.002
2006	0.001	-0.051	-0.012	0.149	-0.105	-0.040	0.037	0.364
2007	0.001			0.163			0.036	0.032
2008	0.006	-0.104		0.277	-0.093		0.094	0.093
2009	0.002	-0.132		0.162	-0.178		0.063	0.061
2010	0.002	-0.286	-0.027	0.145	-0.312	-0.047	0.116	0.115
2011	0.003	-0.090	-0.025	0.255	-0.128	-0.060	0.078	0.077
2012	0.002	0.027		0.203	0.052		0.040	0.039
2013	0.000		-0.047	0.393		-0.117	0.132	0.131
2014	0.002	0.138		0.186	0.243		0.086	0.084

Table 4: Results from Stepwise Multiple Linear Regression Model – Aspect

Biophysical Stepwise Multiple Linear Regression Model Results										
<i>Aspect (Coefficient Estimate)</i>										
Year	NW	W	SW	S	SE	E	NE	Flat	R ²	Adj. R ²
1963	3.034	1.675	-1.994	-2.189	0.564	-0.044	-0.115	-0.752	0.216	0.092
1971	-0.681	0.571	0.035	-0.022	-0.143	-1.002	-1.201	3.068	0.160	0.114
1977	1.297	-0.105	-0.184	-0.933	1.288	-1.580	-2.117	0.877	0.073	0.051
1982	0.183	1.838	-1.042	-0.839	1.592	0.346	-0.616	-1.032	0.022	0.014
1983	1.024	-0.670	-0.202	0.321	-0.275	-0.288	-0.291	-0.136	0.029	0.024
1985	0.074	0.063	-0.297	-0.164	-0.288	0.042	-0.177	0.501	0.023	0.018
1986	0.375	-0.261	-0.093	-0.229	-0.046	-0.119	-0.241	0.220	0.017	0.013
1987	1.264	0.314	-1.045	-1.178	0.689	-0.275	-0.231	0.086	0.055	0.051
1990	0.358	-0.488	-0.375	-0.149	-0.163	-0.100	-0.030	0.536	0.054	0.046
1991	0.344	0.075	-0.384	-0.089	0.199	0.108	-0.152	-0.358	0.029	0.023
1995	-0.183	-0.107	0.005	0.210	1.202	0.355	-0.569	-0.473	0.052	0.046
2003	0.559	-0.152	-0.049	-0.245	-0.213	0.051	0.165	-0.152	0.034	0.029
2004	-0.160	-0.044	-0.101	0.093	0.077	-0.400	0.117	0.199	0.026	0.020
2007	0.343	-0.246	-0.122	0.064	0.064	-0.230	-0.387	0.213	0.036	0.032
2009	0.032	-0.447	-0.294	0.343	-0.044	0.507	0.198	-0.201	0.063	0.061
2010	0.288	0.324	-0.325	-0.033	0.235	-0.035	-0.132	-0.276	0.116	0.115
<i>Aspect (Standardized Beta)</i>										
Year	NW	W	SW	S	SE	E	NE	Flat	R ²	Adj. R ²
1963	0.341	0.202	-0.328	-0.331	0.072	-0.007	-0.016	-0.085	0.216	0.092
1971	-0.107	0.101	0.007	-0.004	-0.030	-0.195	-0.205	0.421	0.160	0.114
1977	0.059	-0.005	-0.011	-0.058	0.077	-0.084	-0.136	0.034	0.073	0.051
1982	0.006	0.070	-0.038	-0.030	0.064	0.014	-0.025	-0.029	0.022	0.014
1983	0.082	-0.059	-0.019	0.029	-0.027	-0.031	-0.029	-0.008	0.029	0.024
1985	0.011	0.011	-0.054	-0.030	-0.056	0.009	-0.035	0.064	0.023	0.018
1986	0.051	-0.043	-0.016	-0.039	-0.008	-0.022	-0.043	0.027	0.017	0.013
1987	0.065	0.019	-0.072	-0.077	0.044	-0.019	-0.015	0.004	0.055	0.051
1990	0.074	-0.116	-0.095	-0.038	-0.041	-0.027	-0.008	0.094	0.054	0.046
1991	0.077	0.019	-0.107	-0.023	0.050	0.029	-0.043	-0.067	0.029	0.023
1995	-0.026	-0.017	0.001	0.035	0.193	0.058	-0.097	-0.057	0.052	0.046
2003	0.095	-0.030	-0.010	-0.047	-0.041	0.011	0.035	-0.020	0.034	0.029
2004	-0.027	-0.009	-0.021	0.019	0.015	-0.087	0.025	0.029	0.026	0.020
2007	0.060	-0.049	-0.024	0.012	0.013	-0.048	-0.077	0.029	0.036	0.032
2009	0.003	-0.045	-0.030	0.034	-0.004	0.054	0.021	-0.015	0.063	0.061
2010	0.021	0.029	-0.029	-0.003	0.021	-0.003	-0.012	-0.017	0.116	0.115

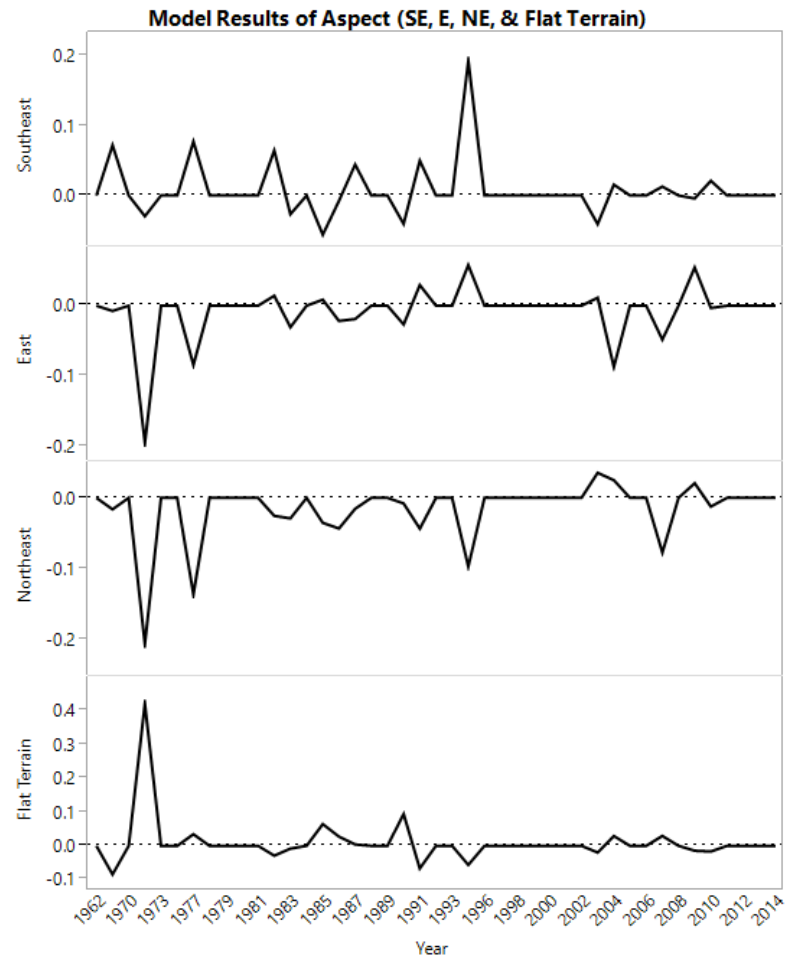
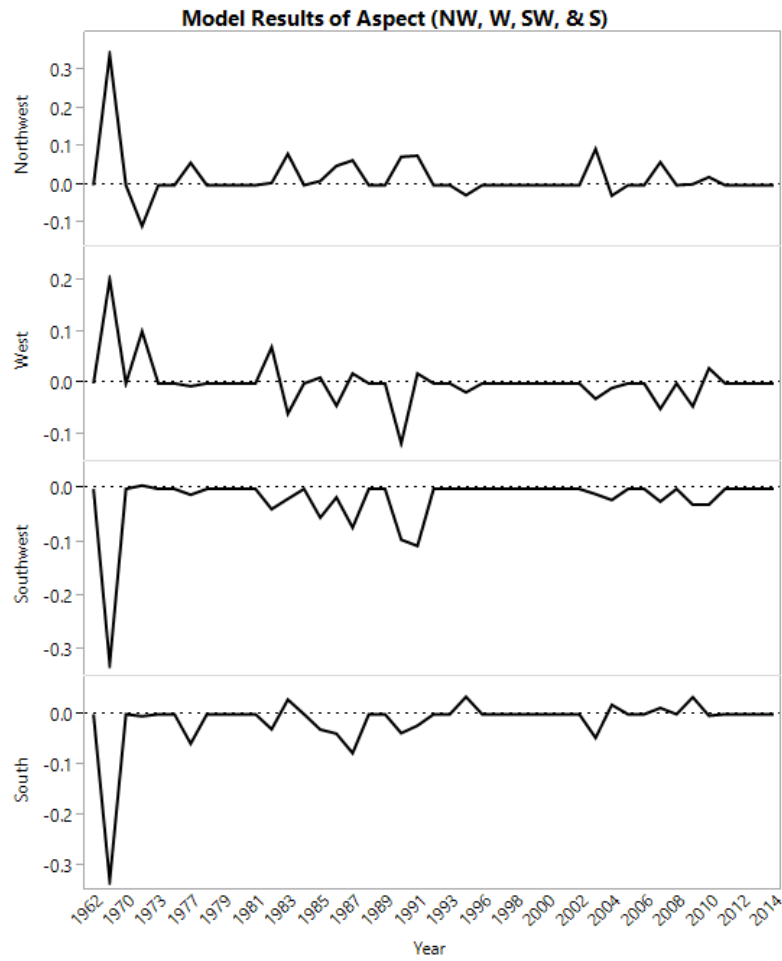


Figure 5: (left) Results from multiple linear regression model - graph of aspect variables in standardized beta. (Right) Results from multiple linear regression model - graph of aspect variables in standardized beta

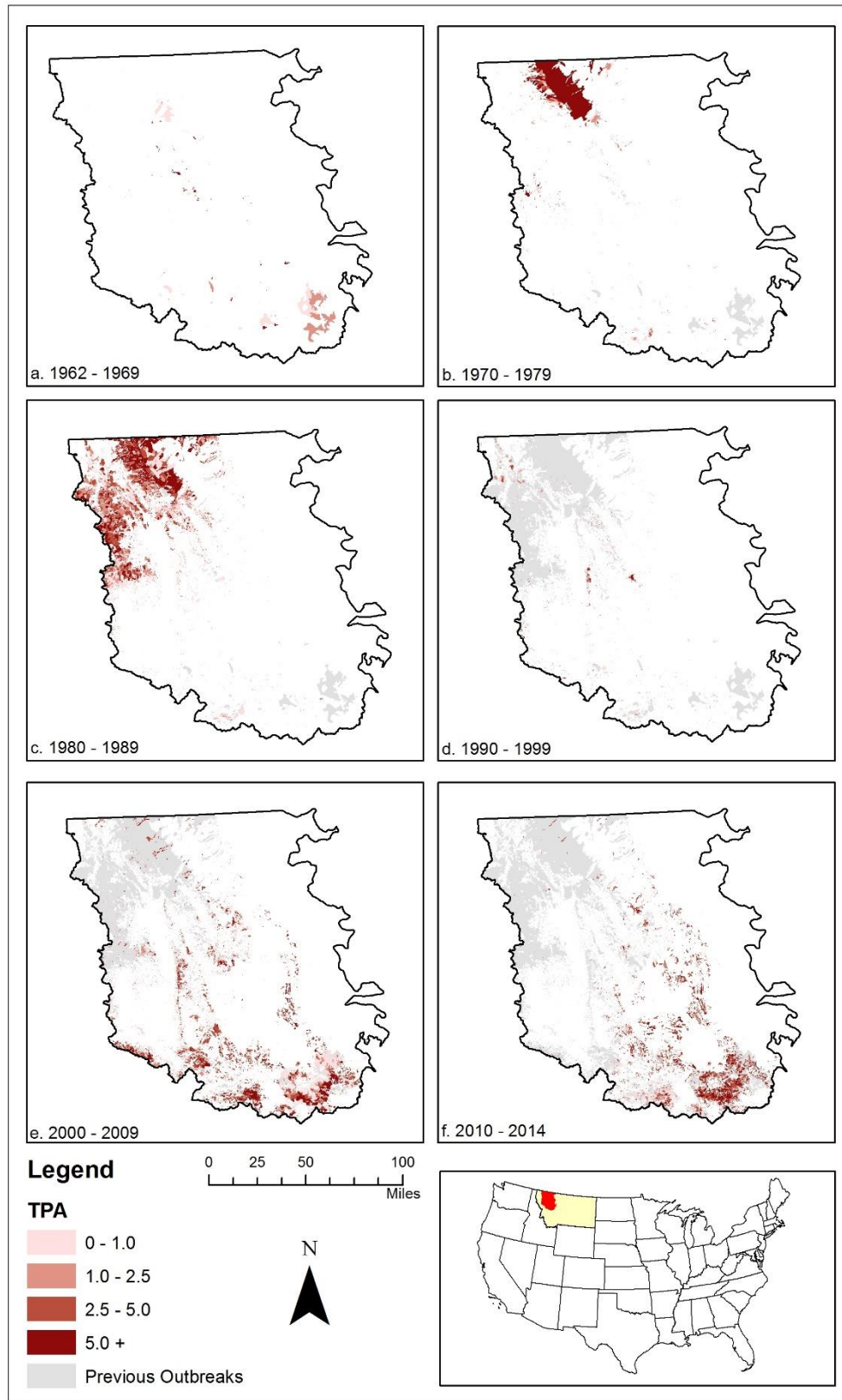


Figure 6: Mountain pine beetle infestation in the Crown of the Continent Ecosystem by decade.

5.2. Objective 2 Results (Climate)

5.2.1 Two-Sample t-Test Results (Local Climate and Global Teleconnections)

I conducted a series of t-tests to determine statistically significant differences between the highest TPA and lowest TPA sets of years (from 1962 to 2014), with respect to the selected climate variables (Table 2). Tables 5 and 6 contain results of the t-tests for local climate variables and global teleconnections based on the season of aggregated climate data for only those variables where significant differences were found. In the winter season, only variables related to precipitation and drought showed significant differences (Table 5), however spring, summer, and fall revealed significance differences with respect to air temperature. Further, spring was the only season that yielded current year temperature differences with high and low TPA along with current year PDSI (Table 5). It should be understood that any trend in temperatures (i.e., increasing temperatures due to a changing climate) was not de-trended, but the stepwise multiple linear regression model will de-trend increasing temperatures to reveal any significance in temperature variability in response with differences in TPA.

Statistically significant differences were found between low and high MPB spread (TPA) for PDO (current year, 1-year lag, and 4-year lag) and indicated that low (high) TPA values were associated with negative (positive) PDO phases (Table 6). The PDO phases are evident by the following mean values: positive for warm-phase PDO and negative values for cool-phase PDO. Both winter and spring had the lowest p-values associated with PDO (Table 6). The positive PNA phase was indicative of high MPB spread (Table 6). The relationship between precipitation and PNA positive phase is strongly correlated in this region (Leathers et al., 1991).

The results from the two-sample t-test for testing low and high TPA with global teleconnections reinforced the importance of a warm phase PDO during the winter and spring with regards to high MPB spread, as evident by positive mean values (warm phase) of PDO corresponding with high TPA (Table 6). Southern Oscillation Index and the three year lags of ENSO, Niño₄, and Niño_{3,4}, showed statistical significance between low and high TPA. There are some conflicting interpretations such as high TPA being associated with lower sea-surface temperatures (La Niña) during the spring and higher sea-surface temperatures (El Niño) during the summer and fall. The mean for high spread MPB for SOI is negative (Table 6), which is

indicative of an El Niño season. The mean values of ENSO, Niño₄, and Niño_{3,4} are also negative (Table 6), which for these values, indicate a La Niña season.

Table 5: Local climate variables used in the two-sample t-test analysis. Yearly lags of 1, 2, 3, 4, 5, and 10 years were also

Two-Sample t-Test: Local Climate									
<i>Climate Divisional Data</i>	Low MPB Spread			High MPB Spread			Two-Sample T-Test		
<i>Winter</i>	Mean ± SD	SE Mean	Mean ± SD	SE Mean	T-Value	P-Value	DF		
PDSI (Avg)	0.55 ± 1.95	0.38	-0.76 ± 1.84	0.36	2.49	< 0.05	49		
PCP (Avg)	3.76 ± 1.01	0.20	2.98 ± 0.89	0.17	2.94	< 0.01	49		
PCP (Avg) 1 Year Lag	3.62 ± 1.11	0.22	3.04 ± 0.87	0.17	2.10	< 0.05	47		
SP01 (Avg)	0.25 ± 0.60	0.12	-0.26 ± 0.67	0.13	2.90	< 0.01	49		
SP01 (Avg) 1 Year Lag	0.16 ± 0.65	0.13	-0.21 ± 0.66	0.13	2.04	< 0.05	49		
<i>Spring</i>	Mean ± SD	SE Mean	Mean ± SD	SE Mean	T-Value	P-Value	DF		
Min Temp* (Min)	-6.22 ± 3.27	0.64	-4.97 ± 2.86	0.56	-2.64	< 0.05	49		
Min Temp* (Min) 4 Year Lag	-6.29 ± 3.56	0.70	-5.12 ± 2.61	0.51	-2.43	< 0.05	45		
Avg Temp* (Avg)	3.54 ± 1.69	0.33	4.32 ± 1.94	0.38	-2.77	< 0.01	49		
Avg Temp* (Avg) 1 Year Lag	3.64 ± 2.06	0.40	4.23 ± 1.69	0.33	-2.02	< 0.05	48		
Min Temp* (Avg)	-2.45 ± 1.48	0.29	-1.73 ± 1.59	0.31	-3.04	< 0.01	49		
Min Temp* (Avg) 1 Year Lag	-2.37 ± 1.65	0.32	-1.79 ± 1.60	0.31	-2.28	< 0.05	49		
Max Temp* (Avg)	9.52 ± 2.19	0.43	10.35 ± 2.47	0.48	-2.29	< 0.05	49		
PDSI (Avg)	0.59 ± 1.73	0.34	-0.48 ± 1.80	0.35	2.19	< 0.05	49		
<i>Summer</i>	Mean ± SD	SE Mean	Mean ± SD	SE Mean	T-Value	P-Value	DF		
Min Temp* (Avg) 2 Year Lag	6.76 ± 1.04	0.20	7.11 ± 0.93	0.18	-2.32	< 0.05	49		
Min Temp* (Avg) 3 Year Lag	6.77 ± 1.03	0.20	7.12 ± 0.97	0.19	-2.25	< 0.05	49		
Min Temp* (Avg) 5 Year Lag	6.74 ± 1.02	0.20	7.07 ± 0.93	0.18	-2.18	< 0.05	49		
<i>Fall</i>	Mean ± SD	SE Mean	Mean ± SD	SE Mean	T-Value	P-Value	DF		
Min Temp* (Min) 1 Year Lag	-4.66 ± 2.74	0.54	-5.8 ± 4.22	0.83	2.08	< 0.05	42		
Avg Temp* (Avg) 4 Year Lag	4.26 ± 2.19	0.43	4.89 ± 1.69	0.33	-2.09	< 0.05	47		
Max Temp* (Avg) 4 Year Lag	9.56 ± 2.76	0.54	10.52 ± 2.35	0.46	-2.42	< 0.05	48		
PDSI (Avg) 4 Year Lag	0.54 ± 1.52	0.30	-0.46 ± 1.86	0.36	2.14	< 0.05	48		

* Temperature Variables in °C

Table 6: Teleconnection variables used in the two-sample t-test analysis. Yearly lags of 1, 2, 3, 4, 5, and 10 years were also analyzed.

Two-Sample t-Test: Teleconnections									
Teleconnection(s)	Low MPB Spread			High MPB Spread			Two-Sample T-Test		
	Mean ± SD	SE Mean		Mean ± SD	SE Mean	T-Value	P-Value	DF	
<i>Winter</i>									
PDO	-0.54 ± 0.79	0.15		0.37 ± 0.93	0.18	-3.83	< 0.001	48	
PDO 1 Year Lag	-0.36 ± 0.87	0.17		0.20 ± 1.01	0.20	-2.15	< 0.05	48	
PDO 4 Year Lag	-0.36 ± 0.93	0.18		0.23 ± 0.94	0.18	-2.24	< 0.05	49	
NAO 3 Year Lag	-0.24 ± 0.77	0.15		0.26 ± 0.66	0.13	-2.50	< 0.05	48	
PNA	-0.10 ± 0.70	0.14		0.41 ± 0.63	0.12	-2.73	< 0.01	49	
PNA 4 Year Lag	-0.06 ± 0.74	0.15		0.35 ± 0.62	0.12	-2.20	< 0.05	48	
<i>Spring</i>									
	Mean ± SD	SE Mean		Mean ± SD	SE Mean	T-Value	P-Value	DF	
SOI	0.63 ± 1.19	0.23		-0.02 ± 1.08	0.21	2.09	< 0.05	49	
Niño ₄ 3 Year Lag	0.20 ± 0.42	0.08		-0.13 ± 0.54	0.11	2.43	< 0.05	47	
Niño _{3,4} 3 Year Lag	0.18 ± 0.52	0.10		-0.15 ± 0.61	0.12	2.07	< 0.05	49	
PDO	-0.22 ± 0.92	0.18		0.59 ± 0.94	0.18	-3.13	< 0.01	49	
PDO 1 Year Lag	-0.14 ± 0.97	0.19		0.51 ± 0.96	0.19	-2.43	< 0.05	49	
PDO 4 Year Lag	-0.08 ± 0.99	0.19		0.53 ± 0.90	0.18	-2.34	< 0.05	49	
PDO 5 Year Lag	-0.09 ± 0.97	0.19		0.47 ± 1.02	0.20	-2.05	< 0.05	49	
<i>Summer</i>									
	Mean ± SD	SE Mean		Mean ± SD	SE Mean	T-Value	P-Value	DF	
Niño ₄	-0.06 ± 0.48	0.09		0.21 ± 0.45	0.09	-2.16	< 0.05	49	
Niño ₄ 1 Year Lag	-0.06 ± 0.51	0.10		0.22 ± 0.41	0.08	-2.14	< 0.05	48	
PDO 1 Year Lag	-0.21 ± 0.95	0.19		0.33 ± 0.95	0.19	-2.03	< 0.05	49	
<i>Fall</i>									
	Mean ± SD	SE Mean		Mean ± SD	SE Mean	T-Value	P-Value	DF	
Niño ₄ 1 Year Lag	-0.13 ± 0.72	0.14		0.30 ± 0.60	0.12	-2.29	< 0.05	48	
PDO	-0.51 ± 0.87	0.17		0.08 ± 0.91	0.18	-2.39	< 0.05	49	

Values shown are representative of the index value of each teleconnection

5.2.2 Stepwise Multiple Linear Regression Model Results: Local Climate and Global Teleconnections

The regression model incorporating seasonal average temperatures and precipitation revealed no significant predictors of TPA. Since the focus of the analysis is to understand the overall trend of climate influence on MPB outbreaks, the stepwise multiple linear regression model was reconstructed without the outlier year for exploratory purposes, which resulted in a slight increase in variance explained (Table 7). The model revealed one predictor of TPA, average precipitation in the winter season.

The stepwise multiple linear regression model showed more significant predictors of TPA when running the model global climate teleconnections variables. The results of the model revealed that the positive-phase NAO in winter is associated with increasing TPA (Table 8). When excluding the outlier year of 2009, it decreased the estimate, but the R² value increased

slightly from 0.388 to 0.404 (Table 8). Spring global teleconnections revealed no significant predictors of TPA (Tables 8 and 9). A negative-phase NAO was the only global teleconnection associated with TPA increase for the summer, with 2009 excluded from analysis (Tables 8 and 9). The fall season global climate teleconnections were the only result of the model that resulted in multiple variables as a predictor of TPA, in which negative-phase NAO, positive-phase AO, and positive-phase PNA were associated with an increase in TPA (Tables 8 and 9).

Table 7: Results from stepwise multiple linear regression model using local climate divisional data.

Season	Average PCP		P-Value	R ²	Adjusted R ²
	Coefficient Estimate	Std. Beta			
Winter (All Years)	-1347.21	-0.25	0.08*	0.06	0.04
Winter (Except 2009)	-1472.72	-0.37	<0.01	0.14	0.12

Table 8: Results from Multiple Linear Regression Model - Global Teleconnection Coefficient Estimate (All Years).

Local Climate Results (All Years)								
Season	Coefficient Estimate			Standardized Beta			R ²	Adjusted R ²
	NAO	AO	PNA	NAO	AO	PNA		
Winter	2299.85			0.31			0.39	0.32
Spring							0.39	0.32
Summer		-6506.23			-0.40		0.39	0.32
Fall	-4197.69	6008.82	4108.16	-0.49	0.55	0.46	0.39	0.32

Table 9: Results from Multiple Linear Regression Model - Global Teleconnection Standardized Beta (2009 Omitted).

Local Climate Results (2009 Omitted)								
Season	Coefficient Estimate			Standardized Beta			R ²	Adjusted R ²
	NAO	AO	PNA	NAO	AO	PNA		
Winter	1333.34			0.25			0.40	0.34
Spring							0.40	0.34
Summer	-1656.04			-0.27			0.40	0.34
Fall	-2895.67	4936.60	3412.40	-0.47	0.62	0.53	0.40	0.34

5.3 Objective 3 Results

5.3.1 Mid-Atmospheric 500 hPa Geopotential Height Anomalies

The geopotential height anomalies showed a consistent pattern of below average heights directly over the CCE region in years that had decreasing TPA from the previous year in all four seasons (Figure 7). The lower heights are indicative of cooler than average lower atmospheric

temperatures over this region, as evident by a negative-phase PNA (Figure 7). Spring and fall were the only seasons that had above average heights over the CCE region. The higher heights over the western coast of the U.S. in spring are characteristic of a positive PNA phase.

5.3.2 Tropical Pacific Sea Surface Temperature (El Niño-Southern Oscillation)

Sea-surface temperature (SST) anomaly composite maps were created for the tropical Pacific Ocean to analyze different phases of ENSO, most commonly known as El Niño and La Niña. These phases had very little influence on increasing or decreasing TPA over the CCE as indicated by the little variation in SSTs in association with decreasing and increasing TPA for both the winter and spring (Figure 8). One commonality is that both in winter and spring during decreasing TPA there was a slight positive phase Niño₁₊₂, which is on the western coast of Peru (Figure 8). Niño₁₊₂ had positive SST anomalies in the summer and fall during an increase in TPA. The biggest differences in SST anomalies for different trends in TPA were in the summer and fall seasons, in which La Niña seasons (lower SST anomalies) were associated with a decrease in TPA, while El Niño seasons (higher SST anomalies) were associated with an increase in TPA (Figure 8).

Geopotential Height Anomalies (Western U.S.)

Decreasing TPA

Increasing TPA

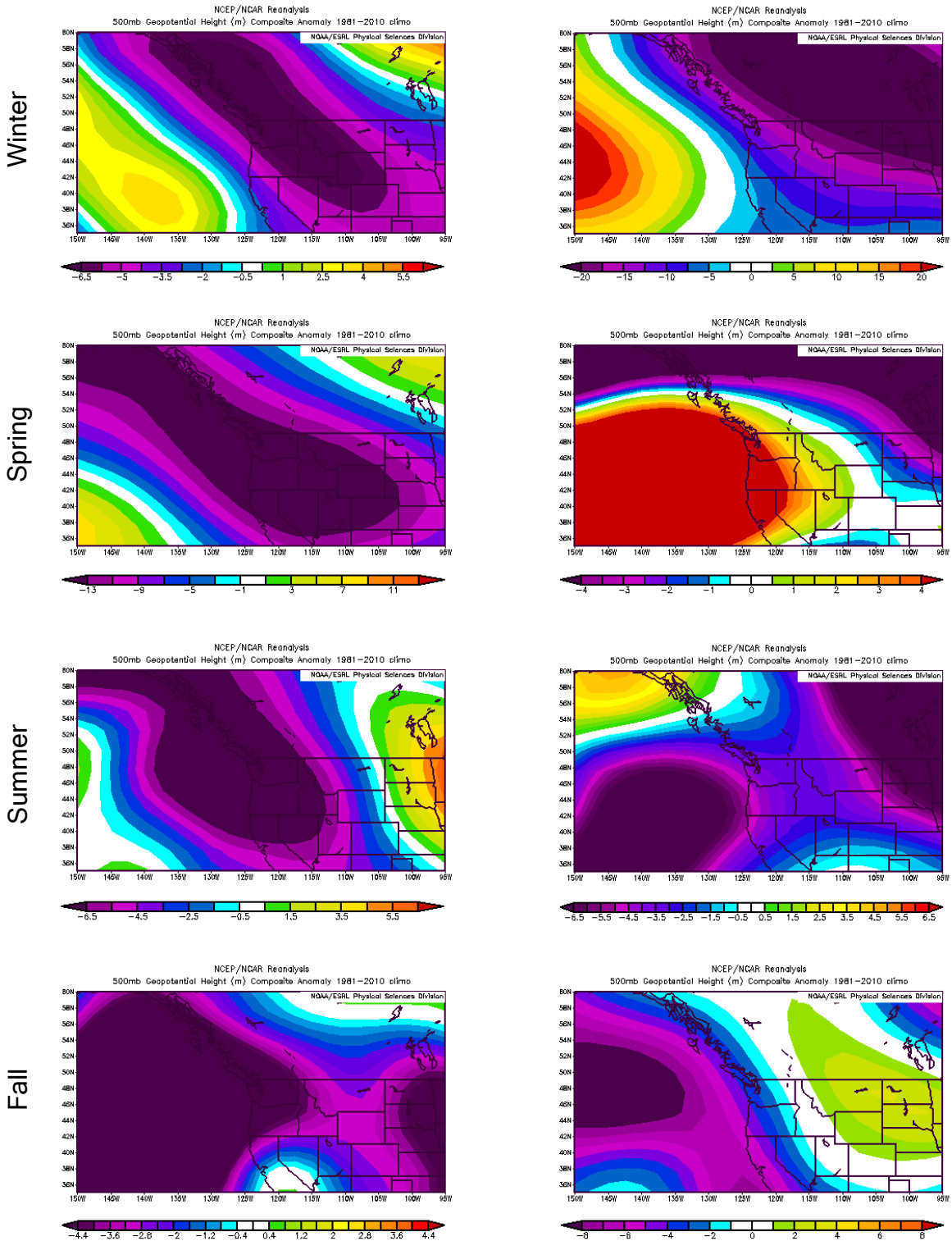


Figure 7: Geopotential Height composites for the western U.S. showing major differences between TPA years of decreasing and increasing TPA from the previous year.

Tropical Pacific SST Anomalies (ENSO)

Decreasing TPA

Increasing TPA

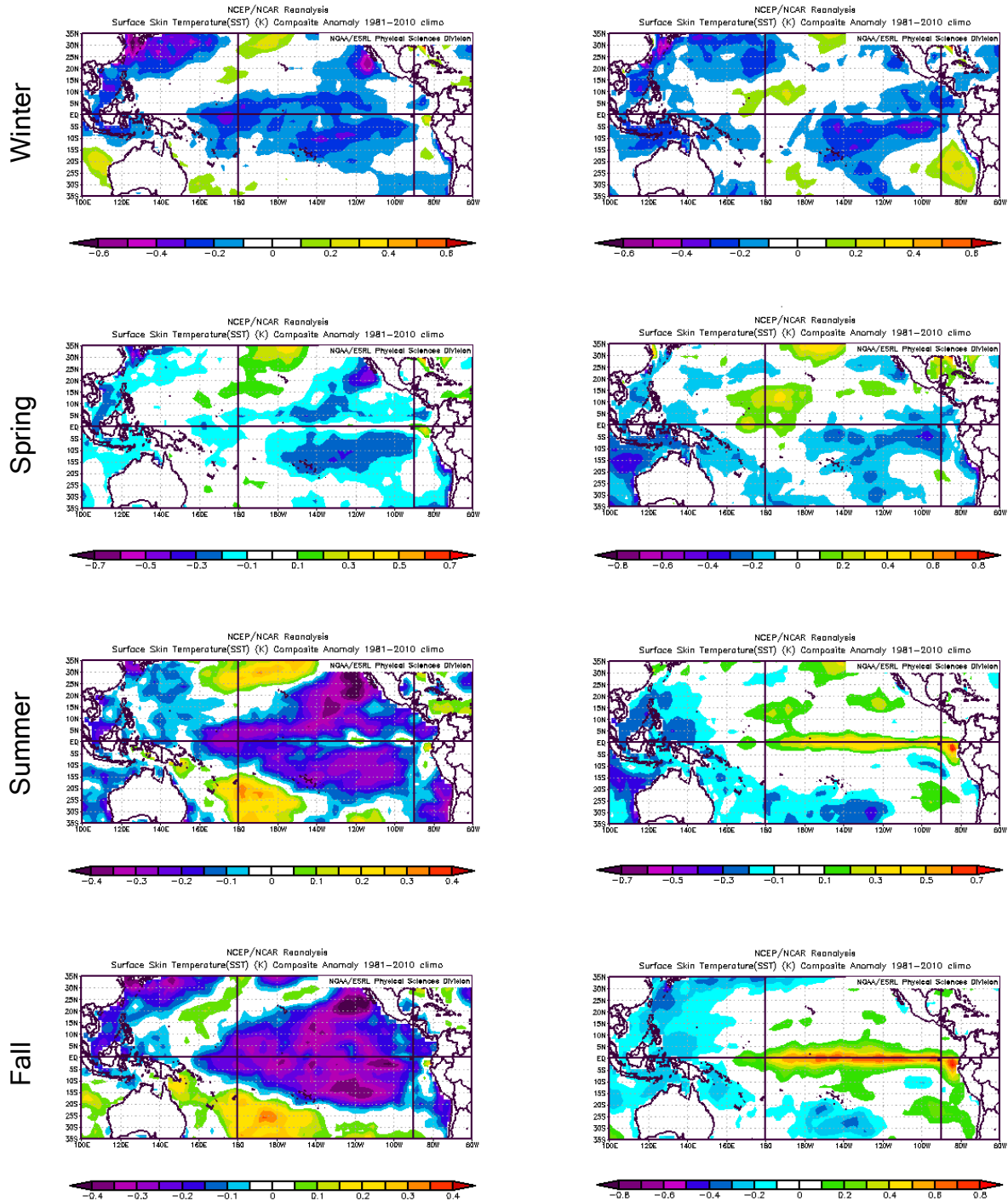


Figure 8: Tropical Pacific Sea-Surface Temperature Anomaly composites (Winter and Spring) were created by summing up years of increase in TPA and then summing up the years of decrease in TPA.

5.3.3 Pacific Decadal Oscillation (PDO)

The sum of the TPA was divided into two categories (low and high TPA) and plotted using box and whisker plots to examine the PDO and TPA relationship (Figure 9). There was a slight significant difference between the low and high TPA categories at the median confidence interval. The lower quantile of the low TPA did not reside in the negative (cool) phase PDO; however, the high TPA category had the lower quantile in the negative (cool) phase. The upper quantile and mean of low TPA were higher than the high TPA category and were in the positive (warm) PDO phase.

Although PDO showed a difference between low and high TPA only at the median confidence interval, a combination of ENSO and PDO showed differences between low and high TPA categories. The TPA response with ENSO and PDO combination showed that positive-phase PDO and negative-phase ENSO (La Niña) had the highest variability of TPA; however, the upper quantile had more TPA than any of the other three combinations (Figure 11). Negative-phase PDO and positive-phase ENSO (El Niño) combination had high variability, but not as extreme as the positive-phase PDO and La Niña combination. Both negative-phase PDO and La

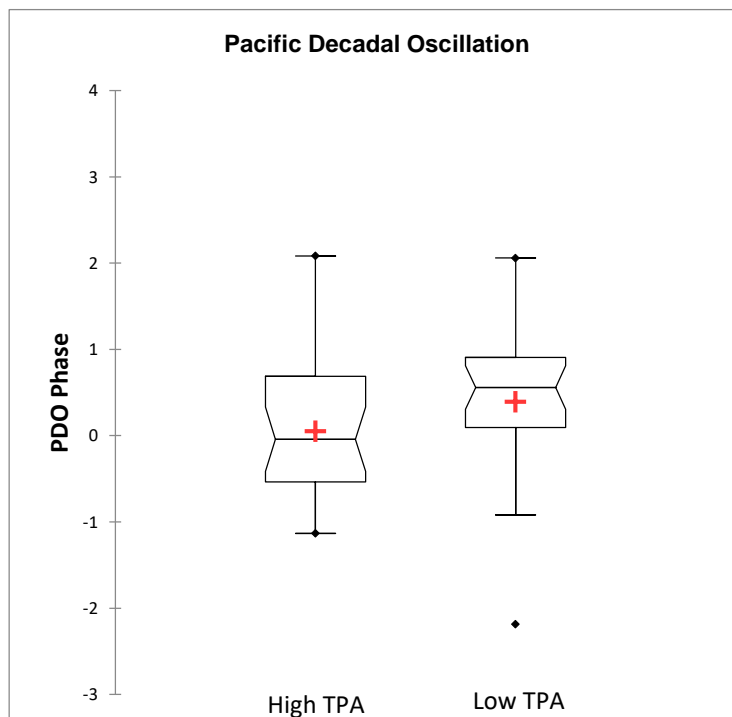


Figure 9: Box and whisker plot of low and high TPA categories in response with PDO phases

Niña had a very narrow distribution between the lower and upper quantiles, but has lower TPA when compared to the inverse combinations of ENSO+PDO. The lowest TPA response with ENSO and PDO combination was with both positive-phases of PDO and El Niño when compared to the other three combinations.

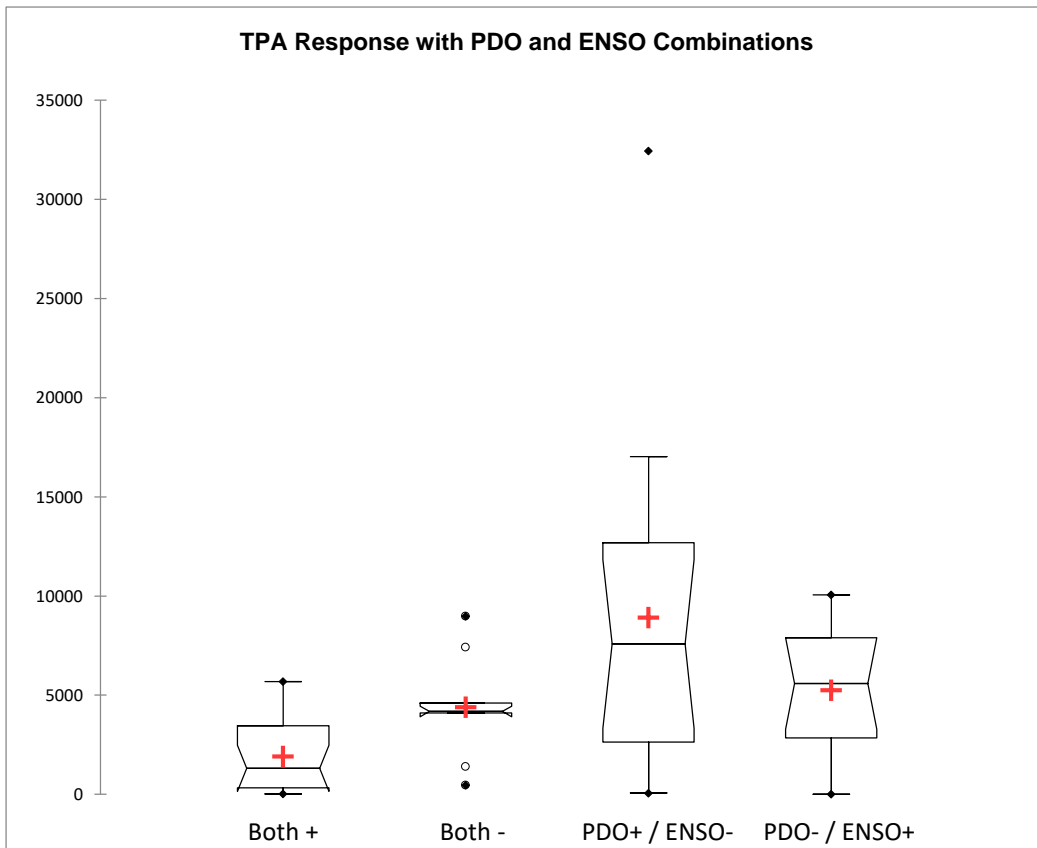


Figure 10: PDO and ENSO Combinations.

Chapter 6. Discussion

Specific objectives of this study were to determine how selected biophysical (slope, aspect, elevation, and latitude) and regional climate variables (temperature, precipitation, and drought), and global climate oscillations (ENSO, PDO, NAO, AO, and PNA) relate to bark beetle infestations in the Crown of the Continent Ecosystem from 1962 through 2014, as measured by ADS-recorded tree mortality (TPA). I used geopotential heights and sea-surface temperatures that may influence CCE climate to contextualize the model results and to further understand how climate may relate to peaks and declines of tree mortality from MBP infestations. Overall, the major findings of this study are: 1) despite its limitations, the ADS data seems suitable for analysis of beetle damage with respect to climate and topographic factors, on a regional scale, 2) there appears to be a link between local biophysical factors, such as latitude, elevation, and winter precipitation and TPA within the CCE, and 3) a combination of a negative-phase PDO and La Niña is important in forecasting a decline in MPB spread during a given year.

6.1 Aerial Detection Survey Data: Advantages and Limitations

Aerial detection surveys have been implemented to some degree in the U.S. since the 1940s (Johnson and Whittwer, 2008). As forest health has become increasingly imperiled by pathogen and insect outbreaks, the demand for this historical data has increased and its uses have diversified (Johnson and Ross 2008). ADS data has been used in some studies for planning purposes to estimate mountain pine beetle outbreaks in the red-attack stage (e.g., Wulder et al. 2006). Many researchers, however, are discouraged by its location inaccuracy and consistent underrepresentation of red-attack area, factors estimated to be the largest source of error associated with aerial surveys at local scales (Leckie et al., 2005; Wulder et al. 2006). For local analysis, ADS clearly may not be appropriate; however, Wulder et al. (2006) and Carroll et al., (2003) suggest that for regional to state level information needs (such as those in this study), aerial overview sketch mapping is thought to be sufficiently reliable for estimating mountain pine beetle damage. This study utilized ADS data in a quantitative analysis of MPB within a region of the western U.S. Despite its cited limitations, I found the dataset to be ideal for its

spatio-temporal resolution and representation of pine beetle damage. One major advantage of the ADS data acquired from the Missoula Field Office in Montana was that it was freely and readily available in GIS format, and thus accompanied with an attribute table with essential mortality information.

One further possible limitation of the ADS data as used in this study was the use of TPA as the primary predictor variable. TPA was calculated in the ADS attribute table number of dead trees (due to beetle attack) per acre, and was a readily available value in the attribute table. In many cases, the total polygon area represented the potential for infestation because they were dominated by host trees. However, some polygons, such as those at higher elevations or in mixed forest stands, may have had areas or species of trees that were not susceptible to attack. Thus, in future research, the proportion of damaged trees relative to total possible host trees could be calculated using supplemental landcover datasets, and may provide a more meaningful assessment.

6.2 Biophysical Analysis

The biophysical analysis revealed a link between local (as opposed to global) factors, such as latitude, elevation, and winter precipitation, and TPA within the CCE. My approach enabled yearly assessment of the changing relationship between outbreaks and the selected biophysical variables. Although the R^2 values of the regression analyses were low overall, latitude, elevation, slope, and aspect were found to influence (by inhibiting and/or promoting) TPA in many instances, and that the relative importance of the variables changed over time, as evident by the standardized coefficients of the regression models. The stepwise multiple linear regression model revealed that TPA increased in latitude in the CCE from the start of the study until 1995, when dead trees from beetle attack were more prevalent in the southern portion of the CCE, resulting in increased host tree mortality. However, the MPB continued to spread to higher elevations throughout the study period regardless of slope, aspect, or latitudinal changes beginning in 1997 (Table 3). The stepwise multiple linear regression model also revealed the increase of outbreak elevation to be even more pronounced starting in 2008 through the end of the study period as evident with larger coefficients than the previous years (Table 3; Figure 4). These results are consistent with findings from other studies that have examined trends in pine

beetle expansion throughout the North American West. For example, Six (2016) noted the expansion of mountain pine beetle into higher, subalpine ecosystems in the Rocky Mountains of the U.S. and Canada since 1999, until they are likely limited at treelines by small diameter trees.

One possible explanation for the upward expansion of MPB is simply that previously uninfected trees at higher elevations provide opportunity for new infestations (Six 2016). It is also possible that the CCE is running out of host trees (Sontag, Scott M – U.S. Forest Service, personal communication); however, Carroll et al. (2003), suggest that range expansion is not limited by available hosts but is rather due to climate change. Bentz et al., (2010) concluded that since the early 1960s, increasing temperatures in North America allows for greater low-temperature survivability and population success in areas already infested. The trend of beetle-induced mortality increasing in elevation within the CCE also suggests that increasing developmental rates and cold survivability of the MPB (Bentz et al., 2010) may be occurring in the study region that would allow beetles to migrate into colder environments where their survivability was previously low. It is possible that in our analysis, elevation, latitude, aspect and slope angle are surrogates for the broader influence of topography/climate interactions, which may in part explain the low R^2 values of these models.

6.3 Climate Analysis

The two-sample t-Test and the stepwise multi-linear regression model both revealed winter season precipitation to be important for the predicting TPA — a finding also supported by the literature. Precipitation provides moisture needed for the host tree to produce the resin to protect itself from the invading MPB (Safranyik et al., 1975; Raffa and Berryman, 1983; Nebeker et al., 1993; Aukema et al., 2006; Safranyik et al., 2010; Lusebrink et al., 2011; Chapman et al., 2012). Thus, a drought or lower than average precipitation can lead to increased TPA. Precipitation was the sole factor for increase or decrease in TPA, as evident by both results of the two-sample t-Test and the stepwise multi-linear regression model.

Geopotential height anomaly analysis revealed a commonality of a low height that appeared to have the CCE in a bullseye. The low heights were consistent during all four seasons for low TPA years. Spring season showed a positive phase (warm) Pacific/North American

(PNA) oscillation in the northwestern U.S. Fall still had a negative-phase PNA, but higher 500mb geopotential heights were located in Montana. The warmer temperatures in the spring and summer seasons are associated with an increase in heights, which has been associated with an accelerated speed in the MPB's developmental cycle and beetle emergence (Logan and Bentz 1999). Crosby and Curtis (1970) and Werner and Holsten (1983) note that that MPB spread is higher during warm summers, a trend possibly attributable to accelerated MPB life-cycle developmental rates (e.g., faster larvae growth and emergence of adult beetles), thus leading to higher TPA (Logan and Bentz 1999). Cooler and drier air is advected southward into this region during a troughing pattern in the polar jetstream, resulting in lower heights. The effect of the cooler and drier air can reduce precipitation in the winter season thus creating stress on the host trees.

A key to long-term forecasting MPB outbreaks in the CCE will be to determine whether neutral or above average height anomalies will be present for the spring and fall in order to forecast for increase in TPA. This study has revealed that PDO should not be the only forecasting tool in predicting TPA, but rather utilizing other climate variables such as analyzing different atmospheric heights that can alter the jetstream pattern during each season of importance. The analysis of the seasonal variation of ENSO did not reveal a profound difference between low and high TPA years in the winter nor spring, which is vital to understanding winter precipitation or spring temperatures influence during high TPA years. NAO in the winter was the only significant variable for the winter season, which could affect the precipitation patterns in this region. Typically, the NAO affects mainly eastern North America toward Europe, but the Geopotential Heights are above average in the eastern North America, and high pressure over north central North America which can limit precipitation and thus cause increasing TPA. The results of the stepwise multiple linear regression model revealed that an increases in PNA and AO with a decrease in NAO in the fall season, which could impact higher TPA.

Aukema et al., (2008) notes that temperature is the most important factor for MPB development and spread, but the regression analysis conducted here did not show temperature as measured to be of importance in predicting TPA. However, the results of the two-sample t-Test indicated that higher mean values of temperatures were associated with high TPA years and lower mean values were associated with low TPA years. Figure 11 illustrates the continuing

increasing trend of annual average temperatures due to a warming climate in this area. There is likely a correlation between the MPB spread and temperature as mentioned by Kurz et al., (2008) and Bentz et al., (2010) that increasingly rising temperatures in this region are accelerating life-cycle development due to climate change. Increasing annual temperature means will make the northern latitudes more favorable for MPB infestation due to rising temperatures, and a shift in range is already being documented in some studies (Kurtz et al., 2008 and Bentz et al., 2010)

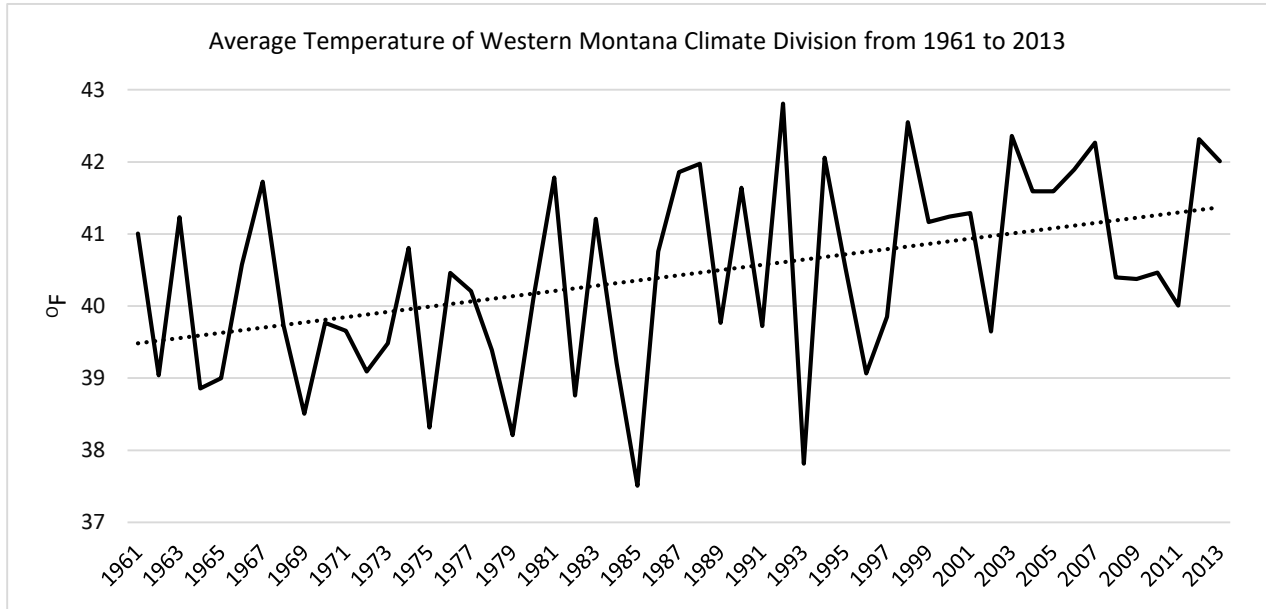


Figure 11: Average Temperature in the CCE continues to increase over time.

6.4 Conclusions and Future Directions

This is the first study to use aerial survey data in a geospatial analysis incorporating biophysical variables for the U.S. portion of the Crown of the Continent Ecosystem. Additionally, this study is unique to explore the potential relationship between global teleconnections and regional climate in the CCE area, and the spatio-temporal spread of MPB.

Future research could involve working with a larger area that incorporates data for both the U.S. and Canada for a more thorough understanding of a geographic range shift of the bark beetle outbreak. It was suggested by Bentz (2010) that the MPB are moving into the boreal forests in Canada, so with Canadian data, it could be possible that the MPB are slowly moving northward each year, or in pulses depending on ideal climatic conditions. PRISM data could

assist in building a better regression model to understanding local climate variables in relation to individual MPB polygons; however, global teleconnections would not be able to utilize this type of method and also eliminates possibility for a trend analysis on temperature and precipitation patterns in this region. Teleconnections would have to be tested on either a seasonal or monthly basis with a different model or other type of statistical test(s). Another method for understanding MPB spread limitations would be to incorporate the spatial extent of forest fire to determine how and where wildfires impede or enhance MPB spread (e.g., McHugh, 2003, Jenkins, 2008, Schoennagel, 2012).

Although there have been several studies on MPB, this is the first study to explore outbreak variation with both local and global climate variables for over fifty years in the CCE. In the future, additional geospatial analyses may enable a landscape assessment of factors contributing to variability of MPB infestation and damage as this insect continues to spread.

References

- Alfaro, René I., et al. "Dendroecological reconstruction of mountain pine beetle outbreaks in the Chilcotin Plateau of British Columbia." *Mountain Pine Beetle Symposium: Challenges and solutions*. TL Shore, JE Brooks, and JE Stone (editors). Kelowna, BC. 2003.
- Alfaro, René I, Elizabeth Campbell, and Brad C Hawkes. *Historical Frequency, Intensity and Extent of Mountain Pine Beetle Disturbance in British Columbia*. Vol. 2009: Pacific Forestry Centre, 2010. Print.
- Amman, Gene D. *Mountain pine beetle emergence in relation to depth of lodgepole pine bark*. Vol. 96. U.S. Dept. of Agriculture, Forest Service, Intermountain Forest & Range Experiment Station, 1969.
- Amman, Gene D. "Population changes of the mountain pine beetle in relation to elevation." *Environmental Entomology* 2.4 (1973): 541-548.
- Amman, G.D. Mountain pine beetle (Coleoptera: Scolytidae) mortality in three types of infestations. *Environmental Entomology*, (1984) 13:184–191.
- Amman, G.D., and Cole, W.E. Mountain pine beetle population dynamics in lodgepole pine forests. Part II. Population dynamics. United States Forest Service General Technical Report INT-145 (1983).
- Amman, Gene D, Mark D McGregor, and Robert E Dolph Jr. "Forest Insect and Disease Leaflet 2." *Mountain pine beetle*. USDA Forest Service, Washington, DC, USA (1990). Print.
- Aukema, Brian H, et al. "Landscape Level Analysis of Mountain Pine Beetle in British Columbia, Canada: Spatiotemporal Development and Spatial Synchrony within the Present Outbreak." *Ecography* 29.3 (2006): 427-41. Print.
- Aukema, Brian H, et al. "Movement of Outbreak Populations of Mountain Pine Beetle: Influences of Spatiotemporal Patterns and Climate." *Ecography* 31.3 (2008): 348-58. Print.

- Bader, Maaïke Y, and Johan JA Ruijten. "A Topography-Based Model of Forest Cover at the Alpine Tree Line in the Tropical Andes." *Journal of Biogeography* 35.4 (2008): 711-23. Print.
- Bakke, Alf. "The Recent Ips Typographus Outbreak in Norway - Experiences from a Control Program." *Ecography* 12.4 (1989): 515-19. Print.
- Bale, Jeffery S, et al. "Herbivory in Global Climate Change Research: Direct Effects of Rising Temperature on Insect Herbivores." *Global Change Biology* 8.1 (2002): 1-16. Print.
- "Bark Beetles in California Conifers - Are Your Trees Susceptible?" United State Department of Agriculture, 1 Feb. 2015. Web. 2 Aug. 2016.
<http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5384837.pdf >.
- Barnston, Anthony G., et al. "NECP forecasts of the El Niño of 1997-98 its U.S. impacts." *Bulletin of the American Meteorological Society* 80.9 (1999): 1829.
- Barras, Stanley J, and John D Hodges. "Carbohydrates of Inner Bark of Pinus Taeda as Affected by Dendroctonus Frontalis and Associated Microorganisms." *The Canadian Entomologist* 101.05 (1969): 489-93. Print.
- del Barrio, Gabriel, et al. "Response of High Mountain Landscape to Topographic Variables: Central Pyrenees." *Landscape Ecology* 12.2 (1997): 95-115. Print.
- Barry, Roger Graham. *Mountain weather and climate*. Psychology Press, 1992.
- Basist, Alan, Gerald D. Bell, and Vernon Meentemeyer. "Statistical Relationships between Topography and Precipitation Patterns." *Journal of Climate* 7.9 (1994): 1305-15. Print.
- Bentz, Barbara J., Jesse A. Logan, and Gene D. Amman. "Temperature-Dependent Development of the Mountain Pine Beetle (Coleoptera: Scolytidae) and Simulation of Its Phenology." *The Canadian Entomologist* 123.05 (1991): 1083-94. Print.
- Bentz, B. J., and D. E. Mullins. *Ecology of Mountain Pine Beetle (Coleoptera: Scolytidae) Cold Hardening in the Intermountain West*. Vol. 28 (1999): Print.

- Bentz, Barbara J., and Greta Schen-Langenheim. "The mountain pine beetle and whitebark pine waltz: Has the music changed." *Proc. conference on whitebark pine: a pacific coast perspective*. 2007.
- Bentz, B., Logan, J., MacMahon, J., Allen, C. et al. (2009). Bark beetle outbreaks in Western North America: Causes and consequences. Proceedings: Bark Beetle Symposium, November 15–17, 2005, Snowbird, Utah. University of Utah Press, Chicago, IL. 42 p.
- Bentz, Barbara J., et al. "Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects." *BioScience* 60.8 (2010): 602-13. Print.
- Bisrat, Simon A. "Modeling Bark Beetle Outbreak and Fire Interactions in Western U.S. Forests and the Invasion Potential of an Invasive Puerto Rican Frog in Hawaii Using Remote Sensing Data." (2010). Print.
- Broberg, Len. "A Climate-Impacts Assessment of the Crown of the Continent." (2012). Print.
- Brown, Daniel G. "Predicting Vegetation Types at Treeline Using Topography and Biophysical Disturbance Variables." *Journal of Vegetation Science* 5.5 (1994): 641-56. Print.
- Carroll, Allan L., et al. "Effect of climate change on range expansion by the mountain pine beetle in British Columbia." *Pages 223-232 in TL Shore et al.(eds) Mountain Pine Beetle Symposium: Challenges and Solutions, Oct. 30-31, 2003. Kelowna BC. Natural Resources Canada, Information Report BC-X-399, Victoria. 2003.*
- Cates, RG, and H Alexander. "Host Resistance and Susceptibility [to Bark Beetles, Scolytidae]." (1982). Print.
- Chapman, Teresa B., Thomas T. Veblen, and Tania Schoennagel. "Spatiotemporal Patterns of Mountain Pine Beetle Activity in the Southern Rocky Mountains." *Ecology* 93.10 (2012): 2175-85. Print.
- Christiansen, Erik, Richard H. Waring, and Alan A. Berryman. "Resistance of conifers to bark beetle attack: searching for general relationships." *Forest Ecology and Management* 22.1 (1987): 89-106.

- "Climate Indices: Monthly Atmospheric and Ocean Time Series." *NOAA Earth System Research Laboratory Physical Sciences Division*. Web. 08 May 2016.
<<http://www.esrl.noaa.gov/psd/data/climateindices/list/#NP>>.
- Climate Prediction Center Internet Team. "Climate Prediction Center - Monitoring & Data: ENSO Impacts on the U.S. - Previous Events." *NOAA Center for Weather and Climate Prediction*. Web. 08 May 2016.
<http://www.cpc.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml>.
- Creeden, Eric P., Jeffrey A. Hicke, and Polly C. Buotte. "Climate, Weather, and Recent Mountain Pine Beetle Outbreaks in the Western United States." *Forest Ecology and Management* 312.0 (2014): 239-51. Print.
- Crosby, D. and D. J. Curtis. *Forest insects and disease conditions in Alaska during 1969*. U.S. Dep. Agric. For. Serv. Publ. 15 pp (1970).
- Cudmore, Timothy J., et al. "Climate Change and Range Expansion of an Aggressive Bark Beetle: Evidence of Higher Beetle Reproduction in Naïve Host Tree Populations." *Journal of Applied Ecology* 47.5 (2010): 1036-43. Print.
- Cullingham, Catherine I., et al. "Mountain pine beetle host-range expansion threatens the boreal forest." *Molecular Ecology* 20.10 (2011): 2157-2171.
- Daly, Christopher, Wayne P. Gibson, George H. Taylor, Gregory L. Johnson, and Phillip Pasteris. "A knowledge-based approach to the statistical mapping of climate." *Climate research* 22, no. 2 (2002): 99-113.
- Eisenhart, Karen S, and Thomas T Veblen. "Dendroecological Detection of Spruce Bark Beetle Outbreaks in Northwestern Colorado." *Canadian Journal of Forest Research* 30.11 (2000): 1788-98. Print.
- Ellison, Aaron M., et al. "Loss of foundation species: consequences for the structure and dynamics of forested ecosystems." *Frontiers in Ecology and the Environment* 3.9 (2005): 479-486.
- ESRI 2015. *ArcGIS Desktop: Release 10.3.1*. Redlands, CA: Environmental Systems Research Institute.

- Fettig, C. J., et al. (2007). "The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States." *Forest Ecology and Management* 238(1–3): 24-53.
- Franceschi, Vincent R., et al. "Anatomical and Chemical Defenses of Conifer Bark against Bark Beetles and Other Pests." *New Phytologist* 167.2 (2005): 353-76. Print.
- Furniss, MM, and JA Schenk. "Sustained Natural Infestation by the Mountain Pine Beetle in Seven New Pinus and Picea Hosts." *Journal of Economic Entomology* 62.2 (1969): 518-19. Print.
- Furniss, MM. American forest entomology comes on stage. *Am. Entomol* (1997). 43: 40-47.
- Guisan, Antoine, Jean-Paul Theurillat, and Felix Kienast. "Predicting the Potential Distribution of Plant Species in an Alpine Environment." *Journal of Vegetation Science* 9.1 (1998): 65-74. Print.
- Guttman, Nathaniel B., and Robert G. Quayle. "A historical perspective of U.S. climate divisions." *Bulletin of the American Meteorological Society* 77.2 (1996): 293-303.
- Hadley, Keith S. "The Role of Disturbance, Topography, and Forest Structure in the Development of a Montane Forest Landscape." *Bulletin of the Torrey Botanical Club* 121.1 (1994): 47-61. Print.
- Hamilton, R. L., D. E. Mullins, and D. M. Orcutt. "Freezing-tolerance in the woodroach *Cryptocercus punctulatus* (Scudder)." *Experientia* 41.12 (1985): 1535-1537.
- Hart, Sarah J., et al. "Drought Induces Spruce Beetle (*Dendroctonus Rufipennis*) Outbreaks across Northwestern Colorado." *Ecology* 95.4 (2013): 930-39. Print.
- Hicke, Jeffrey A, et al. "Changing Temperatures Influence Suitability for Modeled Mountain Pine Beetle (*Dendroctonus Ponderosae*) Outbreaks in the Western United States." *Journal of Geophysical Research: Biogeosciences (2005–2012)* 111.G2 (2006). Print.
- Hicke, Jeffrey A., et al. "Effects of Bark Beetle-Caused Tree Mortality on Wildfire." *Forest Ecology and Management* 271.0 (2012): 81-90. Print.

- Hicke, J. A., et al. "Carbon Stocks of Trees Killed by Bark Beetles and Wildfire in the Western United States." *Environmental Research Letters* 8.3 (2013): 8. Print.
- Jenkins, Michael J., et al. "Bark beetles, fuels, fires and implications for forest management in the Intermountain West." *Forest Ecology and Management* 254.1 (2008): 16-34.
- Jenkins, Michael J., et al. "Fuels and fire behavior dynamics in bark beetle-attacked forests in Western North America and implications for fire management." *Forest Ecology and Management* 275 (2012): 23-34.
- JMP®, Version <12.0.1>. SAS Institute Inc., Cary, NC, 1989-2015.
- Johnson, Erik. "Region 6 - Insects & Diseases." Region 6 - Insects & Diseases. United States Department of Agriculture. Web. 27 Feb. 2015. <http://www.fs.usda.gov/detail/r6/forest-grasslandhealth/insects-diseases/?cid=fsbdev2_027406>.
- Johnson, Philip L, and W Dwight Billings. "The Alpine Vegetation of the Beartooth Plateau in Relation to Cryopedogenic Processes and Patterns." *Ecological Monographs* (1962): 105-35. Print.
- Keane, Robert E. "Modelling Stand Dynamics in Whitebark Pine (*Pinus Albicaulis*) Forests." *Ecological modelling* 51.1-2 (1989): 73-95. Print.
- Keane, Robert E., and Stephen F. Arno. "Rapid Decline of Whitebark Pine in Western Montana: Evidence from 20-Year Remeasurements." *Western Journal of Applied Forestry* 8.2 (1993): 44-47. Print.
- Keane Robert E., and Carl Key. "Transboundary GIS Applications. Sustaining Rocky Mountain Landscapes:" Science, Policy, and Management for the Crown of the Continent Ecosystem" (2010): 281.
- Keeling, Christopher I., and Jörg Bohlmann. "Genes, enzymes and chemicals of terpenoid diversity in the constitutive and induced defence of conifers against insects and pathogens*." *New Phytologist* 170.4 (2006): 657-675.
- Kurz, Werner A., et al. "Mountain pine beetle and forest carbon feedback to climate change." *Nature* 452.7190 (2008): 987-990.

- Leathers, Daniel J., Brent Yarnal, and Michael A. Palecki. "The Pacific/North American teleconnection pattern and United States climate. Part I: Regional temperature and precipitation associations." *Journal of Climate* 4.5 (1991): 517-528.
- Leckie, Donald G., Ed Cloney, and Steve P. Joyce. "Automated detection and mapping of crown discolouration caused by jack pine budworm with 2.5 m resolution multispectral imagery." *International Journal of Applied Earth Observation and Geoinformation* 7.1 (2005): 61-77.
- Lee Jr, Richard E. "Insect cold-hardiness: To freeze or not to freeze." *Bioscience* 39.5 (1989): 308-313.
- Lee Jr, R. E., and Denlinger, D. L. "Principles of insect low temperature tolerance." *Insects at low temperature*. Springer US, 1991. 17-46.
- Liao, X., et al. (2007). "Multiobjective optimization for crash safety design of vehicles using stepwise regression model." *Structural and Multidisciplinary Optimization* 35(6): 561-569.
- Logan, Jesse A., and Barbara J. Bentz. "Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality." *Environmental Entomology* 28.6 (1999): 924-934.
- Logan, Jesse A., and James A. Powell. "Ghost Forests, Global Warming, and the Mountain Pine Beetle (Coleoptera: Scolytidae)." *American Entomologist* 47.3 (2001): 160. Print.
- Logan, Jesse A., William W. Macfarlane, and Louisa Willcox. "Whitebark Pine Vulnerability to Climate-Driven Mountain Pine Beetle Disturbance in the Greater Yellowstone Ecosystem." *Ecological Applications* 20.4 (2010): 895-902. Print.
- Long, Ben. *Crown of the Continent: profile of a treasured landscape*. COCEEC Crown of the Continent Ecosystem Education Consortium, 2002.
- Lusebrink, Inka, et al. "Effect of Water Stress and Fungal Inoculation on Monoterpene Emission from an Historical and a New Pine Host of the Mountain Pine Beetle." *Journal of Chemical Ecology* 37.9 (2011): 1013-26. Print.

- Mantua, Nathan J., et al. "A Pacific interdecadal climate oscillation with impacts on salmon production." *Bulletin of the American Meteorological Society* 78.6 (1997): 1069-1079.
- Mantua, Nathan J., and Steven R Hare. "The Pacific Decadal Oscillation." *Journal of Oceanography* 58.1 (2002): 35-44. Print.
- McConnell, Timothy J., Erik W. Johnson, and Barbara Burns. "guide to conducting aerial sketchmapping surveys." (2000).
- McHugh, C. W., et al. (2003). "Bark Beetle Attacks on Ponderosa Pine Following Fire in Northern Arizona." *Environmental Entomology* 32(3): 510-522.
- Meddens, Arjan J. H., Jeffrey A. Hicke, and Charles A. Ferguson. "Spatiotemporal Patterns of Observed Bark Beetle-Caused Tree Mortality in British Columbia and the Western United States." *Ecological Applications* 22.7 (2012): 1876-91. Print.
- Meyn, A., et al. "Relationship between Fire, Climate Oscillations, and Drought in British Columbia, Canada, 1920-2000." *Global Change Biology* 16.3 (2010): 977-89. Print.
- Miller, R. H., and A. A. Berryman. "Energetics of conifer defense against bark beetles and associated fungi." *The role of the host in the population dynamics of forest insects* (L. Safranyik, Ed.) (1985): 4-7.
- Mock, Cary J. "Climatic controls and spatial variations of precipitation in the western United States." *Journal of Climate* 9.5 (1996): 1111-1125.
- Myers, Judith H. "Synchrony in outbreaks of forest Lepidoptera: a possible example of the Moran effect." *Ecology* 79.3 (1998): 1111-1117.
- Nebeker, T. E., J. D. Hodges, and C. A. Blanche. "Host response to bark beetle and pathogen colonization." *Beetle-pathogen interactions in conifer forests*. 1993.
- Oke, Timothy R. *Boundary layer climates*. Routledge, 1978.
- Pate, Sheena. "Crown of the Continent." *Crown of the Continent*. 2009 Old Town Creative Communications, LLC & National Geographic Society, 2009. Web. 13 Mar. 2015.

- Prato, T., and D. Fagre, Eds., 2007: *Sustaining Rocky Mountain Landscapes: Science, Policy, and Management for the Crown of the Continent Ecosystem*. 1st ed. Resources for the Future Press, 321 pp.
- Prato, Tony, and Daniel B. Fagre. "Sustainable management of the Crown of the Continent Ecosystem." *George Wright Forum*. Vol. 27. 2010.
- PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>, created 4 Feb 2004.
- Quinn, Michael S, et al. "A Collaborative Approach to Assessing Regional Cumulative Effects in the Transboundary Crown of the Continent." *Research and Development Monograph Series* (2002). Print.
- Quinn, Michael, and Len Broberg. "Conserving biodiversity." *Sustaining Rocky Mountain Landscapes: Science, Policy, and Management for the Crown of the Continent Ecosystem* (2007): 102.
- Raffa KF, Berryman AA. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs* 53 (1983): 27–49.
- Raffa, Kenneth F, and Alan A Berryman. "Interacting Selective Pressures in Conifer-Bark Beetle Systems: A Basis for Reciprocal Adaptations?" *American Naturalist* (1987): 234-62. Print.
- Raffa, Kenneth F., and Eugene B. Smalley. "Interaction of pre-attack and induced monoterpene concentrations in host conifer defense against bark beetle-fungal complexes." *Oecologia* 102.3 (1995): 285-295.
- Raffa, Kenneth F., et al. "Chapter Four - Interactions among Conifer Terpenoids and Bark Beetles across Multiple Levels of Scale: An Attempt to Understand Links between Population Patterns and Physiological Processes." *Recent Advances in Phytochemistry*. Ed. John, T. Romeo. Vol. Volume 39: Elsevier, 2005. 79-118. Print.

- Raffa, K. F., et al. "Cross-Scale Drivers of Natural Disturbances Prone to Anthropogenic Amplification: The Dynamics of Bark Beetle Eruptions." *Bioscience* 58.6 (2008): 501-17. Print.
- Reid, R. W. "Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of British Columbia II. Behaviour in the host, fecundity, and internal changes in the female." *The Canadian Entomologist* 94.06 (1962): 605-613.
- Reid, R.W. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay region of British Columbia. III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. *The Canadian Entomologist* (1963); 95: 225–238.
- Reid, R.W., Whitney, H.S. and Watson, J.A., "Reactions of lodgepole pine to attack by *Dendroctonus ponderosae* Hopkins and blue stain fungi". *Can. J. Bot.*, 45 (1967): 1115--1126.
- Reid, R. W., and H. Gates. "Effect of temperature and resin on hatch of eggs of the mountain pine beetle (*Dendroctonus ponderosae*)." *The Canadian Entomologist* 102.05 (1970): 617-622.
- Richmond, J. A., Catherine. Mills, and E. W. Clark. "Chemical changes in Loblolly Pine, *Pinus taeda* L., inner bark caused by blue stain fungus, *Ceratocystis minor* (Hedg.) Hunt." *Journal of the Elisha Mitchell Scientific Society* 86.4 (1970).
- Safranyik, L. "Management of lodgepole pine to reduce losses from the mountain pine beetle." (1974).
- Safranyik, L., Shrimpton, D.M. and Whitney, H.S. An Interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue stain fungi in western Canada. –In: Baumgartner, D.M. (ed.), *Management of Lodgepole Pine Ecosystems Symp. Proc.*, Washington State Univ. Cooperative Extension Service (1975): pp. 406-428.

- Safranyik, L., et al. "Bark Beetle (Coleoptera: Scolytidae) Diversity in Spaced and Unmanaged Mature Lodgepole Pine (Pinaceae) in Southeastern British Columbia." *Forest ecology and management* 200.1 (2004): 23-38. Print.
- Safranyik, L., and A. L. Carroll. "The Biology and Epidemiology of the Mountain Pine Beetle in Lodgepole Pine Forests." Victoria: Canadian Forest Service, 2007. 3-66. Print.
- Safranyik, L., et al. "Potential for Range Expansion of Mountain Pine Beetle into the Boreal Forest of North America." *The Canadian Entomologist* 142.05 (2010): 415-42. Print.
- Schoennagel, Tania, et al. "ENSO and PDO Variability Affect Drought-Induced Fire Occurrence in Rocky Mountain Subalpine Forests." *Ecological Applications* 15.6 (2005): 2000-14. Print.
- Schoennagel, Tania, et al. "Effects of mountain pine beetle on fuels and expected fire behavior in lodgepole pine forests, Colorado, USA." *PLoS One* 7.1 (2012): e30002.
- Seager, Richard, et al. "Model projections of an imminent transition to a more arid climate in southwestern North America." *science* 316.5828 (2007): 1181-1184.
- Seidl, Rupert, et al. "Modelling Bark Beetle Disturbances in a Large Scale Forest Scenario Model to Assess Climate Change Impacts and Evaluate Adaptive Management Strategies." *Regional Environmental Change* 9.2 (2009): 101-19. Print.
- Selkowitz, D. J., Fagre, D. B., & Reardon, B. A. Spatial and Temporal Snowpack Variation in the Crown of the Continent Ecosystem. Proceedings of 70th Annual Meeting of the Western Snow Conference. Granby, CO. 2002. Print.
- Shabbar, Amir, and Madhav Khandekar. "The impact of el Niño-Southern oscillation on the temperature field over Canada: Research note." *Atmosphere-Ocean* 34.2 (1996): 401-416.
- Shabbar, Amir, Barrie Bonsal, and Madhav Khandekar. "Canadian precipitation patterns associated with the Southern Oscillation." *Journal of Climate* 10.12 (1997): 3016-3027.
- Sherriff, Rosemary L., Edward E. Berg, and Amy E. Miller. "Climate Variability and Spruce Beetle (*Dendroctonus Rufipennis*) Outbreaks in South-Central and Southwest Alaska." *Ecology* 92.7 (2011): 1459-70. Print.

- Shrimpton, DM, and AJ Thomson. "Relationship between Phloem Thickness and Lodgepole Pine Growth Characteristics." *Canadian Journal of Forest Research* 15.5 (1985): 1004-08. Print.
- Six, Diana. "Mountain Pine Beetles Expansion in the West." *American Forests*, 06 May 2016. Web. 09 May 2016.
- Smith, Richard Harrison, John P Cramer, and Edwin J Carpender. *New Record of Introduced Hosts for the Mountain Pine Beetle in California*. Vol. 354: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station, 1981. Print.
- Solomon, Susan. *Climate Change 2007: The Physical Science Basis*. Cambridge, UK: Published for the Intergovernmental Panel on Climate Change Cambridge UP, 2007. Print.
- Sontag, Scott M –FS. "RE: Aerial Survey Data" Message to Mario N. Garza. 20 Nov. 2014. E-mail.
- Stahl, K, RD Moore, and IG McKendry. "Climatology of Winter Cold Spells in Relation to Mountain Pine Beetle Mortality in British Columbia, Canada." *Climate Research* 32.1 (2006): 13-23. Print.
- Taylor, S. W., and A. L. Carroll. "Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: A historical perspective." *Mountain pine beetle symposium: Challenges and solutions*. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Information Report BC-X-399, Victoria, BC, 2003.
- Taylor, Steve W., et al. "Forest, climate and mountain pine beetle outbreak dynamics in western Canada." *The mountain pine beetle: A synthesis of biology, management, and impacts on lodgepole pine* (2006): 67-94.
- Temperli, C., H. Bugmann, and C. Elkin. "Cross-Scale Interactions among Bark Beetles, Climate Change, and Wind Disturbances: A Landscape Modeling Approach." *Ecological Monographs* 83.3 (2013): 383-402. Print.

United States Forest Service. Forest Health Monitoring Program and State and Private Forestry Forest Health Protection. Aerial Survey Geographic Information System (GIS) Handbook. Washington. 2007. Print.

United States Forest Service. Forest Health Monitoring Program and State and Private Forestry Forest Health Protection. Aerial Survey Standards. Washington. 1999. Print.

Waldt, R. 2004. Crown of the Continent: The Last Great Wilderness of the Rocky Mountains. Helena, Mont.: Riverbend Publishing.

Werner, Richard A, and Edward H Holsten. "Mortality of White Spruce During a Spruce Beetle Outbreak on the Kenai Peninsula in Alaska." *Canadian Journal of Forest Research* 13.1 (1983): 96-101. Print.

Williams, David W., and Andrew M. Liebhold. "Climate Change and the Outbreak Ranges of Two North American Bark Beetles." *Agricultural and Forest Entomology* 4.2 (2002): 87-99. Print.

Wood, S. L. A revision of bark beetle genus *Dendroctonus* Erichson (Coleoptera: Scolytidae). – *Great Basin Nat.* 23 (1963): 1-117.