Tree-Ring Analysis of Outbreak Dynamics across an Insect’s Entire Range: The Pandora Moth System

A thesis

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In montane forests of the western United States, pandora moth (*Coloradia pandora* Blake) defoliates local pines, primarily ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws.) and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.). This defoliation stresses the tree, leaving a distinct outbreak signature in the tree-rings. The occurrence of pandora moth outbreaks has been recorded in ponderosa pine tree rings in Oregon as far back as 1500 years, however little is known of the outbreak history throughout the rest of the pandora moth range. To gain a better understanding of the spatiotemporal dynamics of pandora moth I have reconstructed outbreaks across the entire range of the insect using 121 tree-ring chronologies from the International Tree-Ring Databank (ITRDB) and 19 chronologies from sites sampled for this study using dendrochronological techniques. I then created a fine resolution habitat model for pandora moth and a gridded tree-ring network of non-host chronologies, which was used to validate statistically confirmed outbreak events across the entire range of the insect. Sites with confirmed outbreaks were then tested against the habitat model for accuracy of model parameters. ArcMap 10 was used to create an animated map of the spatial and temporal distribution of pandora moth across its range. One of my most notable findings is the record of outbreak events further north than previously documented, and the agreement between those northern sites with my habitat model. In my research I have demonstrated the use of dendrochronology to study outbreaks across an insect’s range. The methods I have used here can be applied to other range-wide analyses.
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PREFACE

The goal of this thesis was to better understand the outbreak dynamics of pandora moth across multiple spatiotemporal scales. To perform this investigation of the pandora moth system, a non-host gridded network of tree-ring chronologies and a finer resolution habitat model were constructed. All validated outbreaks were then shown in an animated map of outbreak dynamics over time. Chapter one provides an introduction to the ponderosa pine and pandora moth system in the western united states. Chapter two is a detailed description of the pandora moth habitat, how the insect affects ponderosa pine forests, and how dendrochronology is used to reconstruct past outbreaks. In chapter three the dendrochronological and mapping methods of this research are given in detail, from site selection to statistical programs. Chapter four discusses the use of a gridded network of non-host chronologies as a climate control for pandora moth outbreak reconstruction and presents an animation of outbreaks over time and space. In chapter five a high resolution habitat model is built and tested using ponderosa pine sites in various locations across the western U.S. Chapters four and five have been prepared for submission to the Annals of the Association of American Geographers. Chapter six provides a discussion and chapter seven provides a conclusion of the research as well as a discussion of future methods to be considered.
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CHAPTER 1

INTRODUCTION

In montane forests of the western United States, the pandora moth (*Coloradia pandora* Blake) feeds on the needles of local pines, including ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws.), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and lodgepole pine (*Pinus contorta* Dougl. ex. Loud.) (Patterson 1929). Ponderosa pine is the typical host of pandora moth and the relationship between the two is unique, in respect to other host-parasite relationships. The atypical relationship of pandora moth and ponderosa pine is defined by very low mortality rates in the host trees. During an outbreak, defoliation stresses the tree leaving a distinct outbreak signature in the tree-rings. These signatures indicate when the outbreak occurred and provide a loose estimate of the length of the event (Speer *et al.* 2001). The preservation of outbreak signatures is very useful for determining the frequency of outbreaks through time and the effect of other disturbance events on outbreak dynamics. Pandora moth outbreaks have been recorded using tree rings in Oregon and Arizona, but little is known of outbreak dynamics outside of these two states. In Oregon, the occurrence of pandora moth outbreaks has been recorded in ponderosa pine tree rings as far back as 1500 years (Clark, unpublished data). Historical reports suggest the pandora moth habitat range is centered south of Oregon, in the Sierra Nevada range of California (Figure 1; Carolin and Knopf 1968, USDA 2003). These reports describe the gathering of pandora moth larvae by aboriginal people living near the Sierra Nevada range for a food source.
 Accounts of pandora moth in this area suggest that outbreak signatures will be present in the tree-rings of local ponderosa and Jeffrey pines. Distribution maps were generated based on observations of past outbreaks, but these maps are of a coarse resolution. The Carolin and Knopf map was hand drawn with relative borders and an unknown resolution while the USDA map is at county level (Figure 1).

Figure 1. Maps of pandora moth distribution from 1968 (Carolin and Knopf, left) and 2003 (USGS, right).

The focus of my thesis was primarily on understanding the pandora moth across its entire range. I hypothesize that the pandora moth range extends further than previously documented in maps of collections and outbreaks from the 1900s. The habitat variables (host species, maximum temperature, and soil permeability) necessary to support pandora moth extend well beyond the boundaries of documented pandora moth activity and suggest that outbreaks may have occurred in these areas prior to historical documentation.
In my research I applied dendrochronology, a tool for dating trees and reconstructing past disturbance events such as climate, fire, and insect outbreaks across numerous spatial and temporal scales. One of my objectives was to reconstruct pandora moth outbreaks on a north-south transect covering California to determine if outbreaks occurred in various locations in northern, central, and southern California and to what spatial extent, frequency, duration, and intensity they have occurred. Intensity is variously defined as maximum and average growth reduction per tree, percentage of trees recording on a site, or the number of sites recording in a region depending upon the scale being examined. In addition to reconstructing outbreaks in California, I also looked in others areas of the western U.S. with historical documentation of outbreaks to determine the extent of the pandora moth habitat.

Another objective of my research was to quantify and verify pandora moth outbreaks in the western U.S. by creating a network of non-host chronologies that could be used as a climate control against the ponderosa pine chronologies. I then created an animation of outbreak events from 1400 to 2009 to display the spatiotemporal dynamics of pandora moth outbreaks. Due to the disagreement between historical documents of outbreak sites and previous pandora moth range maps a finer resolution habitat model was developed (Patterson 1929, Carolin and Knopf 1968, USDA 2003). I tested the accuracy of this map using the confirmed pandora moth outbreaks from the non-host climate control study. A range-wide habitat model for pandora moth provided greater detail about the outbreak dynamics of the insect.
CHAPTER 2

LITERATURE REVIEW

In the mountain ranges of eastern California there are three distinct pine forest communities. In the north, ponderosa pine is the most prevalent while in the south Jeffrey pine is more common. In central California, the two species coexist and have hybridized (Burns and Honkala 1990). While there are many natural pine forest disturbances in the western U.S., drought, fire, and insect outbreaks are the most frequent disturbances in California. I will be focusing specifically on pandora moth outbreaks in ponderosa pine forests.

Insect Outbreaks

Phytophagous insects defoliate trees, causing growth reductions which are expressed as narrow rings often in a particular pattern, or ring signature (Speer 2010). Tree-ring measurements can be used to quantify insect outbreaks that predate historical documentation. Spatial and temporal dynamics such as outbreak duration, frequency, intensity, and spread can be reconstructed through dendroecological techniques (Swetnam et al. 1985, Speer 2010). To differentiate between suppressions caused by climate and insect outbreaks, many researchers have used a non-host control species as a climate comparison for the species being defoliated (Wickman 1963, Swetnam 1983, Swetnam et al. 1985, Speer 2010). Ideally, the control species comes from a nearby site to the host species being defoliated, has a similar response to climate,
and is not a host species for another defoliating insect (Swetnam et al. 1985). The chronologies for both species are then used as inputs to the computer program OUTBREAK, which provides the quantitative identification of outbreaks based on parameters set by the user to distinguish specific insect outbreak dynamics (Holmes and Swetnam 1996, Speer 2010).

In some cases a non-host control species is unavailable. In a study of pandora moth outbreaks, Speer et al. (2001) were unable to find a long-lived non-host species growing near the host species, ponderosa pine. Ponderosa pine typically grows in pure stands, making it difficult to sample local non-host trees at outbreak sites. To quantify pandora moth outbreaks, the program OUTBREAK was modified so that only the host species was a necessary input. Once potential outbreaks were determined, instrumental climate data and tree-ring reconstructions of western juniper (Juniperus occidentalis Hook.) were used for climate comparisons (Speer et al. 2001). It has also been suggested that if a non-host species is not available and the host species has not been affected by outbreaks across its entire region, an averaged regional chronology may serve as a suitable climate control as long as spatiotemporal outbreak dynamics have not changed (Swetnam et al. 1985, Paritsis et al. 2009).

Pandora Moth

The pandora moth’s relationship to its host, ponderosa pine, is unique because although it may severely defoliate the trees, it typically does not cause mortality (Speer et al. 2001, Parker et al. 2006). Instead, it leaves a distinctive signature in the growth rings of ponderosa pine, allowing dendrochronologists to study multiple outbreaks that occurred during the lives of these trees (Speer et al. 2001). This makes pandora moth an excellent insect to use in modeling insect outbreak dynamics over long periods of time and large spatial extents.
Pandora moth is an indigenous, phytophagous insect in western North America. The larvae of pandora moth feed mostly on the needles of ponderosa pine, but have also been noted to feed on Jeffrey pine, and lodgepole pine (Patterson 1929). Although it defoliates the pine trees, defoliation occurs over the course of two consecutive summer seasons lessening the overall impact of defoliation. Rarely does defoliation cause mortality (< 2%) but it often causes suppression in growth rings (Blake and Wagner 1987, Speer and Holmes 2004, Pohl et al. 2006). Outbreaks occur in twenty to thirty year intervals and typically last 10 years in Oregon (Speer et al. 2001). While the range of pandora moth is likely to extend into Mexico and Canada, it is mostly restricted to the U.S. and is mostly found in Oregon, California, Arizona, and Colorado, although some small populations are also found in other surrounding states (Carolin and Knopf 1968, Speer et al. 2001, Speer and Jensen 2003, USDA 2003).

Pandora moth has a two-year life cycle that begins in late July or August when the female lays her eggs at the base of the needles. In late August or September the larvae hatch and begin feeding on the needles. The larvae overwinter and begin feeding on the needles again when warmer conditions arrive, usually in late March and April. In August, they move down the tree and burrow into the soil to pupate. They remain in the soil through winter and emerge in late summer as moths (Patterson 1929). Pandora moths prefer sites with loose granitic or pumice soils, open canopies, and low fuel accumulation (McCullough et al. 1998, Speer et al. 2001, Pohl et al. 2006). High soil permeability allows them to burrow during pupation. It is believed that their preference for less dense canopies and low fuel accumulation on forest floors is due, in part, to adaptation to fire (McCullough et al. 1998).
Habitat Models

Previous maps of pandora moth habitat provide a general location for where this insect occurs, but none have attempted to fully cover the insect’s range (Carolin and Knopf 1968, Speer and Jensen 2003, USDA 2003). While the Carolin and Knopf (1968) model recognizes large areas in Oregon, California, and Colorado, it is hand drawn and does not provide much detail. The USGS (2003) map provides more detail of areas likely to support pandora moth but it is at a county level and does not show habitat area at a stand level. Instead it overestimates potential habitat in large counties such as those seen in Arizona (Figure 1). Speer and Jenson (2003) created a hazard model for pandora moth outbreaks. Host species, soil permeability, and climate were used to determine potential habitat. This model was at a much finer resolution (1km) than the two previous models, but was only for the state of Oregon.

Dendrochronology

Tree rings provide a detailed record of disturbance events because they are datable and display climatic and environmental information in the varying sizes of annual rings. A conifer’s growth rings are formed by the division of cambial cells (Speer 2010). During the growing seasons of spring and summer, cells form earlywood which are light in color and have large, thin walls. During late summer to fall latewood is formed by small, thick walled cells that are darker in color. The combination of earlywood and latewood represents one year of growth (Fritts 1976, Bradley 1999, Speer 2010). Environmental and climatic factors such as fire, insect outbreaks, forest succession, precipitation, and temperature correspond with variations in the width of growth rings (Bradley 1999). During years with favorable growing conditions, wide growth rings will form. Conversely, during years when the tree encounters some type of stress, narrow growth
rings are formed (Fritts 1976). These variations in ring width allow dendrochronologists to date disturbance events, measure how long they occurred, and determine the severity of the events.

In the subdiscipline of dendroecology, scientists study the history of disturbances and successional dynamics of forests. They must account for many factors that drive these events such as climate, fire, pathogens, and insect outbreaks. These disturbance events are often studied separately, but there has been a recent growing interest in the scientific community to study multiple facets of natural processes and how they interact as a system (Fleming and Candau 1998, Ehle and Baker 2003, Bigler et al. 2005, Parker et al. 2006, Pohl et al. 2006). The study of interactions between pandora moth and fire is unique due to the fact that ponderosa pines are capable of surviving multiple outbreaks and fires. These events are recorded in the growth rings of the trees, and can be compiled into chronologies dating back hundreds of years (Speer et al. 2001). Drought events are also recorded in tree rings and can be compared with outbreaks and fires to determine relationships between the disturbances. However, in tree ring studies concerning multiple types of disturbance events, dendrochronologists must be able to extract the signal from the noise (Bradley 1999).

Pandora moth outbreaks leave a distinctive signature in the growth rings that is identifiable by thin latewood throughout the signature of recorded outbreak with four to six years of subsequent suppressed rings (Speer et al. 2001). However, one issue with using tree rings to determine outbreak event years is that the trees do not begin recording the outbreak until it reaches its peak a few years into the event when the tree is most stressed and insect populations reach their maximum limit (Speer et al. 2001). So while dendrochronologists cannot determine the precise year an outbreak began, they can verify that an outbreak did occur and approximate
the length of the outbreak based on known outbreak dynamics. More importantly, if temporal lag effects are taken into consideration, triggering factors can be explored.

Fire damage can be easily distinguished from insect outbreaks by the scar left on the tree that corresponds with the year in which an event occurred, although occasionally growth rings can be larger or smaller following fire events depending on nutrient cycling or damage to the tree, respectively (Speer et al. 2001). Climatic events are recorded as suppressed (small) or large growth rings in trees. Small rings indicate some type of stress, typically related to excessive temperature or lack of precipitation while large rings indicate favorable climatic conditions (Fritts 1976, Bradley 1999, Speer et al. 2001). The use of a non-host tree species that responds similarly to climate conditions coupled with documented climate data can be beneficial when distinguishing climate related suppression from fire or outbreaks (Speer et al. 2001).

History of the Climate Grid

Dendrochronology has been and continues to be a prominent tool used in climate reconstructions around the world, largely due to the annual resolution provided by tree-rings. In the United States, instrumental climate data from the National Climate Data Center has only been widely recorded since 1895 (Karl et al. 1990). Dendrochronology has been used to extend the climate record further back in time.

Once it was determined that data from instrumental records could be used to calibrate tree-ring data, extending climate reconstructions further back in time became a possibility (Fritts 2001). Networks of local chronologies were successfully pieced together to contribute to regional climate reconstructions for the western U.S. (LaMarche and Fritts 1971). Once more eastern chronologies were available, they were combined with the western networks making possible a climate reconstruction that covered the continental United States (Meko et al. 1993).
Around the same time tree-ring chronologies were expanding in the U.S., Palmer (1965) was working with temperature and precipitation data, and calculated the Palmer Drought Severity Index (PDSI) for each year of available data. PDSI is a common measure of wet and drought conditions (Palmer 1965). This approach allowed climatologists to examine climate patterns as they had occurred spatially and temporally, but was ultimately confined to an eighty-six year period by the instrumental data record at the time (Karl and Koscielny 1982).

Following the works of Karl and Koscielny (1982) and Meko et al. (1993), a gridded network of climate reconstructions was developed by Cook et al. (1999) for the continental United States using tree-ring chronologies from sites with climate-sensitive trees and based on the PDSI. This climate grid laid the framework for continent-wide climate reconstructions, as it not only covered the entire continental U.S. but also extended the drought record back to 1700. Cook et al. (1999) constructed a 2˚ latitude by 3˚ longitude grid using 1036 single-station PDSI records local to each of the 155 grid points. Monthly PDSI records were assigned to a point using a 150km radius or the five nearest records to a point if none met the first criterion. These records were then interpolated to their assigned grid points using inverse distance weighting (Cook et al. 1999). Tree-ring chronologies from numerous species across the United States were included in the network as long as they started no later than 1700 and ended no earlier than 1979. These chronologies came from the International Tree-Ring Data Bank (ITRDB), an online storehouse for tree-ring chronologies around the world, or were contributed by other researchers. Four hundred and twenty-five chronologies met these criteria. Due to the natural arrangement of species across a landscape, the clustering of species in certain regions and the lack of species in others was observed (Cook et al. 1999). The effects of differences in chronology start and end dates were minimized using a variance stabilization option in ARSTAN, the Autoregressive
Standardization program for tree-ring standardization (Cook and Holmes 1986, Meko et al. 1993).

After standardizing the chronologies, a tree-ring reconstruction of PDSI was made using point-by-point regression (PPR), as opposed to other regression methods that would compare two sets of variables and had been used in the past by other dendroclimatologists. Cook et al. (1999) decided PPR was most appropriate since it would allow for tree-ring chronologies local to each PDSI grid point (within 450km) to be included in the search for the best fit drought correlation and it would also exclude any local tree-ring chronologies that were not responding to drought using a screening probability of $\alpha = 0.10$. To test the accuracy of the PDSI grid points, actual and reconstructed, each point was statistically tested for the explained variance during the calibration period (1928 – 1978), the squared Pearson correlation for the verification period (before 1928), the reduction of error in the verification period, and the coefficient of efficiency also in the verification period. Results from these tests showed that over the majority of the grid, excluding a few problem locations (areas lacking chronologies or having poor quality instrumental records), there was a significant correlation between the verification period made up of tree-ring chronologies and the actual PDSI grid (Cook et al. 1999).

Following the severe drought of 2002, which affected much of western North America including parts of Canada and Mexico, Cook et al. (2004) set out to expand the previous version of the PDSI drought reconstruction created by Cook et al. (1999). This updated version of the grid covered a larger area, extending into Canada and Mexico, and a finer scale than the previous grid, with 286 points on a 2.5° latitude by 2.5° longitude grid. Growing season (June, July, August) PDSI records were averaged instead of using the monthly PDSI records from Cook et al.
(1999), and the reconstructions were updated to the year 2003 and extended further back in time, adding between 600 and 1200 years to the record in some areas of the grid (Cook et al. 2004).

PPR was used to reconstruct drought in the same manner as it was in Cook et al. (1999), and the actual and reconstructed grid portions of the grid were statistically tested in the same manner as before, with one exception. Principal components regressions models were used to extend each reconstruction for a grid point as far back as its longest chronology would allow (Cook et al. 2004). Drought history was then analyzed using the Drought Area Index (DAI), which calculated the number of grid points with drought conditions each year and divided that by 286 (total grid points) to determine the percentage of the grid under drought conditions each year (Cook et al. 2004). Cook’s PDSI grid and an interactive drought map are now available on the internet through NOAA’s website (http://www.ncdc.noaa.gov/paleo/pdsi.html).
CHAPTER 3

METHODS

Site Selection

I have sampled thirteen forested sites throughout National Forest land in California that are believed to be suitable habitats for pandora moths (Figure 2, Table 1). The pandora moth habitat requires the presence of a host species, favorable climate conditions (average temperature not falling below 15.6°C during the summer), and high soil permeability (Speer et al. 2001). These sites have been chosen by the following criteria:

- All sites are on National Forest land in the state of California
- Sites are chosen in northern, central, and southern California to represent the forests of these regions
- Sites are located in clusters, when possible, so that spatiotemporal analysis can be done within sites and between distant sites
- The predominant species present is large diameter (≥60cm DBH) ponderosa and/or Jeffrey pines including hybrid species
- Any locations with historical documentation of pandora moth outbreaks that are also located on National Forest land have been sampled, if possible
In southern California, I sampled in San Bernardino National Forest (two sites) and Cleveland National Forest (one site) (Figure 5). In central California I sampled in Inyo National Forest (three sites), Eldorado National Forest (one site), and Humboldt-Toiyabe National Forest (one site) (Figure 4). In northern California I sampled in Lassen National Forest (three sites), Klamath National Forest (one site), and Tahoe National Forest (one site) (Figure 3).

In addition to the thirteen sites in California, nine other study sites throughout the western U.S. were chosen based on historical reports of pandora moth activity (Figure 6, Table 1). These sites were worked up by Dorothy Rosene for her senior thesis at Indiana State University but were used for various parts of this research. In Arizona, three sites were sampled in Kaibab National Forest and one site was sampled in Sitgreaves National Forest. In New Mexico, two sites in Cibola National Forest were sampled. In Oregon, one site was sampled in Winema National Forest and in South Dakota two sites were sampled in Black Hills National Forest.
Figure 2. Study site locations in California.
Figure 3. Study site locations in northern California.
Figure 4. Study site locations in central California.
Figure 5. Study site locations in southern California.
Table 1. Study site locations in the western U.S. and associated National Forests. Species Abbreviations: PIPO, ponderosa pine (*Pinus ponderosa*); PIJE, Jeffrey pine (*Pinus jeffreyi*); PIPO/PIJE have both species and likely hybrids of the two as well.

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<td>112°13'57.02&quot;</td>
<td>PIPO</td>
</tr>
<tr>
<td></td>
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<td>Kaibab</td>
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<td>112°7'15.15&quot;</td>
<td>PIPO</td>
</tr>
<tr>
<td></td>
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<td>Forest Service Road 22</td>
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<td>36°24'39.82&quot;</td>
<td>112°8'21.64&quot;</td>
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</tr>
<tr>
<td>California</td>
<td>BCC</td>
<td>Butte Creek Camp</td>
<td>Lassen</td>
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<td>121°17'45.86&quot;</td>
<td>PIPO</td>
</tr>
<tr>
<td></td>
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<td>CFC</td>
<td>Chris Flat Camp</td>
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<td>119°27'18.03&quot;</td>
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</tr>
<tr>
<td></td>
<td>CRA</td>
<td>Crestview Research Area</td>
<td>Inyo</td>
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<td>118°59'11.83&quot;</td>
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</tr>
<tr>
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</tr>
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<td>San Bernardino</td>
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<td>116°56'44.97&quot;</td>
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</tr>
<tr>
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<td>HBC</td>
<td>Highbridge Campground</td>
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<td>121°18'31.30&quot;</td>
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<tr>
<td></td>
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<td>Sunflower Flat</td>
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<td>121°17'59.58&quot;</td>
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<td>117°1'56.80&quot;</td>
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</tr>
<tr>
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<td>Tuff Campground</td>
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</tr>
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<td>Telephone Line</td>
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<td>118°56'37.33&quot;</td>
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</tr>
<tr>
<td></td>
<td>WHL</td>
<td>Wooded Hill</td>
<td>Cleveland</td>
<td>32°49'0.54&quot;</td>
<td>116°31'14.02&quot;</td>
<td>PIJE</td>
</tr>
<tr>
<td></td>
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<td>XP Trail</td>
<td>Eldorado</td>
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<td>120°17'45.86&quot;</td>
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</tr>
<tr>
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<td>Sandia Mountain</td>
<td>Cibola</td>
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<td>106°25'50.13&quot;</td>
<td>PIPO</td>
</tr>
<tr>
<td></td>
<td>DMC</td>
<td>Dead Man’s Camp</td>
<td>Cibola</td>
<td>34°59'52.54&quot;</td>
<td>106°20'0.15&quot;</td>
<td>PIPO</td>
</tr>
<tr>
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<td>Hawks Lake</td>
<td>Winema</td>
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<td>121°38'5.05&quot;</td>
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</tr>
<tr>
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<td>Nahant</td>
<td>Black Hills</td>
<td>44°10'40.04&quot;</td>
<td>103°46'23.27&quot;</td>
<td>PIPO</td>
</tr>
<tr>
<td></td>
<td>RUS</td>
<td>Mount Rushmore</td>
<td>Black Hills</td>
<td>43°52'22.39&quot;</td>
<td>103°27'14.75&quot;</td>
<td>PIPO</td>
</tr>
</tbody>
</table>
Figure 6. Study site locations in Arizona, New Mexico, Oregon, and South Dakota.
Field Methods

For all site locations, I searched for large stands of ponderosa and/or Jeffrey pines, and I chose the largest diameter trees in the selected stand to core. Ten to twenty trees with two cores per tree (at breast height) were sampled from each site previously listed, and included in Table 1, using increment borers and standard dendrochronological techniques (Stokes and Smiley 1968, Speer 2010). Cross sections were taken from downed trees that display fire scars, using a chainsaw. Soil samples were collected from all sites using a soil auger (Table 2) to be used in later analyses. DNA samples were collected from all sites visited (and some sites where tree cores were not taken) using Whatman cards to preserve samples taken from tree needles and sent to the University of Hawaii-Manoa genetics lab for genetics analysis of Jeffrey and ponderosa pine. Pandora moths were caught using a light trap, and were preserved in sample vials of isopropyl alcohol. DNA and moths were collected in the field and sent to the University of Hawaii-Manoa for further analysis, not included in this study.
Table 2. Soil samples taken from study sites (Munsell Soil-Color Chart notation used).

<table>
<thead>
<tr>
<th>State</th>
<th>Site ID</th>
<th>Hue</th>
<th>Value/Chroma</th>
<th>Color</th>
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<tr>
<td></td>
<td>JLS</td>
<td>N/A</td>
<td>N/A</td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td>TXC</td>
<td>10YR</td>
<td>3/4</td>
<td>Dark yellowish brown</td>
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<td>SRT</td>
<td>10YR</td>
<td>4/3</td>
<td>Brown</td>
</tr>
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<td>California</td>
<td>BCC</td>
<td>10YR</td>
<td>3/1</td>
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<td>CCC</td>
<td>10YR</td>
<td>3/3</td>
<td>Dark brown</td>
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<td>CFC</td>
<td>5YR</td>
<td>3/1</td>
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<td></td>
<td>CRA</td>
<td>10YR</td>
<td>3/2</td>
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<td>10YR</td>
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<td>GBP</td>
<td>10YR</td>
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<tr>
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<td>SVR</td>
<td>10YR</td>
<td>2/1</td>
<td>Black</td>
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<tr>
<td></td>
<td>TCG</td>
<td>5YR</td>
<td>6/3</td>
<td>Light reddish brown</td>
</tr>
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</tr>
<tr>
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<td>10YR</td>
<td>3/3</td>
<td>Dark brown</td>
</tr>
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<td>10YR</td>
<td>4/3</td>
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</tr>
<tr>
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<td>SAN</td>
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<td>BLACK</td>
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<td>10YR</td>
<td>3/2</td>
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<td></td>
<td>RUS</td>
<td>10YR</td>
<td>3/3</td>
<td>Dark brown</td>
</tr>
</tbody>
</table>
Lab Methods

I used dendrochronological techniques to determine if any outbreaks occurred at these thirteen locations. Samples were mounted on prefabricated core mounts with string so that the cross sectional view is facing up (Speer 2010). Core and cross section samples were then sanded using increasingly finer sand paper, grading from ANSI 120-grit (105-125 µm) to ANSI 400-grit (20.6-23.6µm) (Orvis and Grissino-Mayer 2002). Cores were hand-sanded as needed using 30 micron sanding film.

Skeleton plots were made for all cores to develop a master chronology for each site. Suppressions were noted to visually document pandora moth outbreaks. On graphing paper, time was plotted on the x-axis with the present year on the right. The narrowness of rings was plotted on the y-axis, with the scale ranging from 0 (average) to 10 (absent) (Stokes and Smiley 1968, Speer 2010). A master chronology of each site was made using the skeleton plots from each tree within the site. Marker rings, or narrow rings that repeat between trees, provide a reliable way to crossdate between trees and build a master chronology. The master chronology is simply the stand level record of ring narrowness (Stokes and Smiley 1968, Speer 2010). For all cores and cross sections I measured ring widths to 0.001mm with a Nikon SMZ800 stereozoom microscope, a Velmex unislide measuring system (Velmex Inc., Bloomfield, NY), an ACU-RITE linear encoder (ACU-RITE Inc., Jamestown, NY), and Quick-Check digital readout unit (Metronics Inc., Bedford, NH; Speer 2010).

The output of this measuring device was entered into COFECHA (VER. 6.06P) (VER. 6.06P) (Ver. 6.06p), a statistical program used to double check dating and measurements (Holmes 1983, Grissino-Mayer 2001b, Speer 2010). All COFECHA (VER. 6.06P) analyses were
done on a site-level basis. The dated chronologies from COFECHA (VER. 6.06P) were then entered into ARSTAN for Windows (Ver.41d 2007), autoregressive standardization analysis, to build the final stand-level chronologies and remove intra-stand disturbances, strengthening the common signal (Cook and Holmes 1986, Cook et al. 2007). A 60-year cubic smoothing spline was used to account for autocorrelation in each stand (Cook and Peters 1981). This statistical program is useful for maximizing the signal of interest, such as outbreaks or fire events, and minimizing any noise (Cook 1985, Speer 2010). I visually checked for pandora moth outbreak signatures in the cores. This signature is characterized by thin latewood in the first year where growth is reduced by half, followed by the two smallest rings in the suppressed series, then increasing width for the remainder of suppression. The signature usually extends over four or more years (Speer et al. 2001).

In addition to visually checking for outbreak signatures I used the program OUTBREAK (Ver. 6.00p) which provides a quantitative identification of pandora moth outbreaks from the chronologies, as determined by the ring-width indices produced in ARSTAN (DOS Ver. 1.24d) (Speer 2010). I did not use a non-host chronology for comparison for all sites in OUTBREAK (Ver. 6.00p), since there are no non-host species that grow in the same climate conditions and live as long as ponderosa pine, although I did visually compare them to regional non-host chronologies from the International Tree-Ring Databank (ITRDB). Chronologies from Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), and bur oak (*Quercus macrocarpa* Michx.) were taken from the ITRDB and used to differentiate outbreak events from climate events (Swetnam et al. 1985, Speer et al. 2001).
Animating Outbreaks

An animated map of the spatiotemporal dynamics of all recorded pandora moth outbreaks was constructed in ArcMap 10 to assist in the visualization of the frequency, extent, and spread across the entire range of pandora moth outbreaks. To obtain ponderosa pine chronologies without having to sample in numerous locations, I gathered all available ponderosa pine chronologies from the ITRDB. In addition, all Douglas fir, Rocky Mountain, and bur oak chronologies were gathered for use as a non-host climate comparison. While Douglas fir does have a similar climate response to ponderosa pine, it is also a host species for western spruce budworm (*Choristoneura occidentalis*). Defoliation events in Douglas fir tree-rings could have an effect on ponderosa pine in a climate comparison, but would only lead to a more conservative interpretation of pandora moth outbreak events because of the possible suppression in the non-host chronology.

I compiled all standard chronologies into a dataset and checked the metadata from the chronologies to see how they were standardized in COFECHA (VER. 6.06P). This was done to make sure standardization techniques chosen by ITRDB contributors would not accentuate unrelated noise when run through the program OUTBREAK (Ver. 6.00p), which quantitatively identifies pandora moth outbreaks using the ring-width indices produced as .tre files in ARSTAN (Speer 2010). Standardization notes from many chronologies indicated that negative exponential curves and cubic smoothing splines were used. Some metadata did not include standardization notes, but I assumed them to have used orthogonal polynomials if the chronologies predated 1981, the year when cubic smoothing splines were introduced in dendrochronology (Cook and Peters 1981). While Cook’s (2004) grid is often used for climate interpretation, many of the western trees used in the grid were ponderosa pine (16 percent of trees 95° W longitude) based on
the range of species. Therefore, it would not be a reasonable climate comparison for my particular study. Instead, I have created a gridded network of the chosen non-host chronologies for the climate control.

I built the gridded map in ArcMap 10 using Cook et al.’s (2004) grid points as centroids of grid cells (Figure 7). All the data was referenced to Albers Equal Area Conic UTM (NAD 1983) projection. Ponderosa pine (121), Douglas fir (187), Rocky Mountain juniper (27), and Bur oak (15) chronologies were all added to the map as points. I ran COFECHA (VER. 6.06P) on all ponderosa pine chronologies to check the dating and used a 60 year cubic smoothing spline in ARSTAN to standardize the series. I then entered each tree-level chronology into the program OUTBREAK (Ver. 6.00p) to identify potential pandora moth outbreaks. I assigned ponderosa pine sites to the cells they were contained in and used the closest three chronologies to the centroid of the ponderosa pine chronologies in each grid cell when non-host chronologies were not present in any given grid cell.

In addition to chronology data, I also added divisional PDSI data for the growing season (June, July, and August) to the map. Grid cells contained multiple divisions, so I chose the divisions that were overlapped by centroids. In the case of borders, where centroids did not intersect with a division, I chose the largest division within that cell to represent the area. Using this method, 73% of the divisions that were chosen were, in fact, the largest divisions within the grid cell. The 27% that were not represented by the largest divisions were typically represented by the second largest divisions within the cells. After assigning non-host chronologies to grid cells, I ran principal components analysis on each set of non-host chronologies (for each grid cell). For a few test sites I ran the first eigenvector from PCA in a regression analysis against the assigned divisional summer PDSI data for that cell. Once the reconstruction was created, I ran it...
in OUTBREAK (Ver. 6.00p) along with the ponderosa pine chronologies, as a non-host chronology. Outbreaks detected using this method were checked against the output of OUTBREAK (Ver. 6.00p) without a non-host comparison for similarities and differences. Non-host drought graphs were made for each grid cell and used for climate comparison against the ponderosa pine suppressions. I visually checked for suppression in the COFECHA (VER. 6.06P) master chronologies as well. If there was no suppression in the non-host chronology, the suppression in ponderosa pine had been visually accepted, and OUTBREAK (Ver. 6.00p) also confirmed the event I accepted it as a true pandora moth outbreak event. In instances where OUTBREAK (Ver. 6.00p) called a suppression event an outbreak, but the non-host chronologies also showed suppression, I rejected the event as an outbreak. In cases where ponderosa pine chronologies were recording suppressions and non-host chronologies were not, I looked to the OUTBREAK (Ver. 6.00p) results to confirm or reject the event. In some cases, I visually accepted suppressions as outbreaks when the program OUTBREAK (Ver. 6.00p) did not. I then added the outbreak events to the animated map in ArcMap 10, demonstrating more accurate spatiotemporal outbreak dynamics of pandora moth. However, this estimate is also more conservative because I realize half of my non-host chronologies were identified as having below-normal growth, and so I likely excluded some pandora moth outbreak events in the process.
CHAPTER 4
Mapping an Insect Outbreak System across its Entire Range: Pandora Moth Outbreaks
Reconstructed from Tree-Ring Analysis

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Department of Earth and Environmental Systems, Indiana State University

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Abstract. In the western United States, pandora moth (Coloradia pandora Blake) primarily feeds on the needles of ponderosa pine (Pinus ponderosa Dougl. Ex Laws.). Defoliation during an outbreak stresses the tree, leaving a distinct signature (or sequence of rings) in the tree rings which can be used to determine outbreak events across the pandora moth range. An animated map of outbreaks over time and across the entire range of this insect was constructed in ArcMap 10 using ponderosa pine chronologies from the International Tree Ring Databank (ITRDB). A non-host climate control makes insect outbreak reconstructions more accurate by allowing the researcher to remove suppressions that are due to climatic events. Cook's gridded tree-ring network of the Palmer Drought Severity Index (PDSI) is frequently used for climate interpretation in the U.S. The grid is composed of tree-ring measurements from a mix of species taken from the ITRDB, one of which being ponderosa pine. Since ponderosa pine is the species recording outbreaks in this study, Cook's PDSI grid could not be used. To remedy this, a grid was made from non-host Douglas fir (Pseudotsuga menziesii (Mirb.) Franco),
Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), and bur oak (*Quercus macrocarpa* Michx.) tree-ring measurements taken from the ITRDB. Principal component analysis (PCA) was used to create a new PDSI grid in ArcMap 10 and ponderosa pine chronologies were compared to the nearest Douglas fir, juniper, or oak chronologies within the grid, so that pandora moth outbreaks could be differentiated from climate events. These data were used to construct a more accurate animation of pandora moth outbreaks over time.

**Keywords:** animation, GIS, pandora moth, PDSI grid, ponderosa pine
In dendroecology, the topic of climate and insect outbreak interaction has become more of a focus, as outbreaks have played a major role in North American forests in the past few decades (Mattson and Haak 1987, Fleming and Candau 1998). The need for a more solid understanding of how insect and climate systems can be differentiated in tree-rings and how they affect one another is the basis for this research. In insect outbreak reconstructions, a local non-host species is typically used as a climate control to differentiate outbreak suppressions from drought events (Swetnam et al. 1995). In few cases, a local non-host species is unavailable. Large pure stands of ponderosa pine (*Pinus ponderosa* Dougl. Ex Laws.), a host species of pandora moth (*Coloradia pandora* Blake), are an example of a forest type in which no non-host species is locally available for sampling over much of its range. There are some ponderosa pine stands that are intermixed with Douglas fir or are nearby to juniper, but they are not common (Speer et al. 2001). In our research, we have attempted to rectify this issue by creating a gridded climate reconstruction from species known to have a climate response similar to that of ponderosa pine (Swetnam et al. 1985). This gridded network of reconstructed climate was modeled after the Cook et al. (2004) climate reconstruction of the North America, and was used to ensure no drought caused suppressions were being incorrectly identified as pandora moth outbreaks. The objective of this research was to study the outbreak dynamics of an insect across its entire range. This work is unique in that it is the first range-wide study of its type and uses animation to map insect outbreaks back through time for 600 years, providing the longest outbreak record for the entire range of an insect species.
Background

Because of the annual resolution found in tree rings, dendrochronology is the ideal tool for reconstructing insect outbreaks and climate with annual resolution. The development of a gridded network of tree-ring chronologies made climate reconstructions across the continental U.S. a possibility (LaMarche and Fritts 1971, Meko et al. 1993, Cook et al. 1999, Cook et al. 2004). A widely used climate construction is the updated version of the Cook et al. (1999) Palmer Drought Severity Index (PDSI) drought reconstruction. A large network of tree-ring chronologies from multiple species was used to create this finer scale (2.5° latitude by 2.5° longitude) grid with 286 points that covered more area than previous grids, extended climate reconstructions further back in time, as well as updated them to the year 2003 (Cook et al. 2004). This climate grid is a useful source for many dendrochronological studies, but provides a challenge for projects that require a specific species as the input of the grid. Because the grid is dominated by ponderosa pine in the western U.S., it cannot be used as a climate subtraction for that species in our study.

Tree-ring measurements can be used to determine past insect outbreaks expressed in the wood as a reduction in growth. In some cases, these growth reductions are in a distinguishable pattern, caused by the nature of the defoliating insect and the response of the tree to defoliation (Speer 2010). In many studies quantifying insect outbreaks using dendrochronological methods a non-host climate control species has been used (Wickman 1963, Swetnam et al. 1985, Speer 2010). In cases where a non-host control species is unavailable, such as Speer et al. (2001), visual comparison to the instrumental climate data and a local tree-ring reconstruction of a species with a similar climate response have been used. It has also been suggested in the literature that local chronologies may be averaged together to create a regional chronology for a
species, provided the species has not been affected by an insect across its range and outbreak
dynamics have remained relatively stable over time (Swetnam et al. 1985, Paritsis et al. 2009).

While animation has increased in popularity for mapping temporal geographic data, it has
not been widely used to map past disturbances reconstructed from tree-rings. However,
animated mapping provides great potential for analyzing outbreak dynamics visually and has
been explored for those purposes in this study. We relied heavily on geographic information
science (GIS) in this research to better understand the spatial extent and outbreak dynamics,
specifically the frequency, duration, and intensity (the number of sites recording in a region) of
past outbreaks across the pandora moth range. We used GIS to construct an animated map of all
recorded pandora moth outbreaks in ArcMap 10 to assist in the visualization of outbreak
dynamics across the entire range of pandora moth. The temporal aspect of the map was created
using the time slide tool in ArcMap 10.

Pandora moth is a phytophagous insect that primarily defoliates ponderosa pine
throughout the western United States (Patterson 1929, Carolin and Knopf 1968). It also has been
known to defoliate Jeffrey pine (Pinus jeffreyi Grev. & Balf.), and lodgepole pine (Pinus
contorta Dougl. ex. Loud.); two species that are found throughout areas of the ponderosa pine
range (Patterson 1929). Pandora moth is mostly found in Oregon, California, Arizona, and
Colorado, although some small populations have also been documented in other surrounding
states (Carolin and Knopf 1968, Speer et al. 2001, Speer and Jensen 2003). Outside of the U.S.,
the pandora moth range most likely extends into northern Mexico and potentially extends into
Canada.

Low mortality rates (< 2%) following outbreaks allow dendrochronologists an
opportunity to study outbreak dynamics over hundreds of years (Blake and Wagner 1987, Speer
et al. 2001, Speer and Holmes 2004, Parker et al. 2006). During an outbreak, suppressed rings are formed in the tree leaving a distinct outbreak signature that is characterized by thin latewood in the first year where growth is reduced by half, followed by the two smallest rings in the suppressed series, then by four to six years of subsequent suppressed rings which gradually increase to normal growth (Speer et al. 2001).

While local pandora moth outbreak dynamics have been determined in Oregon (Speer et al. 2001), the full range of pandora moth has not been documented and outbreaks outside of Oregon have not yet been reconstructed. Previous efforts to map the entire range of pandora moth were based on data from the 1900’s and did not provide the length of information we get from tree-ring data.

Methods

Many of the western trees used in the grid by Cook et al. (2004) were ponderosa pine (16 percent of trees 95˚W longitude) so we were not able to use this climate reconstruction as a non-host comparison. Instead, we created a network of non-host chronologies to be used specifically for this study. All available ponderosa pine, Douglas fir (Pseudotsuga menziesii (Mirb.) Franco), Rocky Mountain juniper (Juniperus scopulorum Sarg.), and bur oak (Quercus macrocarpa Michx.) chronologies were gathered from the ITRDB. These species were chosen for non-host climate control based on their proximity to ponderosa pine stands and similar response to climate (Speer et al. 2001, Ryerson et al. 2003). COFECHA (VER. 6.06P) was run on all of the ponderosa pine chronologies to test for accurate dating and a 60-year cubic smoothing spline was used in ARSTAN Ver.41d (2007) to standardize the series. Tree-level chronologies in the form of .tre files produced in ARSTAN (DOS) were run through the program OUTBREAK (Ver. 6.00p) to quantify pandora moth outbreaks. A gridded map was built in ArcMap 10 using grid
points from Cook et al. (2004) as grid cell centroids (Figure 7). *Albers Equal Area Conic* UTM (NAD 1983) projection was used for all data. Ponderosa pine (121), Douglas fir (187), Rocky Mountain juniper (27), and Bur oak (15) chronologies were then added to the grid as points (Figure 7, Figure 8). Ponderosa pine sites were assigned to grid cells and the non-host chronologies (or three closest non-host chronologies to a grid cell centroid) were combined using the first eigenvector from principle components analysis (PCA) to create a non-host chronology for each cell. These non-host chronologies were used for comparison against ponderosa pine suppressions (Figure 9). Master chronologies from COFECHA (VER. 6.06P) were visually checked for suppressions as well. Pandora moth outbreaks were confirmed if OUTBREAK (Ver. 6.00p) noted an outbreak event, the COFECHA (VER. 6.06P) master chronology displayed visual confirmation, and there was no corresponding drought in the non-host chronology. The temporal aspect of the map was created using the time slide tool in ArcMap 10 to demonstrate the spatiotemporal dynamics of pandora moth outbreaks.
Figure 7. Grid with all chronologies (Ponderosa pine=blue, Douglas fir=red, Rocky Mountain juniper=yellow, Bur oak=green).
Figure 8. Ponderosa pine and Douglas fir climate response.
Figure 9. Non-host Chronologies used as climate comparison.
Results

Outbreak Results

Of the 121 ponderosa pine chronologies used in this study, 51 (42 percent) recorded outbreak events. We confirmed 123 outbreaks out of 745 suggested outbreak events (16.5 percent). 95 events were confirmed by OUTBREAK (Ver. 6.00p); 19 of those were also visually confirmed. We visually confirmed 26 outbreaks without an OUTBREAK (Ver. 6.00p) confirmation due to the suppression patterns in COFECHA (VER. 6.06P) and the lack of suppression in the non-host climate comparison. The average length of outbreaks from these sites was 5.9 years with the longest outbreak lasting 13 years and the shortest lasting 3 years. Sites ARS, BSK, BC1, BJS, DLK, PPF, and TLD accounted for 32.5 percent of outbreak events (Table 3).

Table 3. Locations of most outbreak events over time.

<table>
<thead>
<tr>
<th>Site ID</th>
<th>Site Name</th>
<th>State</th>
<th>Latitude N</th>
<th>Longitude W</th>
<th>Chronology Dates</th>
<th>Number of Outbreaks</th>
</tr>
</thead>
<tbody>
<tr>
<td>ARS</td>
<td>Alcova Reservoir Site A</td>
<td>WY</td>
<td>42.5167</td>
<td>-106.7333</td>
<td>1544-1964</td>
<td>5</td>
</tr>
<tr>
<td>BSK</td>
<td>Big Sink</td>
<td>OR</td>
<td>45.7833</td>
<td>-117.9167</td>
<td>1665-1990</td>
<td>5</td>
</tr>
<tr>
<td>BC1</td>
<td>Black Cone</td>
<td>CA</td>
<td>41.1833</td>
<td>-120.1167</td>
<td>1526-1979</td>
<td>5</td>
</tr>
<tr>
<td>BJS</td>
<td>Blue Jay Spring</td>
<td>OR</td>
<td>42.9167</td>
<td>-121.5333</td>
<td>1423-1995</td>
<td>8</td>
</tr>
<tr>
<td>DLK</td>
<td>Diamond Lake</td>
<td>OR</td>
<td>43.0833</td>
<td>-121.95</td>
<td>1513-1995</td>
<td>6</td>
</tr>
<tr>
<td>PPF</td>
<td>Pringle Falls Prescribed Fire</td>
<td>OR</td>
<td>43.7333</td>
<td>-121.65</td>
<td>1493-1991</td>
<td>5</td>
</tr>
<tr>
<td>TLD</td>
<td>Telephone Draw</td>
<td>OR</td>
<td>42.9333</td>
<td>-121.6167</td>
<td>1570-1995</td>
<td>6</td>
</tr>
</tbody>
</table>
Animated Map

With our data we were able to animate outbreak events on a timeline from 1400 to 2009. The non-host chronologies we built demonstrated patterns in suppression across grid cells and also larger regions. From the animated map, we can see that outbreaks occurred further north than previously documented from observations.

The animated map was essential to study the spatiotemporal dynamics of the pandora moth across its range. From this map we were able to visualize the spread of outbreaks within regions. We took screen captures of particular years to demonstrate the animation in still form. Time steps of these screen captures demonstrate the changes in outbreaks over time. From A.D. 1498 to 1503, outbreaks affected southern Oregon and northern California at the same time (Figure 11). Outbreaks occur again twenty years later at these two sites. From A.D. 1577 to 1582, outbreaks occur in Nebraska, an area previously believed to be outside of the pandora moth range (Figure 12). From A.D. 1602 to 1607, there is an occurrence of outbreaks in the Pacific Northwest and the Midwest, not often seen in the animation (Figure 13). There is a clustering of outbreaks in the Pacific Northwest from A.D. 1661 to 1666 (Figure 14). From A.D. 1741 to 1746 there are occurrences of outbreaks from northern Washington to southern Oregon and from Colorado to Wyoming (Figure 15). It is important to note that Washington was also not previously considered part of the pandora moth range. It now appears that outbreaks have occurred further north than previously documented. One of the last recorded pandora moth outbreaks from this animation is occurring in southern Oregon and northern California from A.D. 1948 to 1953 (Figure 16). The animated map not only showed us that outbreaks were occurring outside of previously mapped boundaries in northern areas, but it also showed us spread dynamics in the regions of the pandora moth habitat (Figure 17).
Discussion

Determining Outbreak Events

Instances where OUTBREAK (Ver. 6.00p) called a suppression event an outbreak, but the non-host chronology also showed suppression were considered to be climatically driven and not the effect of a pandora moth outbreak. In other cases the ponderosa pine chronologies were recording suppressions and the non-host chronologies were not. If OUTBREAK (Ver. 6.00p) confirmed an outbreak event, the non-host chronology did not record suppression, and the COFECHA (VER. 6.06P) master chronology for ponderosa pine showed a convincing suppression pattern, we accepted the outbreak event. The events we rejected were obvious climate suppressions related to drought events such as the dust bowl and the Flagstaff signature (a drought caused suppression of tree rings from the American southwest consisting of narrow rings in A.D. 1899, 1902, and 1904.) (Figure 10). The repetition of the events being recorded in OUTBREAK (Ver. 6.00p) as pandora moth outbreaks reinforces the need for a climate control in these studies. While the preferred method for preventing this issue would be to recalibrate OUTBREAK (Ver. 6.00p) on a site-by-site basis based on observations of signatures in the wood, it is still possible to reconstruct outbreaks using our methods but more conservative assumptions have to be made. Because of this, it is likely the actual numbers of outbreaks are under-represented. Our results of 42 percent of chronologies recording outbreaks using a non-host subtraction are more conservative than those using no non-host control, which documented 80 percent of chronologies recording pandora moth outbreaks. We suspect that the actual number of outbreaks lies somewhere between these two estimates.
Figure 10. Outbreak events recorded in OUTBREAK (Ver. 6.00p) were compared with drought graphs created from non-host chronologies (shown here) to visually rule out drought events. The two circled droughts are well-documented events; the dust bowl (left) and the Flagstaff signature (right). These drought events were recorded as outbreak events by the program OUTBREAK (Ver. 6.00p) numerous times.

Comparison with Previous Research

Four of the seven chronologies recording the most outbreaks over time in our study (Table 3) were built and analyzed for outbreaks by Speer et al. (2001). In their research, Speer et al. (2001) had fourteen sites recording pandora moth outbreaks in Oregon. Along with all other ponderosa pine chronologies, we analyzed those sites and found four (29 percent) to be recording pandora moth outbreaks. Within these four sites, 60 percent of the Speer et al. (2001) confirmed outbreak events agreed with our outbreak events or were off by only a few years. Fifteen outbreak events were confirmed in both analyses (Table 4). Speer et al. (2001) confirmed a total of 34 outbreaks from these four sites as well as outbreaks in ten other sites that our study did not record. The fewer outbreaks from our study are a product of the conservative methods we chose, which rejected any outbreak events that were occurring at the same time as drought events. In a similar study, Pohl et al. (2006) recorded six outbreaks at a nearby site (Lava Cast Forest (LCF)).
Half of the outbreaks recorded by Pohl et al. (2006) were in agreement with the outbreak events confirmed in our study and the Speer et al. (2001) study (Table 4). We also compared our results with those of Humbert and Kneeshaw (2011) and noted the difference in the outbreak event lengths from their results compared to Speer et al. (2001), Pohl et al. (2006), and our current study. For the latter three studies, outbreak events typically lasted between 4 and 10 years. Humbert and Kneeshaw (2011) recorded outbreaks lasting from around 20 to 40 years. These results did not correspond with any of our confirmed outbreak events.
Table 4. Comparison of outbreak results from Speer *et al.* (2001) and Pohl *et al.* (2006) with our confirmed outbreaks. The outbreak results from Pohl *et al.* (2006) are from one nearby site not included in our study and are shown repeatedly down the column where all outbreaks occur at the same time. (X = no outbreaks for this site at this time).

<table>
<thead>
<tr>
<th></th>
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</tr>
</thead>
<tbody>
<tr>
<td>BJS</td>
<td>1719 - 1724</td>
<td>1718 - 1725</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>1771 - 1775</td>
<td>1771 - 1778</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>1801 - 1806</td>
<td>1801 - 1808</td>
<td>(1803 – 1811)</td>
</tr>
<tr>
<td>DLK</td>
<td>1623 – 1635</td>
<td>1623 – 1635</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>1661 - 1666</td>
<td>1661 - 1666</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>1948 - 1952</td>
<td>X</td>
<td>(1949 – 1952)</td>
</tr>
<tr>
<td>PPF</td>
<td>1630 - 1636</td>
<td>1630 – 1636</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>1661 – 1666</td>
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<td>1677 – 1685</td>
<td>1677 – 1686</td>
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<td>1776 - 1784</td>
<td>1776 – 1785</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>1802 – 1811</td>
<td>1803 - 1811</td>
<td>(1803 – 1811)</td>
</tr>
<tr>
<td>TLD</td>
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<td>1679 – 1687</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>1747 – 1754</td>
<td>1747 – 1760</td>
<td>X</td>
</tr>
<tr>
<td></td>
<td>1800 – 1808</td>
<td>1800 – 1808</td>
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<td></td>
<td>1875 – 1882</td>
<td>1875 – 1892</td>
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<tr>
<td></td>
<td>1921 - 1928</td>
<td>1920 - 1931</td>
<td>(1922 – 1926)</td>
</tr>
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</table>
Pandora Moth Range and the Animation of Outbreaks

Our results show the pandora moth range extends further north than previously documented (Carolin and Knopf 1968, USDA 2003), which suggests (and is verified in our animation) the lack of outbreaks in the 20th century is the reason why the pandora moth range did not reflect a more northern extent in range maps. With our outbreak reconstruction across the ponderosa pine range, we can revise the pandora moth habitat map to include these northern sites. While we have confirmed outbreaks across the western U.S., a majority of events occurred in Oregon and the surrounding areas of Washington and northern California. These results suggest that Oregon is the heart of the pandora moth range.

We have demonstrated in this study the utility of animation for studying an insect across its entire range. Our animation enabled us to visualize reconstructed outbreak events over the entire range of a species and over 600 years. With our methods we have created the first range-wide reconstruction of outbreak events. We can now begin to look further in the dynamics of outbreak events over time to determine direction of spread, intensity of outbreak events, and when outbreak cessation occurred at each site. All of these details to outbreak dynamics will give us a better understanding of the insect and the ponderosa pine forests as they have changed over time. Once we have a thorough understanding of outbreak dynamics we can begin to look at multiple disturbance interactions. It has been demonstrated in past research (Speer et al. 2001, Pohl et al. 2006) that pandora moth interacts with other disturbances such as drought or wet events and fire. These studies were conducted in Oregon, the heart of the pandora moth range. We can now look at pandora moth interactions with fire and drought across the entire range to determine if results are parallel across all outbreak sites or if there are different drivers for outbreak events in different regions.
Figure 11. Early outbreaks in Oregon and California, displaying spatial clustering.
Figure 12. Clustered outbreaks in Nebraska
Figure 13. Multiple outbreaks occurring across the pandora moth range in the Black Hills region and in the Pacific Northwest.
Figure 14. Clustering of outbreaks in Pacific Northwest
Figure 15. Spread from Washington to southern Oregon and Colorado to Wyoming in 1741-1746
Figure 16. Outbreaks in northern California and southern Oregon.
Figure 17. All recorded outbreaks from 1300 to 2009
Conclusion

While, in our research, the non-host gridded reconstruction was used specifically to strengthen the integrity of pandora moth outbreak reconstructions, the grid concept may be found useful in other outbreak reconstructions where non-host chronologies are inaccessible. Further applications of non-host grids should be explored. An issue in need of further investigation is the possible contamination of dendroclimatic interpretations caused by insect outbreaks (Swetnam and Brown 2011). A comparison of the range-wide pandora moth outbreak reconstruction and the Cook et al. (2004) climate grid should be conducted to determine if outbreaks and drought events are occurring simultaneously. If this is the case, the Cook et al. (2004) drought grid may be reflecting pandora moth and other defoliating insect outbreak signatures as well as drought events. To determine if this is occurring, a study could be done on specific time periods potentially affected by insect outbreaks from each host species and then recalculating the climate reconstructions to see if there are any differences.

Another avenue to explore may be the relationship between disturbance events such as outbreaks and drought, as drought could influence the onset of high intensity defoliation events. In either case, the outcome of further research would be a better understanding of spatiotemporal dynamics of insect outbreaks in the United States and how these outbreaks relate to drought events. Overall, our methods are applicable to other insect outbreak studies. The ITRDB can be used to create a gridded non-host tree-ring network and reconstruct outbreaks across the entire range of an insect and these data can be used to animate outbreaks for visual analyses of outbreak dynamics.
Acknowledgements This research was funded by the National Science Foundation through grant BCS-0926375.

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References


CHAPTER 5

Location and Frequency of Pandora Moth Outbreaks throughout its Entire Range on Ponderosa Pine in the Western United States

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Prepared for submission to the Annals of the Association of American Geographers

Abstract. Ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) is a mid-elevation tree that is defoliated at episodic intervals (around 20 and 40 year cycles) by the pandora moth (*Coloradia Pandora* Blake). Since the tree does not usually die in the process, it can record several outbreaks over its lifespan and it records a distinctive tree-ring signature. We developed a habitat model of where pandora moths would be located based on climate, host species, and soil permeability and sampled locations to test our model. We sampled sites in Arizona, New Mexico, California, Oregon, and South Dakota with 10 or 20 individual trees at each site and two cores per tree. We used chronologies from the International Tree-Ring Databank (ITRDB) to expand pandora moth outbreak reconstructions to most of the range of the insect so that we can examine the outbreak dynamics for the entire range of the species. We took samples from the largest trees at each site to develop the longest possible chronology. We used this analysis of pandora moth outbreaks in the wood to document how pandora moth and ponderosa pine interact throughout its range. We compared our outbreak reconstructions from the ITRDB chronologies
to our habitat model to determine the strength of our habitat model. This resulted in a 73% concurrence between our ITRDB reconstructed outbreaks and our habitat model. Most of the sites that did not match the habitat model were either located in patches of trees that were below the 1km detection threshold of our input vegetation data or were showing pandora moth outbreaks at higher elevation in areas that were excluded because of low temperatures from our climate layer.

Keywords:

*Dendrochronology, Habitat model, ITRDB, Pandora moth, Ponderosa Pine*
Introduction

Landscape level analysis of insect outbreak systems has seldom been attempted, but in order to understand the system, we need to examine it across its entire range encompassing its significant spatial and temporal scales of operation. Few distribution maps based on habitat characteristics have been developed for insects (see Cowley et al. 2000).

Previous research by one of the authors (Speer and Jensen 2003) developed a GIS hazard model for pandora moth throughout Oregon and the current work extends those concepts to the entire range of the insect. Oregon has possibly been the area of the greatest concentration of pandora moth analysis in the past (Pohl et al. 2006, de Graauw et al. unpublished data). Speer et al. (2001) developed a 622-year pandora moth outbreak reconstruction from tree rings for 14 sites throughout south-central Oregon which enabled a temporal analysis of pandora moth outbreaks in this region. As the broader landscape is examined for pandora moth outbreaks in an attempt to understand insect outbreak dynamics across its entire range, these analyses naturally spread out from Oregon to study the other regions of outbreak dynamics. The spatial model of pandora moth habitat is the first step to sampling the entire range of this insect to examine multi-regional insect outbreak dynamics.

In this work, we use habitat requirements for pandora moth (Coloradia pandora Blake) across its entire range throughout the western United States to develop a geographical information systems (GIS) model of pandora moth potential habitat. The biophysical variables used were host species vegetation, average daily maximum temperature, and soil permeability. We compare our model to maps created by Carolyn and Knopf (1968) and the USDA Forest Service (2003) (Figure 18). Both provide only broad scale interpretations of the pandora moth habitat. This model is the first to predict likely pandora moth outbreak locations on a watershed
level. The purpose of this study is to analyze pandora moth across its entire range to determine the operative scales of the system and explore dynamics of the system across spatial and temporal scales. Also, it is to develop an updated habitat model of pandora moth outbreaks to drive future sampling based on pine locations, high soil permeability, and climate.

Figure 18. Maps of pandora moth distribution from 1968 (Carolin and Knopf, left) and 2003 (USGS, right).
Figure 19: Location of field sites sampled in May and July 2010.
Methods

Study Site of Habitat Model

The study site encompasses all of the western United States. Pandora moth has been officially documented in all of the western states excluding Idaho and Washington (Carolyn and Knopf 1968), although pictures of pandora moths from Washington state can be found on the internet. The range of ponderosa pine extends into Canada and Mexico and pandora moth has been documented in northern Mexico although not in very high numbers. Because of the drop off in observations of pandora moth in Mexico, the lack of comparable data layers, and the connection of this work with sampling efforts in the United States, we did not map possible pandora moth habitat into Mexico and Canada.

Data Layers and GIS Analysis

We created a habitat model with 1km resolution in ArcMap 10 using the intersection of the pine, soil permeability, and temperature layers. The vegetation data layer is a raster grid consisting of twenty five forest cover types for the western United States. This data set was derived from Advanced Very High Resolution Radiometer (AVHRR) composite images obtained in 1991 for the entire United States. The spatial resolution of the scene is 1 km. Out of all the forest cover types only the cover types corresponding to lodgepole pine (*Pinus contorta* Dougl. ex Loud.), white pine (*Pinus monticola* Dougl. ex D. Don), and ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) were used for the analysis (note that Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) was not specifically mapped in this dataset but is included in the ponderosa pine layer mentioned above). The extracted data provides conducive vegetation locations where pandora moth can thrive. Ponderosa pine is the primary host species for the insect, with the other species being secondary host species.
The soil permeability data layer is a vector layer obtained from the State Soil Geographic (STATSGO) database (Soil Survey Staff 2009). This layer provides statewide coverage of physical and chemical properties of different soil series. This data is compiled from USGS 1:250,000 scale statewide maps. The soil permeability characteristic was used because pandora moth needs a porous soil that it can burrow into so that it can pupate, otherwise it will desiccate during the search for a borrow site. Soil permeability in the STATSGO database is classified as low, medium, or high permeability and we used the high and medium permeability class in this analysis.

Gridded climate data was obtained from interpolating data collected from weather monitoring stations and an underlying grid using Parameter-elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 2008). This data set contains spatially gridded average monthly and annual maximum temperature for the climatological period 1971–2000. The model uses a 30-yr climatological average point data set and an underlying DEM grid to generate estimates of monthly and annual precipitation and temperature. This data was used as the climate data because the PRISM model takes into account the effect of complex variations in climate of mountainous regions and the resultant interpolated grid that is obtained has the spatial resolution of approximately 900 m. Thirty year average maximum temperature for the months of May, June, July, and August was used to generate the climate layer. The daily maximum temperature had to exceed 15.6 degrees Celsius (60 Fahrenheit) for three months to be included in the habitat zone because pandora moth stops feeding below this temperature. Initially, the raw ASCII gridded climate data was imported into a native ArcMap grid so that the tools provided by the Spatial Analyst toolset of ArcMap can be used for most of the analysis. Once the binary data was obtained for all the four months, a final composite map, which is a grid of all the locations
which have an average maximum temperature of more than 15.6 °C, was obtained by using the "Boolean And" tool in the Spatial Analyst toolset.

All the data were referenced to *Albers Equal Area* projection using the WGS 1984 datum. Most of the data provided by the United States Geological Survey (USGS) is in this projection and the vegetation layer was also in this projection which prompted the use of this projection for all the data used in the analysis.

All analyses were completed in ArcMap 10 following these steps: (a) Generating a high-permeability layer from STATSGO, (b) Extracting climate data from PRISM Group data, (c) Extracting the required pine layers from the AVHRR vegetation layer, (d) Intersecting the high-permeability layer and vegetation to get an intermediate layer, (e) Intersect this intermediate layer with climate data to get the final habitat map of pandora moth.
Table 5: Site names and locations

<table>
<thead>
<tr>
<th>State</th>
<th>Site ID</th>
<th>Site Name</th>
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<th>Longitude W</th>
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<td>Hawks Lake</td>
<td>Winema</td>
<td>42°36'43.83&quot;</td>
<td>121°38'5.05&quot;</td>
</tr>
<tr>
<td>South Dakota</td>
<td>NHT</td>
<td>Nahant</td>
<td>Black Hills</td>
<td>44°10'40.04&quot;</td>
<td>103°46'23.27&quot;</td>
</tr>
<tr>
<td></td>
<td>RUS</td>
<td>Mount Rushmore</td>
<td>Black Hills</td>
<td>43°52'22.39&quot;</td>
<td>103°27'14.75&quot;</td>
</tr>
</tbody>
</table>
Ponderosa pine chronologies were collected from the International Tree Ring Databank (ITRDB) and were analyzed for pandora moth outbreaks. The location information for each chronology was included with the metadata for the chronology from the ITRDB. This provided point data which when intersected with the hazard map results in all the locations (point data) of outbreak which have all the favorable conditions for pandora moth. Different properties of this resultant point data such as total number of outbreaks, or outbreaks per century were used for statistical analysis. Tree ring cores were taken from 19 sites (Table 5) throughout the western United States based on the habitat model (Figure 19). All stands were primarily mid- to old-growth ponderosa with minimal understory. In addition to sites being located within the habitat model, stands were selected based on easy accessibility by road or trails. This habitat model was checked for accuracy with the International Tree-Ring Databank (ITRDB) outbreak data (Figure 22).

Field and Lab Methods

Sites were located based on historical documentation of presence of pandora moth from the US Forest Service Insect Inventories and other documents that recorded the location of pandora moth presence in the past. Throughout the study locations we cored 10-20 trees in each of 19 sites from four states in the Western U.S. Two increment cores were taken at breast height on opposite sides of the tree using a 5.15 mm Haglöf increment borer. Targeted sampling was used by selecting trees with the largest diameter at breast height (DBH) and old-tree characteristics to obtain the longest chronology.

All cores were dried, mounted and sanded. Initial sanding was performed with a belt sander using ANSI 120-, 220-, 320, and 400-grit (105-125, 53-74, 32.5-36.0, and 20.6-23.6 μm) sandpaper to provide a level and smooth surface (Orvis and Grissino-Mayer 2002). Micron
sanding film (30, 15, and 9 μm) was then used until all rings could be clearly identified. We used the standard skeleton plotting cross dating technique (Stokes and Smiley 1968, Speer 2010) to develop a master chronology and obtain accurate dates for cores.

Cores were then measured to the nearest 0.001mm using a Velmex measuring system coupled with the program Measure J2X. We then verified the crossdating with the COFECHA (VER. 6.06P) program on all chronologies (Holmes 1986, Grissino-Mayer 2001b). The dated ring-width series were then standardized using the program ARSTAN (Cook et al. 2007). This standardization was used to remove any age-related growth trends to allow us to more accurately analyze insect outbreak growth variables. We standardized the series using a 60-year cubic smoothing spline to preserve the ring width changes that would happen over shorter time scales (<2 decades) that would be indicative of a pandora moth outbreak.

![Figure 20: Pandora moth signature in Ponderosa Pine showing thin latewood during the initial year of defoliation and subsequent reduced growth following years of defoliation (Speer et al. 2001).](image)
We visually checked for outbreak signatures in the wood (shown in Figure 20) and also used the program OUTBREAK (Ver. 6.00p) which provides a quantitative identification of pandora moth outbreaks from the chronologies, as determined by the ring-width indices produced by ARSTAN as .tre files (Speer 2010). We used the standard options for pandora moth in the program, as determined by Speer et al. (2001). The program OUTBREAK (Ver. 6.00p) typically requires a non-host species input to be used as a climate comparison but because ponderosa pine often grows in pure stands it is difficult to use a local non-host as a climate control. Due to similar climate responses all Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), western juniper (*Juniperus occidentalis* Hook.), and bur oak (*Quercus macrocarpa* Michx.) chronologies were gathered for a non-host climate comparison.

We created a gridded map in ArcMap 10 using the grid points from Cook et al. (2004) as grid cell centroids. Host and non-host species were added to the map as points and each cell containing ponderosa pine was assigned at least three single-species non-host chronologies based on proximity to the host species. Principal components analysis was run on each set of non-host chronologies for each grid cell, and the first eigenvector was chosen for the compiled chronology. Divisional PDSI data for the growing season (June, July, and August) was used to reconstruct climate with the non-host chronologies. These reconstructions were compared with our non-host chronologies for discrepancies, and were found to be positively correlated. Once the non-host chronologies were created, they were run in OUTBREAK (Ver. 6.00p) against the ponderosa pine chronologies. If outbreaks were detected in the program OUTBREAK (Ver. 6.00p) we checked them against the non-host climate graphs for any disagreement.
Results

*Pandora moth outbreaks*

According to OUTBREAK (Ver. 6.00p), numerous sites where we collected samples had possible outbreaks. We checked these potential outbreak events against the master chronologies in COFECHA (VER. 6.06P) and also against the non-host chronology to check that these suppressions were not climate related. After visually checking these 37 potential outbreaks against COFECHA (VER. 6.06P) masters and comparing with non-host chronologies we were left with 7 accepted potential outbreak events (Table 6).

**Table 6. Potential Outbreaks**

<table>
<thead>
<tr>
<th>Site ID</th>
<th>Chronology Dates</th>
<th>Possible Outbreak Years</th>
<th>Accepted (Yes/No)</th>
<th>Accepted Outbreak Years</th>
</tr>
</thead>
<tbody>
<tr>
<td>CPC</td>
<td>1811-2009</td>
<td>1871-1876</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>NHT</td>
<td>1882-2009</td>
<td>1931-1936</td>
<td>Y</td>
<td>1931-1936</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1959-1964</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>CCC</td>
<td>1600-2009</td>
<td>1776-1784</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1821-1827</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1862-1869</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1932-1938</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1973-1974</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1987-1995</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td>DMS</td>
<td>1754-2009</td>
<td>1803-1810</td>
<td>N</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1889-1899</td>
<td>Y</td>
<td>1889-1894</td>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>---</td>
<td>---</td>
</tr>
<tr>
<td></td>
<td>1928-1939</td>
<td>N</td>
<td>1987-1992</td>
<td>N</td>
</tr>
<tr>
<td>GBP</td>
<td>1728-2009</td>
<td>1813-1815</td>
<td>N</td>
<td>1838-1845</td>
</tr>
</tbody>
</table>
Some potential outbreaks were thrown out because of the large suppression events shown in the non-host chronologies which corresponded with the suppressions in the host chronologies (Figure 21). Other events were accepted as potential outbreaks when non-host chronologies did not show similar suppressions.

Figure 21. Drought graph created from non-host chronology (left) and compared with ponderosa pine COFECHA (VER. 6.06P) master (right) for the years of A.D. 1819 to 1825. The suppression seen in the ponderosa pine chronology corresponds with suppression in the non-host chronology. This event was not accepted as an outbreak.

*Habitat Model*

When comparing our habitat model to the ITRDB reconstructed outbreaks we found a 72.6% positive correlation between the model and outbreak location. The pine layer was the most important layer as it restricted the food availability in the habitat and the climate layer ended up not being very limiting at all.
Figure 22: Pandora moth habitat model with ITRDB outbreak locations and correlations.
Discussion

One of the difficulties of this study was including all available habitat space for pandora moth. The 1km pine layer we used to create our model was of a fine resolution but still was not fine enough to include some patches of ponderosa forest. Because these patches were excluded from the pine layer they were not accounted for in our pandora moth habitat model. Due to this issue we recorded outbreaks in areas that didn’t appear to match the habitat of pandora moth, such as in the Great Plains where pine stands are much smaller. However, this 1km resolution is significantly finer than past habitat maps and can still provide greater detail of the pandora moth habitat. Previous maps were only documenting outbreak events and collection sites from the 20th century and did not include habitat parameters (Carolin and Knopf 1968, USDA 2003). Using the Speer and Jensen (2003) habitat model for Oregon, we created the first fine resolution, range-wide habitat model for this insect. From their parameters, we found the climate layer was not limiting to the model, as it covered most of the western U.S., but the pine and soil layers were very strong in limiting the habitat model to specific locations. We then used our reconstructed outbreak events to test the first fine resolution habitat model for this insect across its entire range and found the reconstructed outbreak events generally agreed with our habitat model, strengthening our confidence in the parameters we used.

Little research has been done to quantify pandora moth outbreaks in California, although historical documentation suggests it is an area of high activity (Carolin and Knopf 1968, Weaver and Basgall 1986, Blake and Wagner 1987). Sites chosen for sampling were determined before the habitat model was created and were based on these historical reports of activity. When compared with the habitat model, we found that all of our sites were closely matched with the habitat of pandora moth, however when we quantified outbreaks we only accepted a select few
from these areas in California. This could be due to a sampling issue where we did not sample a large enough area to recover the best representation of outbreaks or it could be that in these areas outbreak signatures are less defined than those seen by Speer et al. (2001) in Oregon. It is clear by looking at the habitat model that there is a large habitat area located on the eastern side of the Cascades in Oregon, where in many other places throughout the pandora moth range habitat areas are scattered across the landscape. This generally agrees with previous habitat models; however our model shows that pandora moth does have potential habitat space that extends north and east past previous range boundaries.
Conclusion

The pandora moth habitat extends well outside of previous outbreak boundaries, but it is clear from the habitat model that there is not much continuous habitat space as past maps would suggest (Carolin and Knopf 1968, USDA 2003). Instead, we found that there are more pockets of habitat area than corridors and continuous habitat. The pine layer we used was created in the 1990s, and so reflects the forested areas after much logging of western forests. It is possible the pandora moth habitat was much more fluid in the past, and did not include so many forest fragments. We can now begin to ask questions about past pandora moth range as compared with the current range and how this might affect the life cycle and outbreak dynamics of this insect.

Our habitat model has provided the first fine resolution map for pandora moth across its entire range. Although we did not record many outbreak events across our sites, those cores were collected prior to building the habitat model. Future methods should include testing the habitat model by sampling in predicted sites and locations not predicted to refine the model. Outbreak events from these tested sites can then be used to demonstrate the potential of the non-host grid as a climate control for the ponderosa pine-pandora moth system. We were able to test our reconstructed pandora moth outbreak events back to the habitat model and found much agreement between the reconstructions and predicted habitat space. Our model can be used for any defoliating insect provided the life cycle parameters for the insect are understood and replace the parameters we used.
Acknowledgements

This research was made possible by the support of the National Science Foundation through grant BCS-0926375. We would like to thank everyone who assisted with field sampling in May and July of 2010: Tony Bailey, Dave Bohnert, Elaina Hughbanks, Joe Ladwig, Peter Rosene, Jennifer Sicking, and Robin Van De Veer. We would also like to thank Vijay Lulla and Idrissa Tiemogo for their early work with the habitat model. Also we would like to thank Lauren Adams and Andrea Kelley for their work with the ITRDB chronologies.

References


Climate, fire, and insect outbreaks are major disturbances in pine forests in the western United States (Veblen et al. 2000, Speer et al. 2001, Brown 2006, Pohl et al. 2006). They are often studied separately, but their dynamic interaction is not well understood. With a range-wide reconstruction of pandora moth outbreaks and related climate data, I can now investigate the interactions between these disturbances and fire in future studies. Interpreting the complexities of such a system would be useful in predicting when future outbreaks would occur and what consequences could ensue. This information would be valuable to forest management personnel.

Fire and Climate

In pine forests of the western U.S., fire has been found to be the most influential disturbance event (Agee 1993). Ponderosa pine forests are well suited for low intensity surface fires. This type of fire typically only causes mortality to the understory layer which is composed of seedlings, keeping stand density in check by limiting the amount of seedlings that reach the canopy (Kulakowski et al. 2003, Brown 2006, Parker et al. 2006). Surface fires are not harmful to older ponderosa pines due to their thicker bark which protects the cambium from mortality caused by fire scorch and high crowns which protect them against crown fire mortality (Brown 2006). The long intervals between fires allow for those saplings (>10 cm diameter at breast
height) that did survive the previous fire to establish themselves within the canopy (Brown 2006).

In the southwestern ponderosa pine forests, interannual and multidecadal climate changes related to El Niño Southern Oscillation (ENSO) heavily influence fire (Swetnam and Betancourt 1998). ENSO is the connection between the oceanic and atmospheric system where El Niño refers to the broad scale warming of sea surface temperature and associated pressure changes in the Pacific Ocean and La Niña essentially refers to the opposite effect (Veblen et al. 2000, Brown 2006, Pohl et al. 2006). In the year following the beginning of an El Niño event, precipitation tends to be higher than average during winter and spring in the American southwest. This greater moisture availability allows for enhanced tree and understory plant growth during the El Niño years. During La Niña events, more extensive fires typically occur in this region due to lower than average precipitation leading to drought in the winter and spring months which is exacerbated by the high accumulation of fuels from previous El Niño events (Veblen et al. 2000, Pohl et al. 2006). El Niño and La Niña have the opposite effect in the Pacific Northwest. In the Pacific Northwest, the Pacific Decadal Oscillation (PDO) has a greater influence on fire frequency. PDO refers to changes in sea surface temperature in the North Pacific Basin (Brown 2006). During sequential dry years that are indicative of the warm, positive phases of PDO, fires occur with more frequency than during the cool, negative phases (Brown 2006, Pohl et al. 2006). More recently, the Atlantic Multidecadal Oscillation (AMO) has been linked with drought induced fires in central and western parts of the U.S. during warm, positive phases (Brown 2006). In the central U.S., Brown (2006) found that there was a very strong link between fire and the combination of warm AMO, cool PDO, and La Niña phases. He
found that fewer intense fires occurred with the opposite combination of cool AMO, warm PDO, and El Niño phases.

In the early part of this century, policymakers made efforts to suppress natural wildfires believing that they were destructive and harmful to forests (McCullough et al. 1998). The introduction of livestock grazing also played a major role in fire suppression, causing a reduction in fuels, which are necessary to continue the spread of fire (Savage and Swetnam 1990). The effects of fire suppression are now known to negatively impact forests, changing species composition and successional dynamics while also making more trees vulnerable to insects, pathogens, and more intense fires (McCullough et al. 1998). In ponderosa pine forests of the western U.S., fire was once a natural regulator of canopy density and understory vegetation. Before settlement, density in ponderosa pine forests was approximately nine trees per hectare whereas now, due to fire suppression, density has increased to more than 300 trees per hectare (McCullough et al. 1998). This increased density of trees has connected once isolated stands and has led to the accumulation of surface fuels such as dead needles and branches, thus allowing wildfires to burn hotter and spread more quickly than they would have before fire suppression (McCullough et al. 1998, Veblen et al. 2000, Brown 2006).

The result of heightened fire intensity caused by fuel accumulation has been shown to cause more stand replacement in forests than that caused by fires with lower fuel accumulation (McCullough et al. 1998, Veblen et al. 2000). All of these factors indicate that although forest management personnel are still actively suppressing fires, those fires that go unmanaged are causing greater damage to forests than ever before. Greater fire intensity coupled with the changing forest structure and density due to fire suppression is making trees less resistant to
other disturbances, such as insect outbreaks (Veblen et al. 2000). This increase in canopy density along with new understory growth can create an uninterrupted and plentiful source of nutrition for invading insects (Swetnam and Lynch 1989).

Disturbance Interaction

Fire and insect outbreaks not only affect the forests they are altering, but they also play a major role in affecting one another. Fire suppression has been found to increase the risk of mountain pine beetle (Dendroctonus ponderosae Hopk.) and western spruce budworm (Choristoneura occidentalis Freeman) outbreaks in various coniferous forests (Kulakowski et al. 2003). To remedy this issue, prescribed burning has been used to reduce bark beetle species, mountain pine beetle, and pine engraver (Ips pini (Say)) populations while also reducing the risk of wildfires after timber harvest in ponderosa and lodgepole pine stands (McCullough et al. 1998). Although fire suppression has been identified as a factor in the timing of insect outbreaks, it is not the only driving force. For instance, drought can sometimes encourage outbreaks of insects such as the mountain pine beetle, various bark beetles, and phytophagous insects (Mattson and Hack 1987, Brown 2006). As trees try to protect themselves against drought, many of their natural defenses are reduced, increasing their risk of insect outbreak. For example, due to a decrease in resin secretion (a defense mechanism for survival during wood boring insect attacks) conifers tend to be more susceptible to insect outbreaks than during times of favorable climatic conditions (Mattson and Hack 1987).

Although fire suppression likely contributes to increased insect outbreak activity such as with bark beetles, studies have also shown that prescribed burning has had variable success and can induce outbreak activity in some host species by weakening the host trees (McCullough et al. 1998).
1998, Parker et al. 2006). Trees wounded by fire have been found to be more prone to attacks by spruce beetle (*Dendroctonus rufipennis*) and various bark beetle species (McCullough et al. 1998, Kulakowski et al. 2003). Generally, western pine beetle attacks old growth ponderosa pine, but because of increased harvest of these larger trees, outbreaks are occurring in younger fire scorched ponderosa pine stands where there is decreased resistance to insect attacks (McCullough et al. 1998, Parker et al. 2006). Conversely, fire can be brought on by outbreaks. In lodgepole pine forests, outbreaks of mountain pine beetle result in a heavy accumulation of fuels. This accumulation determines the severity of what are often stand replacing fires. The increase in fire occurrence is short lived, only three to four years, because of the decay of fine fuels (needles and leaf litter) and increase of moisture due to the lack of transpiration (Kulakoswki et al. 2003, Speer 2010). In this condition, subsequent lodgepole pine stands will serve as a future feeding location during later outbreaks. If no fire occurs after an outbreak, lodgepole pine is generally replaced by ponderosa pine at lower elevations and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) at higher elevations; thus reducing the habitat for mountain pine beetle (McCullough et al. 1998). This case contradicts the first interaction in which fire suppression increased the risk of mountain pine beetle which demonstrates that fire severity, insect species, and the order in which events occur are not the only important factors involved in the interactions of disturbance regimes. These contradictions are likely due to more complex interactions within the system such as the presence of serotinous cones (those that require fire to expel seeds) or the lack of viable seed from lodgepole pine.

Fire directly and indirectly affects insects by causing mortality and by changing their habitat, respectively. Some studies, however, have shown that prescribed fire caused little to no mortality to pandora moths (McCullough et al. 1998, Pohl et al. 2006). Prescribed burning has
often been used to cause mortality in bark beetles, but has only had minimal success in controlling defoliators, such as pandora moth (Schmid et al. 1981, Schmid and Bennett 1988, Miller and Wagner 1984, Parker et al. 2006). In a few instances prescribed burning has been determined to be somewhat successful in reducing pandora moth populations, but it must be applied when the insect burrows in the soil to pupate (usually August) as this is the most vulnerable stage of its life (Gerson and Kelsey 1997, McCullough et al. 1998). An interesting study conducted by Gerson and Kelsey (1997) found that the Pacific Northwest fire season was aligned with the last stage of the pandora moth life cycle and wildfire attracted some of the moths they tracked. They determined that moths were typically attracted to artificial lights, but also flew toward fire. This suggests that prior to fire suppression, forest fires that burned at night could have been a local, natural regulator of pandora moth populations during outbreaks (Gerson and Kelsey 1997). This would only be true for the Pacific Northwest however, because the southwest fire season is earlier and does not occur with moth flight.

The introduction of Euro-American settlement in North America had a great effect on forests and fire regimes. The late nineteenth century also brought along increased climate variability, some of which has been attributed to anthropogenic causes beginning with the Industrial Revolution (Veblen et al. 2000). Due to drastic changes in fire regimes such as fire suppression and timber harvesting during the twentieth century, it is thought that insects may have also changed in their outbreak behavior and timing (Swetnam et al. 1995). There is also the probability of displacement of insects due to habitat loss in some areas as well. Before Euro-American settlement, the aboriginal people of California were known to use pandora moth larvae for subsistence purposes (Weaver and Basgall 1986, Blake and Wagner 1987). While they may
not have affected the outbreak dynamics of pandora moth on a regional scale, this gathering of larvae certainly would have affected local populations.

To determine if pandora moth outbreak dynamics have changed over time due to fire suppression and climate changes, more ponderosa pine forests will need to be studied. It is still not completely understood whether one part of the disturbance system is driving the others. What is known is that fire and insect outbreaks are closely associated components of forest dynamics, and human activity has begun to play a major role in disturbance as well (McCullough et al. 1998, Speer et al. 2001, Kulakowski et al. 2003, Pohl et al. 2006).

Dendrochronology is the key to determining how disturbance events interact and how they have changed over time due to climatic and anthropogenic causes. It provides a record of past events that can be compared to current events to determine if there are any differences between early and modern disturbance interactions. Once the relationship between pandora moth, fire, and ponderosa pine is understood, other defoliators can be studied using this system as a model. With the understanding of this complex system future forests can be properly managed.

Conclusion

In this research, I was able to contribute a few important pieces to the field of dendroecology. I created 10 new ponderosa pine chronologies in California; an area severely lacking them in comparison to the rest of the western U.S. I created a gridded non-host climate comparison for a species that was lacking a local non-host control. This gridded network will not only be useful in future pandora moth studies, but the design concept can be applied to any other
study of defoliation that is lacking a non-host control. My reconstruction of pandora moth outbreaks is also useful for forest managers. Now that there is a history of outbreaks in the western U.S., managers can look at past outbreaks for their forests and use this information to understand how frequently outbreaks have occurred on their sites and what may have changed forest health in areas lacking 21st century outbreaks.

The habitat model, which I tested all of my accepted outbreaks against, is now the highest resolution pandora moth habitat model currently available. This model not only verified the locations of my outbreak as falling within the pandora moth habitat, but it can also be used in the future as a test for all study sites related to pandora moth outbreaks. The animation of outbreaks over time provided a visual display of outbreak dynamics that is difficult to imagine in still form. This animation may lend to studies of wind pattern influence in the spread of pandora moth outbreaks from one location to another. My animation design can be applied in any long-term ecological disturbance study such as outbreak or fire events over time.

One of the most notable findings in this research is the occurrence of outbreaks much further north than previously documented in Washington, Idaho, Montana, and Wyoming. Through the non-host comparison test, outbreak events in these states were accepted as true outbreaks. These events then matched the habitat model’s prediction of where pandora moth could be found. These results not only demonstrate the performances of the non-host network and habitat model, but also draw attention to how little is known about the pandora moth.
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