

**MODELING ENDEMIC BARK BEETLE POPULATIONS IN SOUTHWESTERN
PONDEROSA PINE FORESTS**

A Thesis

by

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ABSTRACT

Bark beetle populations phase between epidemic, outbreak levels, and low population density, endemic levels. The majority of scientific research is focused on outbreak populations because of the associated economic, ecological, and social impacts. Endemic populations are rarely studied but could provide information about the triggers that cause outbreaks. The goal of this thesis was to gain a better understanding of how endemic populations persist in a landscape through time by looking at the spatial distribution and susceptibility of host trees in southwestern US forested landscapes. To do this, I (1) analyzed 21 years of field data to examine the population dynamics of bark beetles and the factors that affect them, (2) created a statistical model for predicting the absolute risk of individual trees to bark beetle-cause mortality using tree, stand, and beetle pressure variables, and (3) simulated a forest landscape to develop a framework for applying tree-level risk assessments.

In 1995, forty-five sites were established throughout the southwestern US to measure bark beetle activity and associated tree and stand characteristics. The plots were periodically revisited through 2012 resulting in over twenty years of bark beetle data with highly variable population densities over time and space. Site maximum dbh and the number of ponderosa pines per acre were significant ($P < .029$) for predicting the probability a rise in the population density of bark beetles. Tree, stand, and beetle pressure were significant ($P < .001$) in predicting the probability of beetle caused tree mortality per year. Using GIS, remote sensing, and ground truth data, a ponderosa pine forest was simulated with information about the size and configuration of trees in the landscape. This simulated landscape was used to develop a framework for tree-level risk assessments. The results are discussed further in the context of bark beetle management and further research opportunities.

DEDICATION

This thesis is dedicated to my parents, Maria Guadalupe Davila and Mario Alberto Garza, who have supported me in pursuing a higher level degree. I love you and appreciate all you have done for me.

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TABLE OF CONTENTS

	Page
I INTRODUCTION.....	1
I.1 Introduction.....	1
I.2 Study organisms.....	1
I.3 Landscape ecology and disturbances.....	5
I.4 GIS and remote sensing in landscape ecology.....	7
I.5 Goal and objectives.....	9
II ANALYSIS OF BARK BEETLE POPULATION DYNAMICS.....	12
II.1 Introduction.....	12
II.2 Methods.....	14
II.3 Results.....	21
II.4 Discussion.....	24
III HOST SUSCEPTIBILITY TO BARK BEETLE-CAUSED MORTALITY.....	28
III.1 Introduction.....	28
III.2 Methods.....	32
III.3 Results.....	35
III.4 Discussion.....	40
IV FRAMEWORK FOR DISPLAYING TREE-LEVEL RISK ASSESSMENTS.....	43
IV.1 Introduction.....	43
IV.2 Methods.....	47
IV.3 Results.....	61
IV.4 Discussion.....	68
V CONCLUSIONS.....	74
V.1 Bark beetle population dynamics.....	74
V.2 Modeling host susceptibility to bark beetle-caused mortality.....	75
V.3 Developing a framework for tree-level risk assessment.....	76
V.4 Management implications.....	77
V.5 Further work.....	78
REFERENCES.....	80

LIST OF FIGURES

FIGURE		Page
1	Data and analysis flowchart for this study.....	10
2	The National Forests and National Parks where sites were established in the southwestern US within or near the Colorado Plateau.....	15
3	Site and plot design for field collection of tree/stand and bark beetle data.....	16
4	The three regions used to group study sites.....	20
5	Annual proportions of beetle-caused mortality across all sites and regions.....	22
6	Mean site-level measurements in epidemic and endemic sites.....	23
7	Surface chart of how stand variables influence population densities.....	24
8	The study area for simulating a ponderosa pine forest.....	48
9	A Normalized Difference Vegetation Index (NDVI) developed for the study.....	50
10	The ponderosa pine simulation flowchart.....	51
11	The GAP land cover data for the study area.....	52
12	The GAP land cover classes clipped to the NDVI-VEG raster.....	53
13	Ponderosa pines randomly generated for the different vegetation classes.....	56
14	VBA script of the acceptance-rejection model in Microsoft Access.....	57
15	Frequency distributions for the dbh of sampled and generated ponderosa pines...	63
16	Mean risk maps for epidemic and endemic populations (2 acre cell size).....	66
17	Maximum risk maps for epidemic and endemic populations (2 acre cell size)....	67
18	The relationship between tree density and tree susceptibility.....	68

LIST OF TABLES

TABLE		Page
1	The output coefficients from the stepwise logistic regression analysis.....	24
2	A correlation matrix of all tree and stand variables.....	36
3	The logistic regression coefficients and associated statistics for the standardized tree and stand variable measurements when analyzed independently.....	37
4	The logistic regression coefficients and associated statistics for the standardized beetle pressure variable measurements when analyzed independently.....	37
5	The stepwise multiple logistic regression analysis output for the best predictive model.....	39
6	The vegetation types within the study area that had a density of ponderosa pines according to the FIA subplot data.....	62
7	The logistic regression output that was used to develop equations for applying the probability of bark beetle caused mortality per year to individual host trees in the simulated forest landscape.....	64
8	The average beetle pressure values from epidemic and endemic years.....	64

I INTRODUCTION

I.1 Introduction

In the southwestern US, a number of bark beetle species phase between outbreak conditions and low population density endemic populations. These bark beetle species utilize a mass attack strategy to overcome the natural tree defenses. If successful, the beetles colonize and kill their host trees. Outbreaks lead to widespread tree losses over a number of years while endemic populations affect fewer scattered trees over a period of decades. The majority of the research on bark beetles has been performed on outbreak populations because of the damage that they cause. Information about endemic populations is also lacking because these populations are difficult to study. An improved understanding of endemic populations could provide information about the triggers that cause outbreaks. This thesis aims to gather information about host susceptibility to endemic bark beetle populations in southwestern ponderosa pine (*Pinus ponderosa* Dougl.) forests. I was able to provide some insight about forest management given the results of this study and other literature. Here, I will describe the primary organisms of interest to this study, related concepts in landscape ecology, and the goal and objectives of this study.

I.2 – Study organisms

I.2.1 – *Ponderosa pine*

Ponderosa pine is a species that can be found throughout the western US. Variants of the ponderosa pine have been divided into five subspecies. Throughout the Colorado Plateau, there is a transition and hybridization between the Rocky Mountains ponderosa pine, *P. ponderosa* subsp. *scopulorum*, to the north and southwestern ponderosa pine, *P. ponderosa*

subsp. *brachyptera* (Callaham 2013) in the south. Ponderosa pine grows as a climax tree in xerophytic forests while in mesophytic forests it is considered a seral species that is succeeded by other conifers like spruces and firs (Dick-Peddie 1999). In the Colorado Plateau, ponderosa pine can be found interspersed with junipers (*Juniperus* sp.) and pinyon pines (*P. edulis* Engelm.) in drier, lower elevations while it grows among quaking aspen (*Populus tremuloides*), Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), white fir (*Abies concolor* (Gord. & Glend.) Lindl.), and blue spruce (*Picea pungens* Engelm.) in higher elevations. Limber pine (*Pinus flexilis* James) is a five-needle pine that can be found among ponderosa pines although it is generally not as dominant as ponderosa pines in the Colorado Plateau. Both ponderosa pine and limber pine are hosts to native pine beetle species within their range.

Southwestern ponderosa pine forests provide habitats for a variety of wildlife species such as mule deer, elk, black bears, Abert's squirrels, and a number of bird species including the Mexican spotted owl which is listed as threatened under the Endangered Species Act. Heterogenous ponderosa pine forests composed of stands in various successional phases support a high diversity of wildlife (Allen et al. 2002). For example, areas affected by fires can support higher wildlife diversity than late successional forests (Lowe et al. 1978).

A number of studies have investigated categorizing the ponderosa pines into class ratings based on their age and vigor for timber-marking and selective removal of susceptible trees (Hornibrook 1939, Thomson 1940). Ponderosa pines are generally classified into sixteen classes based on four age groups and four vigor classes. The data can be used to analyze the susceptibility of pines to mortality from bark beetle attacks (Keen 1943)

Swetnam and Baisan (1996) suggested that before Europeans settled in the western US, fire was a frequent disturbance agent in ponderosa pine forests resulting in an open grassy understory. The ponderosa pine's thick bark is an adaptation that provided the trees with the ability to withstand lower intensity fires which maintained different forest conditions than current forests as a result of fire suppression. Forests that have been influenced by fire suppression may be less healthy than before European settlement because of increased competition among woody plant species. This decrease in forest health could make these forests more susceptible to other forms of disease and mortality from insects such as bark beetles.

1.2.2 – Bark beetles

Bark beetles are within the Order Coleoptera and the Family Curculionidae, Scolytinae. These beetles feed in the phloems of trees and though not all bark beetles kill trees to reproduce, many of these beetles have received considerable attention from researchers because of the damage caused to their respective hosts. This study will focus primarily on three pine beetle species within the genus *Dendroctonus* that are each present in and around the Colorado Plateau and can successfully attack and kill southwestern ponderosa pines.

The mountain pine beetle (*Dendroctonus ponderosae* Hopkins, hereafter MPB), western pine beetle (*D. brevicomis* LeConte, hereafter WPB), and roundheaded pine beetle (*D. adjunctus* Blandford, hereafter RHPB) are native insects to the southwestern US. These beetles share a similar life cycle although the number of generations per year and the timing of their life stages can differ. Adults of these beetle species select pine trees as hosts and

chew into the phloem. Healthy pines have a natural defense in which they exude pitch to push out or engulf invading beetles. After pine beetles have selected a suitable host, they use pheromones to attract others so that they can mass attack trees and overcome the tree defenses. Resource partitioning within a single pine is not uncommon for pine beetles (Amezaga & Rodriguez 1998, Paine et. al. 1981). In the Colorado Plateau, it can occur between the aforementioned species, *Ips* sp., and turpentine beetles (Furniss & Carolin 1977). Once beetles successfully chew beneath the bark, they mate and reproduce. Eggs are laid in a gallery and the hatched larvae feed in the phloem until they pupate. When the beetles eclose from the pupal stage, they emerge from the tree as adults to find another suitable tree to attack and reproduce in. Bark beetle populations phase between high population densities and low population densities. Epidemic or outbreak populations can impact contiguous acres of forests while smaller population densities, or endemic populations, tend to attack scattered trees within forest landscapes (Carroll et al. 2006).

There are also two species in the genus *Ips* and a turpentine beetle that were found in trees throughout the forests of the Colorado Plateau. The pine engraver beetle (*Ips pini*) and *Ips knausii* are two of the common *Ips* species that attack ponderosa pines in the southwestern US. These *Ips* sp. are typically attack and kill low vigor hosts (Hulcr et al. 2011). The red turpentine beetle (*Dendroctonus valens* LeConte) is another insect that attacks ponderosa pines, but this beetle typically does not kill trees. Turpentine beetles attack the base of trees often leaving pitch tubes visible right above the ground on the bole. Attacked trees are often fire scorched, low vigor, or recently dead although healthier trees may be attacked when populations rise. Native turpentine beetles rarely kill healthy trees even when populations are high.

I.3 – Landscape ecology and disturbances

This study can be described in the context of landscape ecology. The terms described here are important to this scientific study. Ecology is often defined as the study of organisms and their interactions with the environment. As the definition implies, the levels at which ecology is studied is generally beyond the level of the individual. It is instead primarily comprised of population, community, ecosystem, and landscape-level studies. At the landscape scale, the influence of the components (such as ecosystems) and their distribution within the landscape can be analyzed with respect to the ecology of the study organisms. A study with these characteristics can be referred to as landscape ecology.

Landscapes are characterized as having structure and function. The structure of the landscape typically refers to the ecosystem components that make up the landscape. The structure of the landscape affects how organisms perceive and use the landscape, or their “functional heterogeneity” (Coulson & Tchakerian 2010). Landscape function involves the movement of materials, energy, and information within or between components of the landscape. For example, warming temperatures in the spring can cause an emergence of adult pine beetles which move through the landscape to find another susceptible tree to attack and attempt to kill to reproduce.

When landscape structures and functions have been altered, the result is a landscape change. Landscape change is a very broad term though it is often used when a substantial area within a landscape has been altered which either impacts humans or other organisms of interest. Although the natural switch of dominant species in an area over time is a result of ecological succession, it is rarely referred to as a landscape change. The successful spread of an invasive organism, however, is usually credited with causing a landscape change. This

paper is focused on native pest insects with population dynamics that provide them with opportunities to go from small population sizes, which have little influence on tree mortality in the landscape, to outbreak populations that kill large, contiguous acres of forest landscapes. I refer to this type of landscape change as a disturbance.

Disturbance is a term often discussed in ecological settings although it is frequently used without a clear definition, likely because it is assumed that the reader has a general understanding of the word. The definition of the word is not quite as clear perhaps because the term is broad and there have been a number of separate classifications of the word disturbance. I will therefore define a disturbance as any event that results in a rapid change in ecosystem processes or features.

Disturbances by bark beetles in southwestern ponderosa pine forests primarily become an issue when they have economic costs associated with them. Although southwestern ponderosa pines are generally considered to have a lower timber value compared to some other trees in the western US, in 1974, ponderosa pine made up approximately 11 million acres of the 26.5 million acres of commercial forest land in Utah, Arizona, Colorado, and New Mexico (Schubert 1974). Ponderosa pine forests have aesthetic value (Brown 1987) and throughout the southwestern US, ponderosa pine is a dominant tree species in a number of state parks, national parks, national monuments, and national forests, including the Grand Canyon National Park (hereafter NP), Bryce Canyon NP, Mesa Verde NP, and Zion NP. Because of the prevalence of this pine in areas of recreation throughout the southwest, standing dead ponderosa pines can also be dangerous near trails, roads, campgrounds, or structures and require time and costs in removal and reduction of those associated dangers (Cole & Amman 1980).

There are also some potential negative ecological impacts that can occur after a bark beetle outbreak. One study showed that bark beetles acting as a secondary disturbance after fires in lodgepole pine systems can often lead to a shift in succession to subalpine fir depending on the severity of the disturbances and the age of the stands affected (Sibold et al 2007). Hydrological changes have also been seen after bark beetle outbreaks (Bethlahmy 1974, Potts 1984, Moore 2013) which can influence erosion. Many southwestern landscapes are very susceptible erosion due to friable soils and a higher prevalence of sandstone. Dead pines after bark beetle outbreaks can also provide fuel for both canopy and surface fires at variable times after the outbreaks (Allen 2007, Page & Jenkins 2007, Hansen 2015).

I.4 – GIS and remote sensing in landscape ecology

Geographic information systems (GIS) and remote sensing are two powerful tools for landscape ecology studies. Modern GIS applications involve computer software that allows the users to display, alter, and analyze spatial data. Before computer software, performing spatial analyses was difficult and landscape ecological studies were far less common than they are today. It was not until 1992 that ESRI released ArcView 1. GIS technology has rapidly improved and scientific studies using GIS are now commonplace (Coulson & Tchakerian 2010). Using GIS and remote sensing, allow for countless opportunities to perform landscape ecological studies.

In landscape ecology, remote sensing involves the collection of spatial data through electronic sensors instead of physical field collection. Perhaps the most common form of remotely sensed data used in this field is imagery either taken by some form of aircraft or satellite. Often, humans can visually distinguish many characteristics of landscapes when

viewing aerial imagery although current remote sensing technology and software allows the users to classify landscapes into the component features without having to manually outline each feature. Software can perform classifications through spectral signatures. Object-oriented classifications use size and shape to classify objects in the landscape such as houses or trees. Classifications can also take advantage of textures and patterns in the imagery.

Another form of remotely sensed data is LiDAR. This technique involves using laser reflectance to estimate the distance of an object in a landscape. The data is returned as a three dimensional point cloud that reflects the heights and locations of objects in the landscape. Among other things, this information can be used to develop forest canopy height models or estimate the aboveground biomass of trees in a landscape. LiDAR data can be expensive to acquire and is not readily available for most locations. I did not utilize LiDAR data for my analyses but future work using the framework developed in this study could greatly benefit from LiDAR data.

Remote sensing and GIS can be used independently but can also function together synergistically in scientific studies. While GIS can be used in a number of different fields, most landscape ecology studies inherently require some use of GIS. Remotely sensed aerial imagery offers forest ecologists with the opportunity to view the landscape from a perspective that provides information over a broad spatial extent. In this thesis, I use both GIS and remote sensing to (1) simulate ponderosa pines in a landscape and (2) develop a framework for mapping the susceptibility of those pines using the results of extensive field data.

I.5 – Goal and objectives

In this thesis, I analyzed data from both endemic and epidemic populations of pine beetles in southwestern ponderosa pines forests within or near the Colorado Plateau. The goal of this study was to gain a better understanding of the shifts between endemic and epidemic populations and to develop tree-level risk models for predicting bark beetle-caused mortality. To do this, I had three main objectives (Figure 1):

- 1) I used extensive field data of bark beetle populations and the associated stand conditions from sites throughout the Colorado Plateau to assess what factors might contribute to a shift in the population densities of bark beetles.
- 2) The same field data was then used to develop the best statistical and ecological model for determining the absolute risk of bark beetle-caused mortality in ponderosa pines.
- 3) Using remotely sensed imagery, GIS layers, and ground truth data I estimated the spatial distribution and conditions of host trees across a large landscape setting and then used the landscape to develop a framework for applying tree-level risk assessments.

To complete the first objective, I used over 20 years of field data to assess the spatial and temporal changes in the bark beetle population dynamics within southwestern ponderosa pine forests. After grouping sites based on epidemic and endemic conditions, I was able to analyze any differences between the stand conditions associated with the population densities. I then used logistic regression to determine how stand variables interact to influence the probability of a shift in the population phase from endemic to epidemic conditions.

The second objective required logistic regression analyses to develop a model for predicting the probability of beetle caused mortality for individual trees per year. To do this, I first standardized tree, stand, and beetle pressure variables and then assessed the relative influence of each variable by analyzing them independently using logistic regression. I then entered non-correlated variables into a multiple logistic regression analysis to develop the best ecological and statistical predictive model for assessing the risk of individual trees.

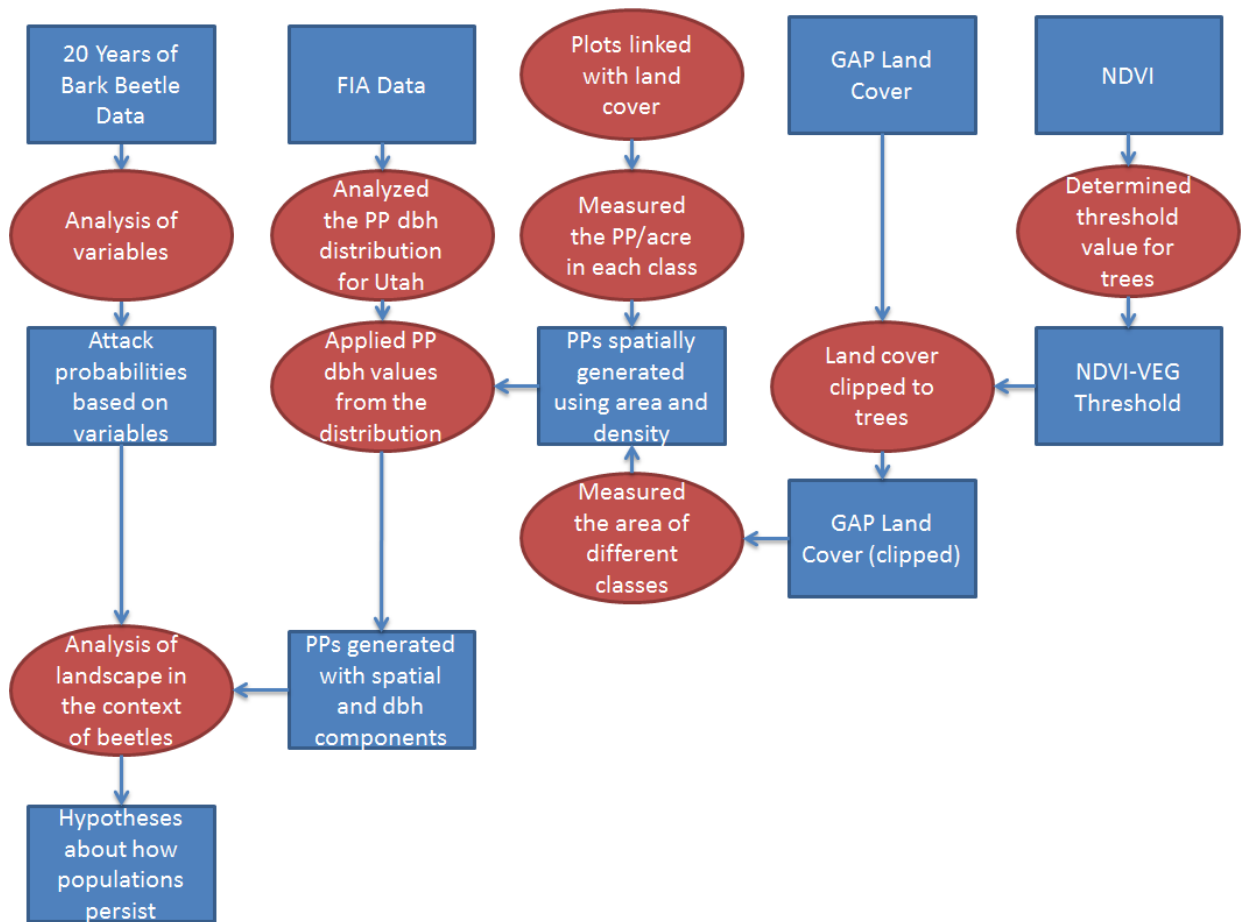


Figure 1: Data and analysis flowchart for this study. The left-most column describes the first objective of analyzing host susceptibility variables. The second objective includes the Forest Inventory & Analysis (FIA) ground truth data, GAP land cover data, and a normalized difference vegetation index (NDVI) to simulate a ponderosa pine (PP) forest with information about each pines diameter at breast height (dbh). Last, the susceptibility of individual trees was displayed in a simulated forest landscape

The final objective involved developing a framework for displaying a tree-level risk model in the landscape. To simulate a realistic forest landscape I used 1 meter spatial resolution remotely sensed aerial imagery and other GIS layers. The US Geological Survey's National Map Viewer was used to download 1 meter resolution imagery for the Cedar City Ranger District of the Dixie National Forest. The imagery was processed to create a normalized difference vegetation index (NDVI) which allowed me to classify healthy green vegetation, primarily trees, within the landscape. Forest Inventory and Analysis (FIA) data provided by the US Forest Service were linked to GAP vegetation classes to gain estimates of the density of ponderosa pines in each vegetation class. Locations to represent ponderosa pines were randomly generated within the "green" locations of each vegetation class according to the average densities that were calculated. Dbh values for each pine were randomly selected using the dbh distribution of ponderosa pines from the FIA data and an acceptance- rejection method. Using both susceptibility data as well as a simulated landscape with information about the configuration and conditions of individual trees, I used the landscape to develop a framework to assess the risk of bark beetle-caused mortality of individual trees.

II ANALYSIS OF BARK BEETLE POPULATION DYNAMICS

II.1 – Introduction

Dendroctonus pine bark beetles in southwestern ponderosa pine forests phase between periods of high epidemic population densities and periods of low density, endemic populations. During epidemic population phases, high numbers of beetles are available to mass attack trees. After a variable number of years, epidemic populations reduce in number and persist as separate metapopulations or endemic populations. Raffa and Berryman (1980) define endemic populations as those in which the “reproductive gains are offset by losses during the host-searching stage” although host resistance, weather, natural enemies and other factors also contribute to losses in the population (Safranyik 2003). Carroll et al. (2006) considered endemic populations to attack fewer than three trees per hectare. Endemic populations that are unable to find suitable hosts are incapable of reproduction. Eventually, some of the endemic bark beetle populations will have suitable conditions for an increase in the population density of epidemic levels again. Because there are many potential circumstances that could prompt the transition from an endemic population to an epidemic population, there is a high degree of unpredictability as to when and where populations will transition from the one phase to the other.

Although bark beetles are a natural part of western forests, outbreaks can have large economic, ecological, and social impacts associated with them. Because of these impacts, the majority of research is devoted to studying current outbreaks or forest conditions following outbreaks. Some scientists, however, have noted that understanding the endemic populations could contribute to what is known about the triggers for outbreaks (Cole & Amman 1980, Bentz et al. 1993, Schmid & Amman 1992). One reason that endemic populations have

largely remained unstudied is likely due to the difficulties associated in their detection since they tend to affect few trees over a large landscape. It is also more difficult to obtain funding for studies of endemic bark beetle populations since they are not directly responsible for considerable tree losses.

The exact causes of outbreaks are often unclear though many hypotheses have been developed to explain the triggers that cause epidemics. Berryman (1982) developed a theoretical model in which low stand resistance and wide phloem thickness are the factors that can trigger an endemic population to develop into an epidemic population. Thick phloems are associated with actively growing, healthy trees (Skov 2008) which often have stronger defenses than those that are over-mature or diseased and therefore require high beetle populations for successful attacks. On the other hand, the unhealthy trees commonly attacked by endemic populations tend to have low quality phloems (Bleiker 2014) and produce fewer offspring (Boone et al. 2011). If bark beetle populations have high densities, they can successfully attack healthy trees, the thick phloem of these trees tends to result in higher counts of offspring (Amman et al. 1977, Raffa et al. 2008). Widespread losses in host vigor due to climatic factors, such as drought and excess soil moisture, have also been attributed with causing outbreaks of pine beetle species (Preisler et al. 2012, Negrón et al. 2009, Kalkstein 1976, Kalkstein 1981, Raffa et al. 2008).

The goal of this section was to analyze over 20 years of bark beetle data in southwestern ponderosa pine forests to discern differences in stand conditions between epidemic and endemic population phases. I think that the stand variables would differ between sites with low and high population densities. If this is true, the stand conditions could be used to predict a shift in the population. The objectives that were performed to

achieve the goal were to (1) detect changes in the population size over time, (2) determine differences between stands with high population densities and those with low population densities, and (3) develop a model that uses stand conditions to predict the probability of a shift from a low population density to a higher population density. These analyses provide insight into the stand conditions that could trigger outbreak populations in southwestern ponderosa pine forests.

II.2 – Methods

II.2.1 – Study area

Throughout the Colorado Plateau and surrounding areas, a total of 45 two acre sites were established in national forests (hereafter NFs) and national parks (hereafter NPs). The Colorado Plateau encompasses approximately 130,000 square miles in parts of Utah, Colorado, Arizona, and New Mexico. The southern slopes of the Uinta Mountains mark the northern boundary of the plateau in Utah while the contiguous ranges of the Rocky Mountains bound the eastern range of the plateau in Colorado. The plateau also includes the Grand Canyon in the southwest and is bounded by the Rio Grande rift to the southeast. Nearly all of the Colorado Plateau falls within the Upper and Lower Colorado River Basins. Most of the Colorado Plateau is comprised of arid, high elevation desert characterized by sandstone cliffs and canyons. As elevations increase and temperatures remain cooler throughout the year, the Colorado Plateau may transition from pinyon-juniper forests to ponderosa pine, mixed conifer, and aspen forests. Despite the area being relatively dry most of the year, a summer monsoon season often occurs in July and August particularly seen in the southern part of the plateau. Despite the fact that the most valuable material natural

resources from the Colorado Plateau are chemical and mineral as opposed to timber, the plateau is renowned for its aesthetic natural beauty most of which includes forested areas that are susceptible to a variety of insects and pathogens. Widespread tree mortality could result in increased hazard in areas of high recreation use as well as economic losses from tourism and management expenses.



Figure 2: The National Forests and National Parks where sites were established in the southwestern US within or near the Colorado Plateau. The Colorado Plateau boundary shapefile was acquired from: http://perceval.bio.nau.edu/MPCER_OLD/sage/coplant.htm

The bark beetles of the Colorado Plateau that attack and kill ponderosa pines include *Dendroctonus ponderosae*, *D. brevicomis*, *D. adjunctus* as well as several species of *Ips* and *D. valens*. Sites were established within the Dixie NF, Kaibab NF, Manti-La Sal NF, San Juan NF, Fishlake NF, Uncompahgre NF, Bryce Canyon NP, and the North Rim of the Grand Canyon NP (Figure 2). The location of the sites was based on the status of beetle activity when sites were first established in 1995. Beetle activity was labeled endemic, epidemic, or post-epidemic. In 1998, plots were made permanent within each site. Ten 0.1 acre circular plots were placed along each of two parallel transects that were 66 feet apart (Figure 3). In 1995-96, two plots at each site were permanently marked with plot center stakes and tags on each tree in the plot. In 1998, a decision was made to permanently mark all 20 plots at each site. Because plot centers were estimated in 1998, it is possible that the trees tagged may differ slightly from trees originally measured in 1995-96. All plots were revisited for data collection periodically through 2012.

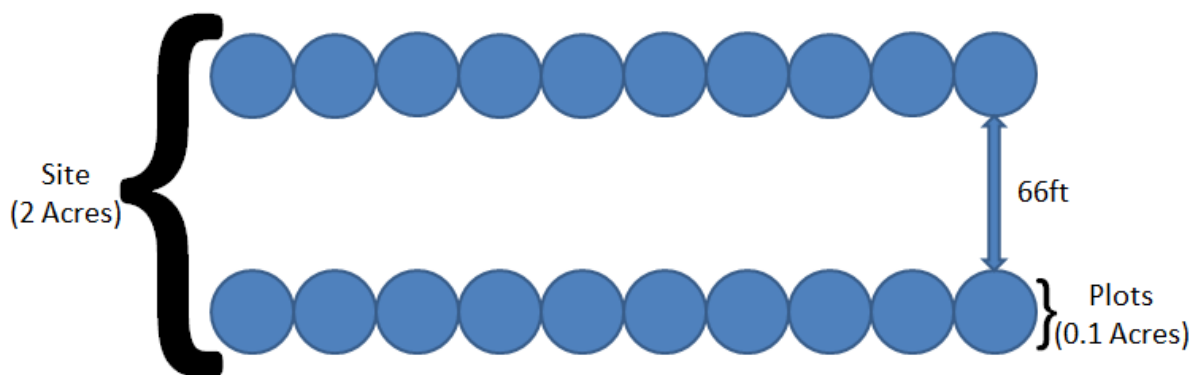


Figure 3: Site and plot design for field collection of tree/stand and bark beetle data.

II.2.2 – Field data

Plots were initially installed in 1995-96, made permanent in 1998, and re-measured in 2002, 2004, 2006, and 2012. In 2012, I collected data at the sites with a field crew. Within each 0.1 acre plot at each site, all trees with a diameter at breast height (dbh) greater than 3 inches were tagged and sampled for species, dbh, and whether they were alive, dead, or down. All pines were given a Keen's vigor rating based on a visual assessment of age as 1) young, 2) immature, 3) mature, and 4) overmature, as well as A) full vigor, B) good to fair vigor, C) Fair to poor vigor, and D) very poor vigor (Keen 1943). All pines were also given a dwarf mistletoe rating based on Hawksworth (1977). Trees were checked for any sign of bark beetle attacks and the type of attack was recorded (i.e., pitchout, strip attack, tree killed). Estimates of the year of attack were made based on the hardness of pitch tubes, the condition of the bark attachment, and the color and number of needles on the trees. In 1995-96 at each plot, the first two trees encountered in a clockwise direction from north were cored on opposite sides of the tree bole to measure previous 5 and 10 year growth. Beginning in 1998, if new bark beetle attacked trees were observed in a plot during a survey year, the attacked tree and an un-attacked tree of similar dbh and height were both cored to pith. In all years, total height and height of the crown base were measured on all cored trees. Additional notes were taken about host tree conditions including lightning scars, snapped tops, and *Armillaria*. If any trees killed by bark beetles were observed within 132 ft. of plot center, surrounding bark beetle activity was assigned 1, and 0 if no trees were observed. In 2012 many of the sites had burned since the last survey. Because fire injury can influence bark beetle attack, all pines in each plot were rated for fire injury based on the presence/absence of scorch on the bole, and an estimate of percent crown damage (see Hood et al. 2007).

II.2.3 – Data analysis

II.2.3.1 – Data organization

Before analyses were performed, data collected from the field had to be organized electronically. Data were collected periodically and then entered for each survey period. The survey periods varied in the number of years over which bark beetle activity could have occurred (e.g., 2 years between 2002 and 2004, and 6 years between 2006 and 2012). Instead of analyzing survey periods over variable numbers of years, I wanted all the data normalized for a single year including the number of live trees and beetle attacked for each year. To do this, all live trees at the end of a survey period were considered alive during each year within that survey period. Also, any beetle attacked or killed trees from later years in a survey period were added to the previous year within that survey period as live trees. This is because up until the year that the trees were beetle attacked, their statuses would have been labeled “live.” For example, to make a dataset for the year 2008, which was not a survey year, trees alive in the 2012 survey were considered live in 2008 and trees estimated in 2012 to be attacked by beetles in 2008 were coded as beetle attacked. In addition, all beetle-attacked or killed trees in 2009, 2010, 2011, and 2012 were considered live in 2008.

Since mortality from other causes was not dated, I assumed that the mortality of these trees was evenly distributed for each year within that survey period. For example, the 2012 survey period encompassed 6 years of data. If 30 trees were marked as dead or down from causes other than beetles in that survey period, I assumed that in 2007, the first year of that survey period, a random sample of 25 of those trees were alive. The next year, 20 trees were sampled from the 25 trees that were displayed as alive from the previous year. By 2012, all the trees originally surveyed that year as dead or down were classified as dead.

II.2.3.2 – Annual proportions of beetle-caused mortality

Once the data was organized, I calculated the annual proportions of bark beetle killed pines out of the number of total number of pines surveyed each year. These proportions provided information about the probability of beetle-caused mortality of any ponderosa pine in the forest being killed by beetles for each year. Confidence intervals were calculated using bootstrapping methods.

To examine any regional differences in the population phases, sites were grouped into three regions and the annual proportions of beetle caused mortality within the regions could then be compared (Figure 4). The sites were grouped into regions of the four corners (N = 15), southern Utah (N = 20), and northern Arizona (N = 10).

These analyses showed how the population phases changed within sites throughout the surveyed years however, these proportions did not provide any information about the tree or stand characteristics that could be responsible for changes in the population sizes. Further analyses were required to examine differences in stands that became epidemic and those that remained endemic.

III.2.3.3 – Comparing epidemic and endemic sites

To examine differences between epidemic sites and endemic sites, I first needed to determine how to group sites as endemic or epidemic. Carroll et al. (2006) considered endemic populations to attack fewer than three trees per hectare. Since sites were composed of 2 acres (0.809 hectares), I decided to use a similar threshold of more than two beetle killed trees per site to represent epidemic conditions. All sites that exceeded the threshold within the 21 surveyed years were considered susceptible to epidemic populations while all other

sites were used to represent stand conditions that would not lead to epidemic populations. More specifically, the stand conditions used for epidemic sites were from the first year that the number of attacked trees exceeded the epidemic threshold. Because endemic sites never exceeded a threshold, the stand conditions used for analyses were those from the first surveyed year.

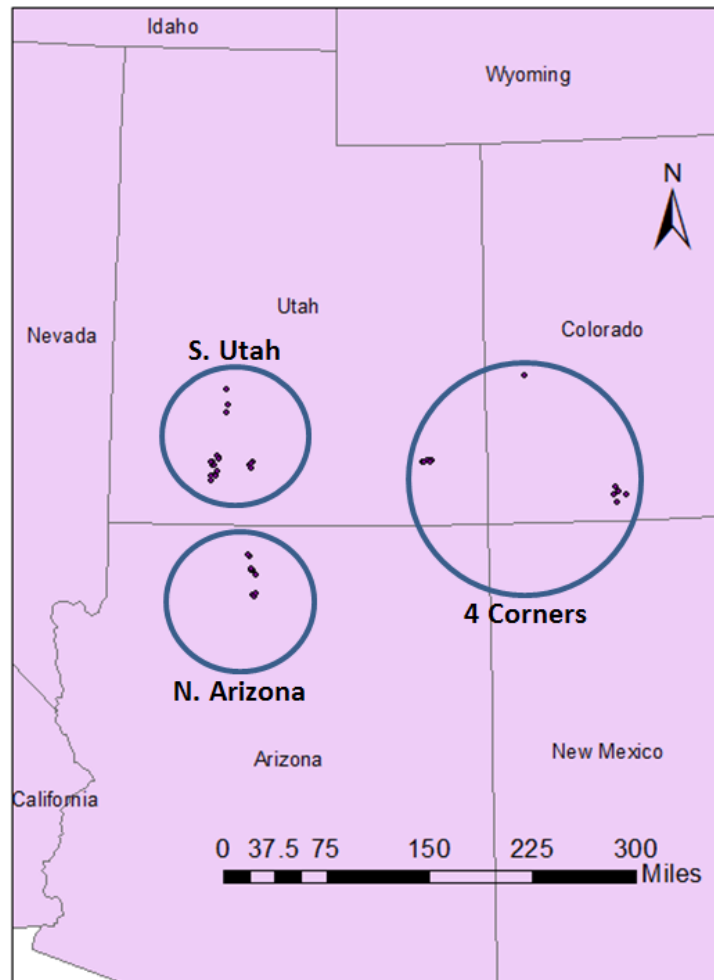


Figure 4: The three regions used to group study sites. These include the four corners (N = 15), southern Utah (N = 20), and northern Arizona (N = 10).

Site level measurements of epidemic and endemic sites were compared with one-way ANOVA analyses to observe any differences between average ponderosa pine dbh,

maximum ponderosa pine dbh, basal area, ponderosa pine basal area, trees per acre, ponderosa pines per acre, and percent ponderosa pine. Stepwise multiple logistic regression was also used to analyze the relationship between these variables and whether or not the population densities increased beyond epidemic conditions. The resulting model could be used to estimate the probability that a site would become epidemic based on stand conditions.

II.3 – Results

The annual proportions of beetle-killed ponderosa pines across all sites shows that 1992-1996, 2003, 2007, 2012 were all years with relatively high mortality (Figure 5). In southern Utah, 1992-1996, 2007, and 2012 were all years with high beetle-caused mortality. Northern Arizona had high beetle caused mortality in 1992-1994, 1996, 2003, 2006, and 2008. There was relatively high beetle-caused mortality in the 4 corners region in 1993, 1995-1997, 2003, 2007.

A total of 30 sites exceeded the epidemic threshold while 15 remained endemic throughout the study. The one-way ANOVA analyses showed that site maximum dbh ($P = 0.0146$), ponderosa pine basal area ($P = 0.0085$), total basal area ($P = 0.0046$), the number of trees per acre ($P = 0.0138$) were all higher significantly higher in sites that exceeded the epidemic threshold. Site average dbh ($P = 0.9583$), the number of ponderosa pines per acre ($P = 0.1038$), and the percent of ponderosa pines ($P = 0.3756$) within sites were not significantly different between endemic and epidemic sites. The mean and standard error for all site variables were plotted to show the differences between epidemic and endemic stand conditions (Figure 6).

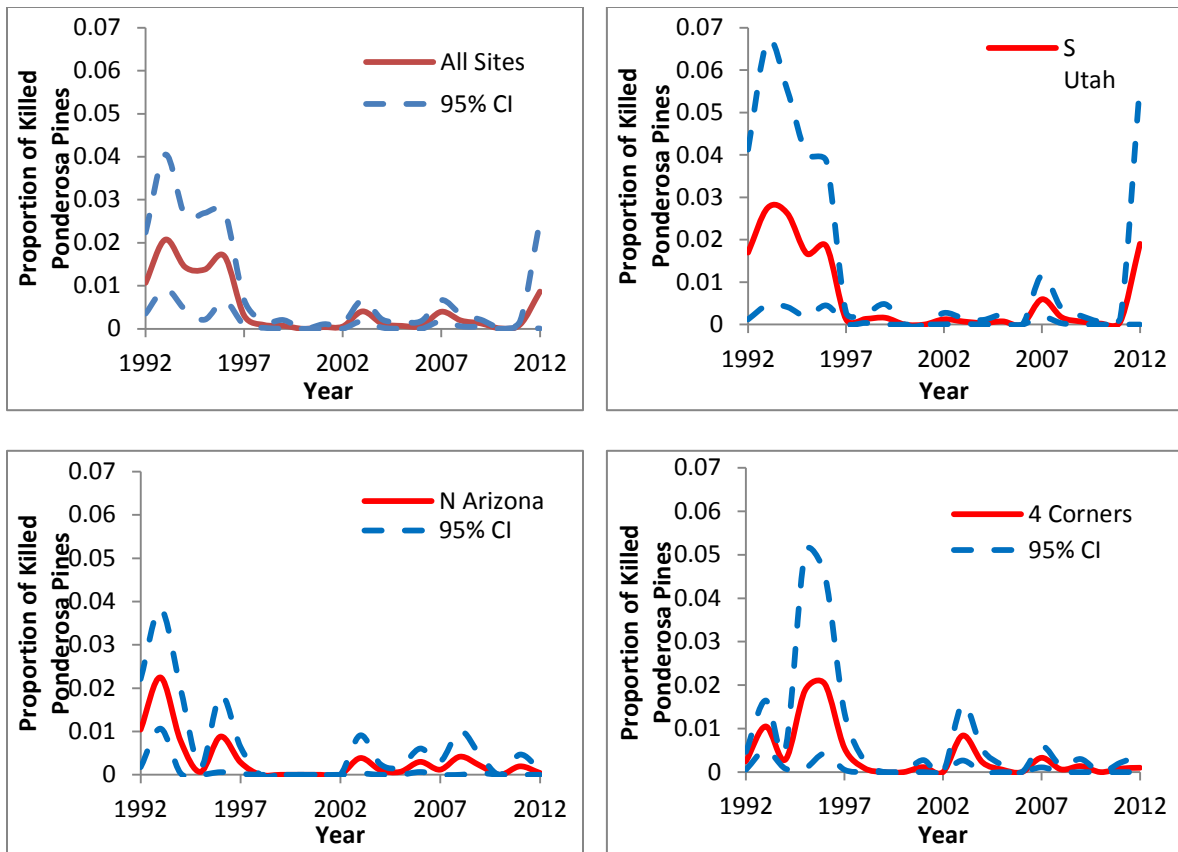


Figure 5: Annual proportions of beetle-caused mortality across all sites and regions

Stepwise logistic regression was used to select the model with the highest predictive power. The best model ($P < .028$, Nagelkerke R square = .402) used site maximum dbh and the site-level estimate of the number of ponderosa pines per acre to predict the probability of increase in the population density (Table 1). The predictive equation developed from this analysis was

$$\text{Probability of an increased population density} = -8.806 + (.227 \times \text{site max dbh}) + (.025 \times \text{site PP per acre})$$

which showed that sites with a site maximum dbh of 30 inches and approximately 225 ponderosa pines per acre has nearly a 100% chance of a positive increase in the population density beyond endemic levels (Figure 7).

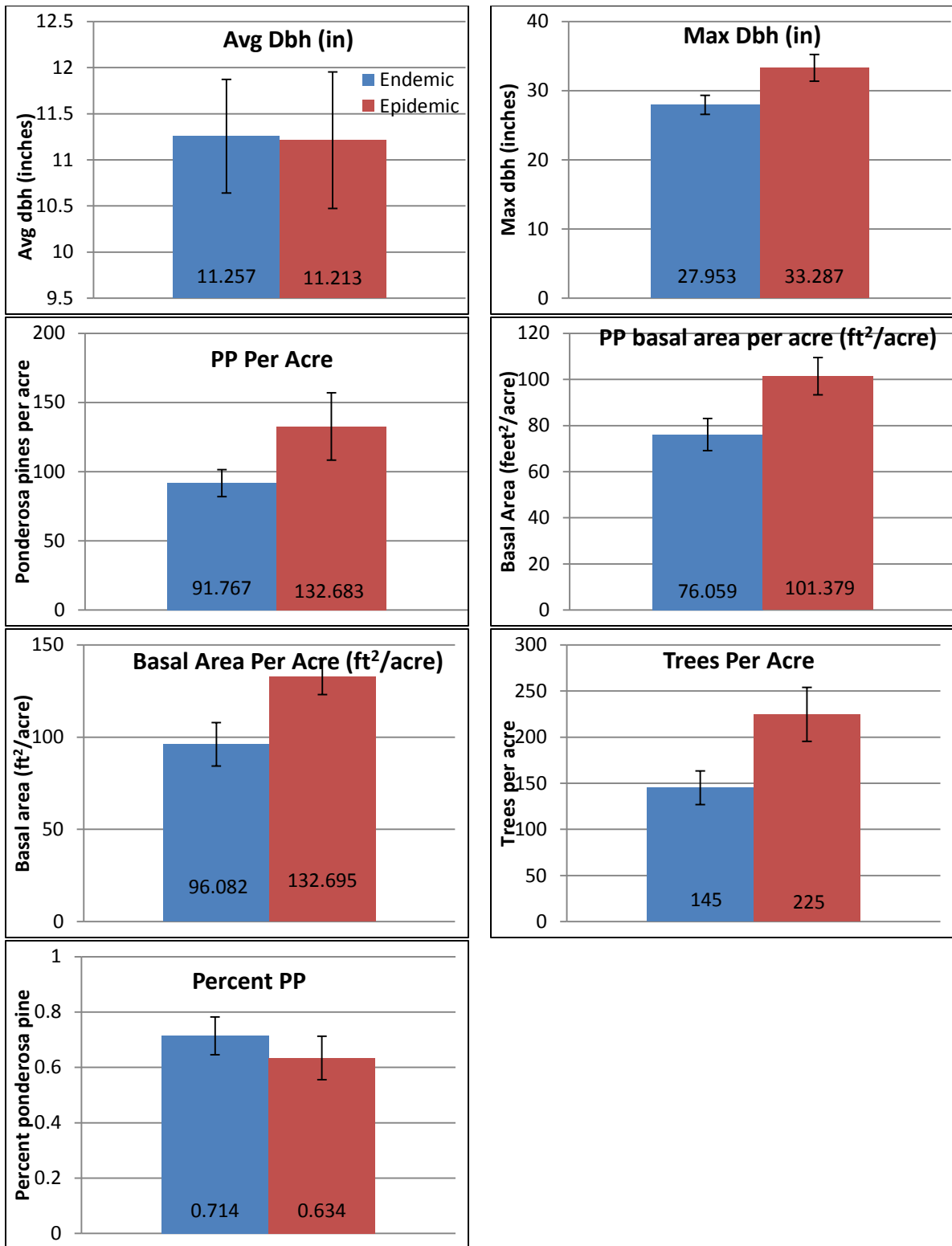


Figure 6: Mean site-level measurements in epidemic and endemic sites. Error bars represent the associated standard errors.

Table 1: The output coefficients from the stepwise logistic regression analysis. B is the regression coefficient, S.E. is the standard error, Sig. is the significance of each variable in the independent model

	B	S.E.	Sig.	95% C.I. for EXP(B)	
				Lower	Upper
Site max dbh	.227	.085	.007	1.063	1.481
Site PP/acre	.025	.011	.028	1.003	1.049
Constant	-8.806	3.291	.007		

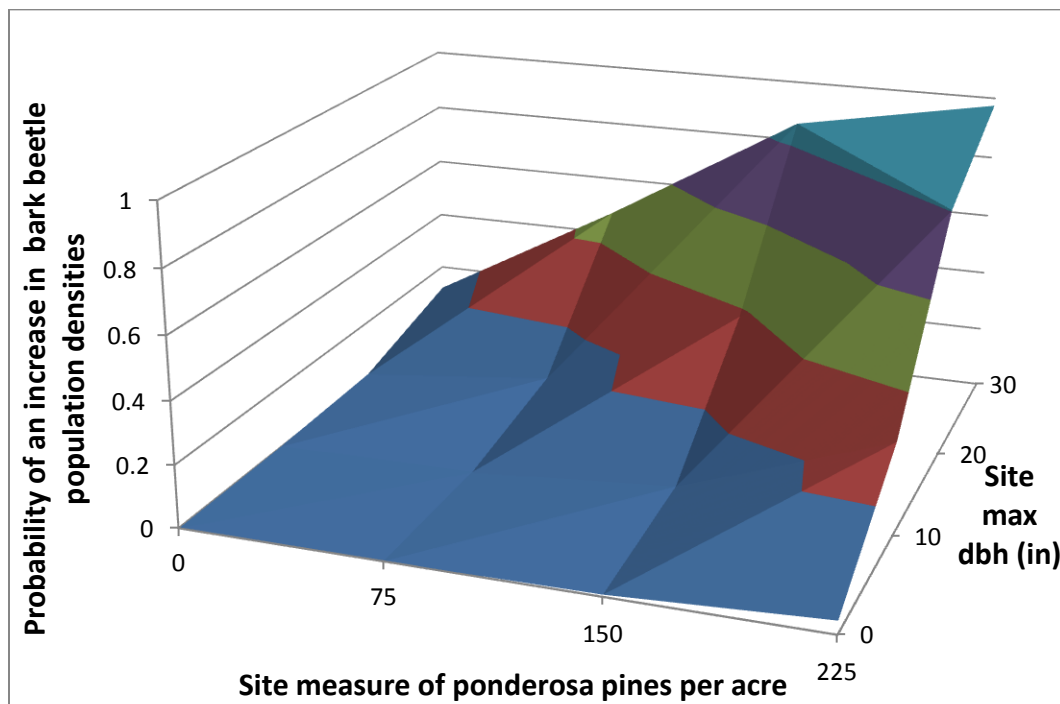


Figure 7: Surface chart of how stand variables influence population densities. Specifically, the number of ponderosa pines per acre and the site max dbh influence the probability of an increase in bark beetle population densities beyond endemic level within a site (more than 2 beetle-killed trees per site)

II.4 – Discussion

The annual proportions of bark beetle-caused mortality across each of the regions was similar to the mortality across all sites. Throughout 1992-1996, the proportions of beetle-killed trees was consistently high across the three regions that sites were grouped into with

the exception of low mortality in northern Arizona in 1995. Northern Arizona and the four corners both had high mortality in 2003 while southern Utah and the 4 corners had peaks in 2007. Northern Arizona also had two small peaks in 2006 and 2008. There was a relatively high proportion of bark beetle-caused mortality in 2012 in a site in southern Utah. The site with 50 beetle-killed trees in 2012 was located in the Fishlake National Forest and many of the trees within the site had been damaged by the Twitchell Canyon fire in 2010. Although the trends seen in the population dynamics within three regions were reflective of the pattern seen across all study sites, a number of sites never had high numbers of beetle killed trees. The other analyses performed provided information about differing stand conditions between sites that reached epidemic levels and those that remained endemic throughout the study.

Using a threshold of greater than two beetle killed trees per acre per year to represent epidemic conditions, sites were analyzed using the stand conditions from the first year that they exceeded the threshold. If sites did not exceed the threshold, the stand conditions were used from the first surveyed year. A total of 30 sites exceeded the threshold over the 21 years while 15 sites never had more than two beetle killed trees in one year. The stand conditions were compared between the epidemic and endemic sites using one-way ANOVA analyses. Site maximum dbh, ponderosa pine basal area, total basal area, the number of trees per acre were all significantly higher in sites that exceeded the epidemic threshold while there were no significant differences in site average dbh, the number of ponderosa pines per acre, and the percent of ponderosa pines per site. Sites with high maximum dbh values might be significant due to the large diameter trees in epidemic sites being preferred hosts for pine beetles (Cole & Amman 1969). Sites with high basal area either also have large diameter trees, or have a high density of trees (number of trees per acre). These factors could also

contribute to making trees within the sites susceptible (Chojnacky et al. 2000, Olsen et al. 1996, Negrón & Popp 2004) which, in turn, could lead to populations increasing beyond endemic levels.

Logistic regression analyses of the variables provided more insight as to how the stand conditions interact to influence the probability of bark beetles reaching epidemic levels within a site. The model with the highest predictive power used the site maximum dbh and the estimate of the number of ponderosa pines per acre. The model shows that as the variables increased, so did the probability of bark beetles reaching epidemic levels within a site. A site with a maximum dbh of 30 inches and approximately 225 ponderosa pines per acre has nearly a 100% probability of an increase in population densities above endemic levels. Specifically, the increase in the population density defined in the model would mean that there would be more than 2 mass attacked trees within a site in a given year.

One issue with the predictive model is that there is no temporal aspect. The probabilities do not mean that the sites will become epidemic within one year. Also, the scale for all of the variables was calculated on the site-level. The sites are composed of 2 acres of non-contiguous forested areas (Figure 3). This might not be a scale of measurement that the beetles select on. Regardless, there were significant differences between a number of variables and two of the variables seemed to interact to play a role in the probability of bark beetles populations increasing beyond the epidemic threshold within the sites. Climatic data was not used in the analyses performed here, although there is evidence that climate plays a role in the population dynamics of bark beetles (Preisler et al. 2012, Negrón et al. 2009, Kalkstein 1976, Kalkstein 1981, Raffa et al. 2008).

Another issue was the bias in site selection for this study which likely played a role in the accuracy of the analysis. Some sites were selected in locations where bark beetle populations were already epidemic. This can be seen from the annual proportions of bark beetle attacks (Figure 5). Any information about the population phase that beetles were in at sites before 1992 is unknown. Similarly, if bark beetle populations were higher than the threshold before 1992, the stand conditions at that time would also remain unknown.

The analyses performed showed that there were some regional differences in the population dynamics throughout the southwest, although the general trends in the population sizes was relatively similar. The population dynamics across sites tended to be more variable. A number of sites never had more than two beetle-killed trees per year over a period of 21 years. Sites that had higher population densities of beetles also had significantly higher measurements of basal area, site maximum dbh, and trees per acre. Using stepwise logistic regression, the number of ponderosa pines per acre and the site maximum dbh were used to predict the probability of an increase in the population density of bark beetles. In the next section, I use logistic regression analyses to determine the best predictive model for determining the probability of individual trees being killed by bark beetles within one year given the beetle pressure and tree/stand conditions. In section 4, a landscape is simulated to the level of the individual tree using remote sensing and GIS so that a framework could be developed for applying the model to individual trees in a landscape.

III HOST SUSCEPTIBILITY TO BARK BEETLE-CAUSED MORTALITY

III.1 – Introduction

A long term goal of forest entomologists has been to develop susceptibility and risk rating systems that would allow forest managers to identify areas where the probability of trees being infested by forest insects is high so that they can implement actions to reduce losses of timber and other associated costs. In the case of bark beetles, goals also include preventing outbreaks and minimizing damage during epidemic conditions. Terms associated with predicting areas of locations where attacks might occur include: risk, susceptibility, and beetle pressure. According to Haimes (1998), “risk is often defined as a measure of the probability and severity of adverse effects.” Shore and Safranyik (1992) defined risk in the context of bark beetles as a function of 1) beetle pressure and 2) mortality of host trees that would be associated with it. Bentz et al. (1993) agree that the term risk is to be used when beetle pressure is included. Birt (2011) noted that a number of risk assessment models in southern pine beetle systems are poor predictors of where outbreaks occur because there are weak relationships in between attacks and stand conditions. However, older risk rating systems provide a foundation for improved methods of determining host susceptibility to bark beetles.

For this study, I define susceptibility as the variables and conditions that affect the probability of host trees being attacked by bark beetles. In terms of risk, the adverse effect associated with the susceptibility is the death of host trees. There is also a temporal scale that of interest to this study. Because of the way the data was organized, the probability of a tree being attacked in one year could be calculated.

The term “beetle pressure” is used to describe the number of beetles at a location and time period of interest. Specifically, “high beetle pressure” means a high level of bark beetle activity while “low beetle pressure” means that there is a smaller presence of beetle at a site or perhaps there is no detectable presence of beetles at all. Beetle pressure often plays a significant role in understanding the risks of attack because it can have a direct influence on the likelihood of successful attacks. Because pine beetles often use mass attack strategies to overcome tree defenses, high numbers of beetles often allow for an increased likelihood of successful attacks. In some cases where populations get very high, beetles can even successfully kill healthy trees. On the other hand, when beetle populations are very low, their chances of successful attacks may decrease unless trees are particularly susceptible. It is possible that some areas may have characteristics that would generally make trees susceptible, but a lack of beetle pressure would mean that there is no risk of pine beetle attacks. This thesis will primarily focus on tree susceptibility based on tree and stand characteristics as well as some beetle pressure data.

A major bias can occur when attempting to research susceptibility associated with outbreaks if the assumption is made that the stand conditions at the location of the outbreak are representative of a susceptible stand. The influence of high beetle pressure or other conditions might result in an epidemic while the associated stand conditions were not the cause of the outbreak. Other stands could be better suited for an epidemic population but if there is no beetle pressure, there is no risk for trees at those sites. Studying the conditions that lead to bark beetle outbreaks requires studying areas of infestation along with information about the forest where infestations did not occur and some measure of beetle pressure in the landscape.

Many studies have neglected to use beetle pressure data and focused solely on susceptibility to determine what tree, stand, or external factors might be influencing host selection. Stevens et al. (1980), for example, developed a susceptibility model for ponderosa pines in the Black Hills. The model did not involve any form of beetle pressure and instead ranked forest conditions based on the average dbh, stand structure, and stand density. Keen (1943) developed a rating system for ponderosa pine age and vigor and developed mortality ratios for each pine class using beetle attack data and other causes of pine mortality in sampling plots in Washington, Oregon, and Northern California. For ponderosa pine in the Colorado Plateau, the Munson/Anhold risk rating technique (Munson & Anhold 1995) proved to be a better than the Stevens/McCambridge/Edminster technique though neither technique was a great predictor of attack probably due to other factors. (Chojnacky et al. 2000). The Munson/Anhold risk rating technique takes into account basal area, average ponderosa pine dbh, proportion of ponderosa pine in the canopy, and the number of currently infested trees per acre while the Stevens/McCambridge/Edminster technique includes stand structure but lacks any information about beetle pressure.

Other research in susceptibility has been for determining the causes of outbreaks or attacks on primary trees (the first trees attacked in an outbreak). A susceptibility study, in Oregon, looked at the relationship between attacks on ponderosa pine and tree vigor as measured by the amount of wood produced per square meter of leaf area and showed that low vigor trees were more susceptible while nearby trees of higher vigor were likely attacked due to “switching over” once the primary tree had been thoroughly attacked (Larsson et al. 1983). Another study of ponderosa pine in the black hills showed that the majority of the first trees attacked in infestations in 1991 and 1992, had root-rotting fungus (*Armillaria mellea*)

infections, physical damage, previous pitchouts, or had been struck by lightning (Eckberg et al. 1994). This would suggest that most beetles were not selecting hosts in response to dbh, basal area, or some other general tree or stand variable

Climate stressors such as droughts and excess soil moisture have been known to have an influence on tree susceptibility to bark beetle attacks (Kalkstein 1976, Kalkstein 1981, Raffa et al. 2008, Chapman et al. 2012). In a study of ponderosa pine in the Black Hills, Olsen et al. (1996) showed that trees per acre, basal area, minimum dbh, range in dbh, and the coefficient of variation on dbh all played a significant role on host selection while maximum dbh did not. In northern Colorado, ponderosa pine stand density index and basal area had the biggest stand-level effect on attack probabilities in ponderosa pine forests while trees with larger dbh and dominance or co-dominant trees were more frequently attacked than smaller trees or those that are intermediate, suppressed or open-growth trees (Negrón & Popp 2004).

When endemic populations are discussed in the literature, diseased or damaged trees are usually described as the only forms of suitable hosts and there are few studies that look at the other tree and stand characteristics that could influence host selection during the endemic phase. Raffa et al. (2008) concluded that large trees are often more resistant to endemic populations. Spruce beetles (*Dendroctonus rufipennis*) have been shown to attack healthy trees during epidemic phases while endemic populations seem to occur in windthrown or other damaged trees (Raffa et al. 2005). A study of lodgepole pine during an endemic phase of mountain pine beetle populations found that trees with *A. mellea* were attacked with higher frequency than trees without the fungal disease (Tkacz 1985). Safranyik (2003)

reported that dbh has no clear relationship with the probability of attack under endemic conditions.

The goal of this section was to develop a risk model to calculate the absolute probabilities of beetle caused mortality for individual trees over a year. I hypothesized that tree, stand, and beetle pressure variables are related to bark beetle-caused mortality in southwestern ponderosa pine forests. The analyses performed in this section were also aimed at discovering which spatial scales are important for the tree/stand characteristics as well as beetle pressure measurements. In the following section, I modified the statistical model to develop a framework for calculating and displaying tree-level risk assessments across a landscape.

III.2 – Methods

III.2.1 – Study area & data collection

The sites used in this study and the methods used for data collection were described in the previous section. A brief summary of the study area and data collection has been described here. All sites were located in the southwestern US within national forests and national parks (Figure 3). Sites were selected within areas where ponderosa pines were present and the status of beetle populations was either endemic, epidemic, or post-epidemic. Sites were a total of 2 acres comprised of twenty 0.1 acre plots along two parallel transects (Figure 4). Sites were periodically visited from 1995 through 2012. Ponderosa pines were identified, measured, and classified and stand measurements could then be calculated at different scales. If ponderosa pines had been attacked or killed by bark beetles, the beetle species were identified and the year of mortality was estimated.

III.2.2 – Data analysis

III.2.2.1 – Data organization

Although data was collected and entered for each survey period, the data was re-organized so that there were estimates of all live, attacked, and killed trees for each individual year. The same methods for the annual estimation of tree data described in the previous section were used in this study. All plot and site-level stand measurements were attributed to the trees that fell within the respective plots and sites each year. To analyze beetle pressure, different spatial scales were selected to measure basal area killed per acre the previous year and the number of beetle killed trees per acre the previous year. These measurements were done at the plot and site-level but also at a regional and “global” level. For regional measurements, sites were grouped into the four corners region (N=15), southern Utah region (N=20), and northern Arizona region (N=10) as seen in the previous section (Figure 4). The “global” beetle pressure measurements were performed across all of the study sites. All beetle pressure measurements were calculated per acre of sampled area. This is a particularly important distinction for the regional and “global” measurements.

After all tree, stand, and beetle pressure measurements were linked to the individual trees each year, all live and beetle killed trees from each year were compiled into one data set. This would allow for logistic regression analyses to represent all the data collected for trees across all of the sites and all of the years. Each of the measurements, however, has different ranges of values and many have different units. To compare the relative influence of the variables, all of the variables were standardized by calculating their Z-scores. The Z-score was calculated using this equation:

$$z = \frac{x - \text{mean of the population}}{\text{standard deviation of the population}}$$

where x is a raw data value of the population. The Z-score standardizes values in relation to the mean value. Values that are identical to the mean will equal zero while those higher than the mean will be positive and vice versa. By doing this, the coefficients obtained when performing logistic regression express information about the relative influence of each variable on host susceptibility to bark beetle-caused mortality.

III.2.2.2 – Logistic regression analyses

Data was analyzed with regression analyses using SPSS statistical software. To determine the relative influence of each variable on the probability of tree mortality, all tree, stand, and beetle pressure variables were analyzed with logistic regression analyses independently. Beetle-caused tree mortality was used as a binomial dependent variable where 0 was used for live trees and 1 was used for beetle-killed trees. The independent variables were analyzed and those with larger regression coefficients had stronger influences on host susceptibility to bark beetles. These coefficients were used to interpret the ecological influences of insect-host interactions. These coefficients also provide information about which spatial scales of measurement are the most important for stand conditions and beetle pressure because those variables were examined over different spatial extents. The strength of the coefficients was also used to determine the order that variables would be entered when stepwise multiple logistic regression was used later.

Before running a stepwise multiple logistic regression analysis on the variables, a correlation matrix was performed for all tree and stand variables. If any of the variables were highly correlated (>0.6), only the variables with the higher regression coefficients, when analyzed independently, were included in the multiple logistic regression analysis. The

correlated variables with lower coefficient values in the independent analyses were not entered into the multiple logistic regression analysis. For beetle pressure, only the variable with the highest regression coefficient was included.

With preliminary analyses to assess the relative importance of variables and the correlations between those variables, I ran a stepwise multiple logistic regression analysis. The variables were entered based on the correlation of variables and the regression coefficients when analyzed independently. The resulting model was considered to be the best predictive model given the data that was analyzed. Specifically, equations could be used to predict the susceptibility of individual trees given the proper tree, stand, and beetle pressure conditions.

III.3 – Results

All tree and stand variables were analyzed for correlations with each other (Table 2). Any highly correlated variables were not used in multiple logistic regression analyses performed later in the study. Age and vigor classes were highly correlated with each other. Plot average dbh was also highly correlated with plot maximum dbh and site average dbh.

To compare the relative influence of each variable on the probability of beetle-caused mortality of individual trees, each of the variables was standardized and was then analyzed independently with logistic regression. The variables with the higher absolute values for the regression coefficients were then used to rank the relative importance of each variable. Not including beetle pressure variables, tree-related variables had the highest relative influence on the probability of beetle-caused mortality (Table 3). Of the tree variables, the Keen age class had the strongest influence followed by the Keen vigor class and dbh.

Table 2: A correlation matrix of all tree and stand variables. PP = ponderosa pines, * denotes variables with correlations greater than 0.6

	Dbh	Age (Keen)	Vigor (Keen)	Plot avg dbh	Plot max dbh	Plot PP basal area	Site avg dbh	Site max dbh	Site PP basal area
Dbh	1	0.2889	-0.231	0.5863	0.3137	0.1413	0.4466	0.1857	0.0053
Age (Keen)	0.2889	1	*0.6584	0.1015	0.0312	-0.0391	0.0291	0.0487	-0.1516
Vigor (Keen)	-0.231	*0.6584	1	-0.1787	-0.1088	-0.0316	-0.1809	-0.0445	-0.0969
Plot avg dbh	0.5863	0.1015	-0.1787	1	*0.6165	0.3089	*0.6385	0.2531	0.0226
Plot max dbh	0.3137	0.0312	-0.1088	*0.6165	1	0.4236	0.3723	0.3825	0.1877
Plot PP basal area	0.1413	-0.0391	-0.0316	0.3089	0.4236	1	0.0656	0.0608	0.5597
Site avg dbh	0.4466	0.0291	-0.1809	*0.6385	0.3723	0.0656	1	0.3984	0.012
Site max dbh	0.1857	0.0487	-0.0445	0.2531	0.3825	0.0608	0.3984	1	0.1106
Site PP basal area	0.0053	-0.1516	-0.0969	0.0226	0.1877	0.5597	0.012	0.1106	1

Table 3: The logistic regression coefficients and associated statistics for the standardized tree and stand variable measurements when analyzed independently. The absolute values of the regression coefficients provide information about the relative influence of each variable on the probability of bark beetle caused mortality of individual trees. B is the regression coefficient, S.E. is the standard error, Sig. is the significance of each variable in the independent model

	Standardized Variables (Z-score)	B	S.E.	Sig.	95% C.I. for EXP(B)	
					Lower	Upper
Tree Variables	Dbh	.366	.028	.000	1.367	1.522
	Age class	.642	.031	.000	1.787	2.020
	Vigor class	.388	.038	.000	1.369	1.587
Plot Variables	Plot avg dbh	.248	.028	.000	1.213	1.353
	Plot max dbh	.076	.031	.013	1.016	1.146
	Plot pp basal area	.212	.031	.000	1.162	1.314
Site Variables	Site avg dbh	.160	.032	.000	1.102	1.249
	Site max dbh	.197	.031	.000	1.145	1.295
	Site pp basal area	-.174	.035	.000	.785	.900

Table 4: The logistic regression coefficients and associated statistics for the standardized beetle pressure variable measurements when analyzed independently. The absolute values of the regression coefficients provide information about the relative influence of each variable on the probability of bark beetle caused mortality.

	Standardized Variables (Z-score)	B	S.E.	Sig.	95% C.I. for EXP(B)	
					Lower	Upper
Plot-level	Basal area killed at the plot-level (year – 1)	.182	.008	.000	1.180	1.220
	Beetle killed trees at the plot-level (year – 1)	.198	.007	.000	1.202	1.236
Site-level	Basal area killed at the site-level (year – 1)	.348	.009	.000	1.391	1.441
	Beetle killed trees at the site-level (year – 1)	.319	.008	.000	1.354	1.398
Regional-level	Basal area killed regionally (year – 1)	.696	.023	.000	1.915	2.100
	Beetle killed trees regionally (year – 1)	.652	.021	.000	1.842	2.001
Global-level	Basal area killed globally (year – 1)	.811	.028	.000	2.130	2.377
	Beetle killed trees globally (year – 1)	.824	.030	.000	2.152	2.416

After tree-level variables, plot-level measurements had a higher relative influence than site-level measurements. Plot average dbh had the highest relative importance followed by plot ponderosa pine basal area and plot maximum dbh. Site-level measurements had the lowest relative importance with site maximum dbh have the highest site-level importance followed by site ponderosa pine basal area and site average dbh.

Beetle pressure variables were also standardized and entered independently with logistic regression analyses. Basal area killed per acre and the number of beetle killed trees per acre the previous year were used at the plot, site, regional, and “global” scale. The regression coefficients showed that the “global” scale beetle pressure variables had the highest influence on the probability of bark beetle-caused mortality of individual trees followed by the regional, site and plot-level scales (Table 4). At the “global” scale and plot-level, beetle killed trees per acre the previous year was more important than basal area killed per acre the previous year. The opposite was true at the regional and site-level although across all scales, the differences between the coefficients for the two variables were relatively small. The results of these analyses imply that the susceptibility of trees to bark beetle-caused mortality is dependent on the population size across relatively broad spatial extents. Specifically, the data implies that when population densities are high throughout study sites in the southwest, the probability of host mortality the following year tends to be higher as well. Beetle pressure was significant at the plot and site-level as well ($P < 0.001$) although the influence tree mortality at these levels tended to be lower than the influence at the “global” and regional levels.

After assessing the correlations between tree, stand, and beetle pressure variables and analyzing the relative importance of each variable by analyzing them independently using

logistic regression, variables were selected to be entered into a stepwise multiple logistic regression analyses. Variables were entered in the order of their relative importance. Of the highly correlated variables, only the variable with the highest relative importance was included in the model. Also, only the beetle pressure variable with the highest relative importance was used. The variables were entered in the following order: Beetle killed trees per acre at the global level the previous year, Keen age class, dbh, plot average dbh, plot ponderosa pine basal area, site maximum dbh, site ponderosa pine basal area.

Table 5: The stepwise multiple logistic regression analysis output for the best predictive model. The regression coefficients for “global” beetle pressure, tree, and stand variables could be used to predict the probability of beetle caused mortality for individual trees. PP stands for ponderosa pine

Variables (Raw Data)	B	S.E.	Sig.	95% C.I. for EXP(B)	
				Lower	Upper
Beetle killed trees globally (year – 1)	.669	.023	.000	1.866	2.044
Age class	.504	.054	.000	1.489	1.841
Dbh	.033	.006	.000	1.022	1.046
Plot PP basal area	.004	.001	.000	1.003	1.005
Site max dbh	.034	.005	.000	1.025	1.045
Site PP basal area	-.008	.001	.000	.989	.994
Constant	-7.864	.183	.000		

Using stepwise logistic regression, all the variables entered were significant ($P < .001$, Nagelkerke R square = .115) except for plot average dbh (Table 5). All of the variables had a positive relationship with the probability of beetle caused tree mortality except for the site ponderosa pine basal area per acre measurement. To calculate the probability of a tree being killed by bark beetles within one year, the following equations were used:

$$\text{Logit} = -7.864 + (.669 \times \text{BP}) + (.504 \times \text{Keen age}) + (.033 \times \text{Dbh}) +$$

$$(.004 \times \text{plot PP BA}) + (.034 \times \text{site max dbh}) + (-.008 \times \text{site PP BA})$$

$$\text{Logit}^{-1} = \frac{\exp(\text{Logit})}{\exp(\text{Logit}) + 1}$$

where BP is the beetle pressure variable (beetle killed trees the previous year across all sites), Age is the Keen class, PP is ponderosa pine, and BA is basal area per acre.

III.4 – Discussion

To develop a tree-level risk assessment model, I used over twenty years of bark beetle data in southwestern ponderosa pine forests. Before performing any regression analyses, I first examined correlations between tree and stand variables (Table 2). The Keen age and vigor classes were highly correlated with each other. This suggests that younger trees tended to have high vigor and older trees were more frequently less vigorous. Plot average dbh was also highly correlated with plot maximum dbh and site average dbh. It makes sense that as the plot average dbh increases, the plot maximum dbh and site average dbh would also tend to increase.

Tree, stand, and beetle pressure variables were standardized using a z-score and analyzed independently. The regression coefficient values obtained from logistic regression analyses determined the order of variables to be entered in multiple logistic regression analyses. Tree variables had a stronger influence on bark beetle caused tree mortality than stand variables (Table 3). All tree variables had a positive relationship with the probability of mortality. Keen age and vigor had a stronger influence than dbh. Vigor has been associated

with tree susceptibility (Gara and Vité 1962, Larsson et al. 1983) as well as dbh and age (Stevens et al. 1980).

Plot-level stand variables tended to have a stronger influence on bark beetle caused mortality of individual trees than site-level stand variables (Table 3). Plot average dbh and plot ponderosa pine basal area both had relatively strong positive influences on mortality. Since the dbh of individual trees has a positive influence on mortality, it is not surprising that the average dbh and maximum dbh of a stand also has a positive influence. Higher basal areas have been shown to influence the susceptibility of trees to bark beetles (Chojnacky et al. 2000). At the site-level, basal area had a negative influence on the susceptibility of individual trees while the relationship was positive at the plot-level. This could mean that large trees in areas of high local densities at the 0.1 acre scale are susceptible in areas where there is a lower density of trees over a scale of two acres.

The beetle pressure variables were all standardized and analyzed independently to estimate their relative influence on tree mortality. All beetle pressure variables were also significant ($P < .001$) and had positive relationships with the probability of tree mortality (Table 4). Beetle pressure had the highest relative influence at the “global” level, followed by the regional level, site-level, and plot-level. Despite the fact that beetle pressure was significant across all spatial scales, the data suggests that beetles pressure has the strongest influence at larger spatial extents. This could also be interpreted to mean that beetles can disperse over long distances to select hosts, which has been previously described (Safranyik 2003, Gara and Vité 1962). To determine if this is actually the case, further research would be needed.

Variables were then entered into a multiple logistic regression analysis to develop the best statistical model for predicting the probability that individual trees would be killed by bark beetles in a year based on tree, stand, and beetle pressure variables. Instead of using the standardized variables, the raw data was used to develop the model. A single beetle pressure variable was used in the model and no highly correlated variables were entered into the model together. The order that variables were entered in depended on the regression coefficients when the variables were analyzed independently. The variables were therefore entered as follows: the “global” number of beetle killed trees the previous year, the Keen age class, tree dbh, plot average dbh, plot ponderosa pine basal area, site max dbh, and site ponderosa pine basal area. All variables were significant ($P < .001$) together except for plot average dbh which was removed from the model (Table 5).

According to the analyses of 21 years of field data, this model best predicts the probability of beetle caused mortality of individual trees per year based on the tree, stand, and beetle pressure variables. On the other hand, the model is not easy to apply to large numbers of trees across large spatial extents because obtaining realistic measurements of many of those variables is not feasible. It would either require field measurements of each individual tree or significant improvements in remote sensing technologies. In the next section, I used GIS, remote sensing, and ground truth data to simulate a realistic forest landscape to the level of the individual trees and then developed a framework for applying a tree-level risk assessment to the trees with the landscape.

IV FRAMEWORK FOR DISPLAYING TREE-LEVEL RISK ASSESSMENTS

IV.1 – Introduction

Forests are often mapped to aggregate stands of various characteristics such as vegetation types, age, or density. This is useful for forest managers and scientists who primarily work or analyze forest landscapes at the stand level. Remotely sensed imagery is a primary tool for mapping forest stands. The US Geological Survey, for example, provides land cover data through the National Land Cover Database (NLCD) and from the Gap Analysis Program (GAP) both of which use aerial imagery and other GIS layers to create land cover maps and distinguish between different types of forests. Remotely sensed imagery can provide details about forest stands through a number of contextual analyses. For example, computer measures of texture can be used to separate classes of stands nearly as well as the human eye (Kim et al. 2009). Crabb et al. (2012) used a number of different spatial data resources to develop a 30 meter resolution pine density raster dataset to model MPB populations. Stand data is useful for studying outbreaks because it is believed that beetles act at a scale beyond the level of the individual tree (Bone et al. 2013b).

While remotely sensed detection of forest damage from outbreak populations is possible using relatively low spatial and spectral resolution imagery, damage from endemic bark beetle populations requires high spatial and spectral resolution imagery due to attacks on scattered individual trees (Wulder & Dymond 2003). Studies have shown that the population density of bark beetles has influences on host selection behavior and the spatial patterns of attacks (Nam et al. 2013, Wallin and Raffa 2004). Bentz et al. (1993) stress the importance of individual tree health and vigor for endemic populations as opposed to stand conditions which have a strong influence on outbreak populations. I was interested in

mapping individual trees in the landscape and, like the methods for detecting tree damage from endemic populations, my methods still required high resolution imagery. I did not, however, require high spectral resolution but did benefit from 4 band imagery including a near-infrared band.

Individual trees are rarely mapped in the forest for scientific studies with large spatial extents probably as a result of historical software limitations. Information about individual trees in the forest can be useful for land managers, forest scientists, and wildlife biologists. Despite useful applications for the spatial configuration and conditions of trees in the forest, there are a number of associated difficulties with mapping these landscapes. Manually collecting the coordinates and conditions of trees in a landscape is time consuming and not feasible when examining an area with a large spatial extent. Boyden et al. (2005) studied the spatio-temporal pattern of old-growth trees in a 9.2 ha study area requiring the coordinates and dbh of all trees to be measured. Remote sensing can provide information about the locations of individual trees although the most common methods are often quite expensive. These methods include the use of high resolution imagery, object-oriented classification software, and LiDAR data. Other difficulties with mapping trees in the forest include size limits with data sets when examining a large area and the maintenance of temporally accurate data of the conditions of the trees.

Minor (1960) developed methods for estimating the dbh of Arizona ponderosa pine trees using crown and height measurements derived from aerial imagery. LiDAR and aerial photography have also been used to determine the locations and characteristics of individual trees conditions (Pollock 1996, Suárez et al. 2005, Korpela et al. 2007). Bright et al. (2012)

used LiDAR and multispectral imagery to estimate the reduction of carbon stocks in mountain pine beetle damaged forests.

Logan et al. (1998) developed a model which showed that environmental determinism, or the spatial pattern of susceptible hosts directly influenced how endemic bark beetle populations would be distributed throughout the landscape. Epidemic populations can attack healthy trees while endemic bark beetle populations are believed to select weakened trees since low vigor trees can often be successfully attacked by these smaller populations (Alcock 1982).

Risk and susceptibility maps are commonly made to assess areas where trees may be vulnerable to bark beetle attacks, particularly to outbreak populations of beetles. These are often done using forest susceptibility data from outbreaks that have previously occurred. In some instances, susceptibility data can be misleading because attacked trees are likely the result of being near a location with high beetle pressure. Host trees in locations with high beetle pressure are likely vulnerable to attack not strictly because of the tree or stand conditions but because the presence of beetles is high enough to mass attack them. Many studies are able to correct for this by sampling other areas of the forest not affected by bark beetles for tree and stand conditions as well as beetle pressure.

A number of recent studies have incorporated GIS to perform risk rating systems for bark beetles. Bentz et al. (1993) concluded that the inclusion of the spatial distributions of beetle populations into risk models will lead to more accurate results. Shore and Safranyik (1992) have found utility in a risk model that included beetle pressure which was further validated in a study mapping risk of lodgepole pine stands in British Columbia (Shore et al. 2000). The same model was updated by Shore et al. (2006) to look at “pine” factors instead

of including non-host factors into the model. In a study in British Columbia, Dymond et al. (2006) mapped stand susceptibility using a modified risk model from Shore and Safranyik (1992) which showed attacks were common in areas of high and low susceptibility which is likely the result of high beetle populations even where susceptibility was low. Hicke and Jenkins (2008) used the Shore et al. (2006) model to look at lodgepole pine stand structure to display county-level susceptibility to outbreak populations in the western US. One study used aerially detected areas of forest damage from bark beetles to develop a risk mapping technique based on beetle pressure (Bone et al. 2013a). When mapping the MPB outbreak within Canada, aspect and elevation played roles in the susceptibility of forest stands (de la Giroday 2011). Aukema et al. (2008) developed a spatial model for estimating outbreak activity by primarily incorporating spatial beetle pressure data and climate data which was relatively successful.

The goal of this section was to develop a simulated ponderosa pine landscape using aerial imagery, GIS, and ground truth data. From my previous analyses, there was evidence that the condition and spatial distribution of individual trees are important for pine beetle populations. While outbreak populations might be more influenced by stand conditions because of their capability to mass attack high numbers of trees, the conditions of individual trees are likely more important for endemic populations because the smaller number of beetles are limited to attacking trees based on certain characteristics that make those trees susceptible. Although risk and susceptibility have been mapped for bark beetles using a number of different methods, my framework for mapping susceptibility is unique in the large spatial extent of the landscape, the susceptibility to both epidemic and endemic populations,

and the inclusion data regarding the spatial configuration and conditions of individual hosts in the landscape.

To simulate trees in the landscape, I used aerial imagery, vegetation layers, and ground truth data to gather information about the density of ponderosa pines and estimate their diameters. As seen from previous analyses, beetle pressure, dbh, and other related stand variables have an influence on host susceptibility to attacks by bark beetles. In this section, I developed a framework for analyzing susceptibility of trees in the forest using a simulated forest landscape. Because of the influence of individual tree characteristics on host selection for endemic populations, I focused on modeling the susceptibility for each individual tree. Using the same data and methods as the previous section, a new model was developed based on the applicability to the simulated landscape. I selected values to use within the models to describe the probabilities of beetle-caused mortality in epidemic and endemic years and applied them to the simulated forest landscape.

IV.2 – Methods

IV.2.1 – Study area

Comprising of nearly two million acres, the Dixie National Forest is the largest national forest in Utah (Figure 8). The national forest is located in south-central Utah within the Colorado Plateau. The range in elevation within the NF goes from approximately 2,800 to 11,322 feet above sea level which allows for dramatic temperature differences. The geology of the NF can vary from reddish sandstones to areas of dark basaltic rock lava fields. Lower, drier elevations support juniper and pinyon forests, while higher elevations provide suitable conditions for ponderosa pines, aspen, and other conifers. Rainfall tends to be low throughout

the year with a peak during the later months of the summer. The Dixie NF has a number of hiking trails, established campsites, as well as dispersed camping opportunities, four wilderness areas, and encompasses segments of the Scenic Byway 12. Nearby are a number of national parks and national monuments including Bryce Canyon NP, Zion NP, Cedar Breaks National Monument and the Grand Staircase-Escalante National Monument. Because of the nearby tourist destinations, many people travel through the Dixie NF. Since there are a number of tree species in the Dixie NF susceptible to pests and disease, losses of these trees can result in a lower aesthetic value and economic costs from a decrease in tourism. Potentially, widespread epidemics could affect valuable stands of ponderosa pines. There are also associated costs with the management of dead trees that are dangerously close to roads, hiking trails, campgrounds, or other structures.

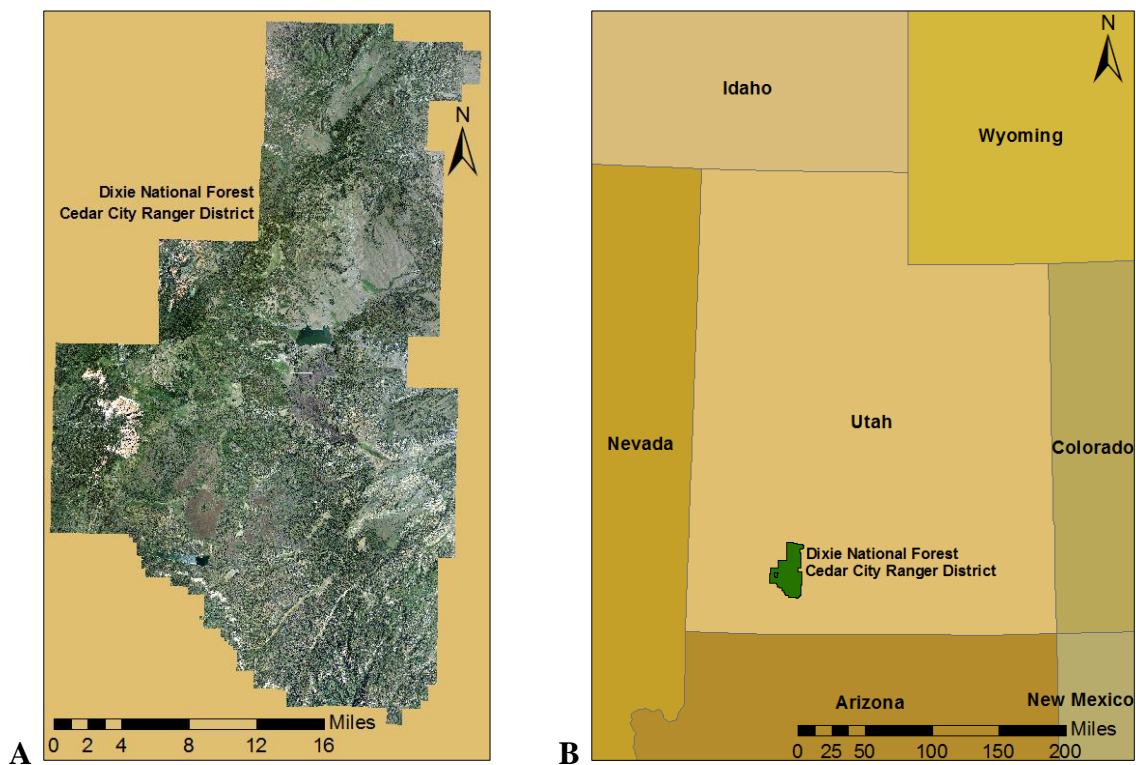


Figure 8: The study area for simulating a ponderosa pine forest. (A) Aerial imagery of the Cedar City Ranger District of the Dixie National Forest which is located in (B) southwest Utah.

IV.2.2 – Image processing

One meter resolution aerial imagery from 2010 was downloaded from the US Geological Survey (USGS) National Map Viewer (<http://viewer.nationalmap.gov/viewer/>). All of the aerial imagery that was downloaded for this study was part of the National Agriculture Imagery Program (NAIP). NAIP is part of the USDA Farm Service Agency and publicly provides up to date, 4-band, orthorectified aerial imagery. Using ArcMap 10.1, each downloaded tile, comprised of approximately 6300 acres, was mosaicked together and then clipped to the boundary of the Cedar City RD within the Dixie NF. Red and near-infrared bands were used to make a normalized difference vegetation index (NDVI) using the following equation:

$$NDVI = \frac{(NIR - RED)}{(NIR + RED)}$$

where NIR is the near-infrared band and RED is the red band. The NDVI layer provides a range of values from -1 to 1 (Figure 9). Green, healthy vegetation absorbs radiation in the red wavelengths but reflects near-infrared wavelengths. Therefore, when viewing the NDVI layer, locations in the imagery that show actively photosynthesizing plants result in higher values. Within the study area, the high values typically represented trees in the landscape but also included some shrubs and herbaceous vegetation in areas of high moisture, such as low-lying basins. Other herbaceous vegetation showed lower reflectance which is likely a result of the lower photosynthetic rates of grasses and forbs in the arid climate at the time the imagery was taken. For this study, I decided to create a NDVI-VEG layer by giving the NDVI a threshold of approximately 0.175 where any value above that was considered a tree or some other actively photosynthetic plant while anything below that was ignored since there was no chance of it being any kind of susceptible pine.

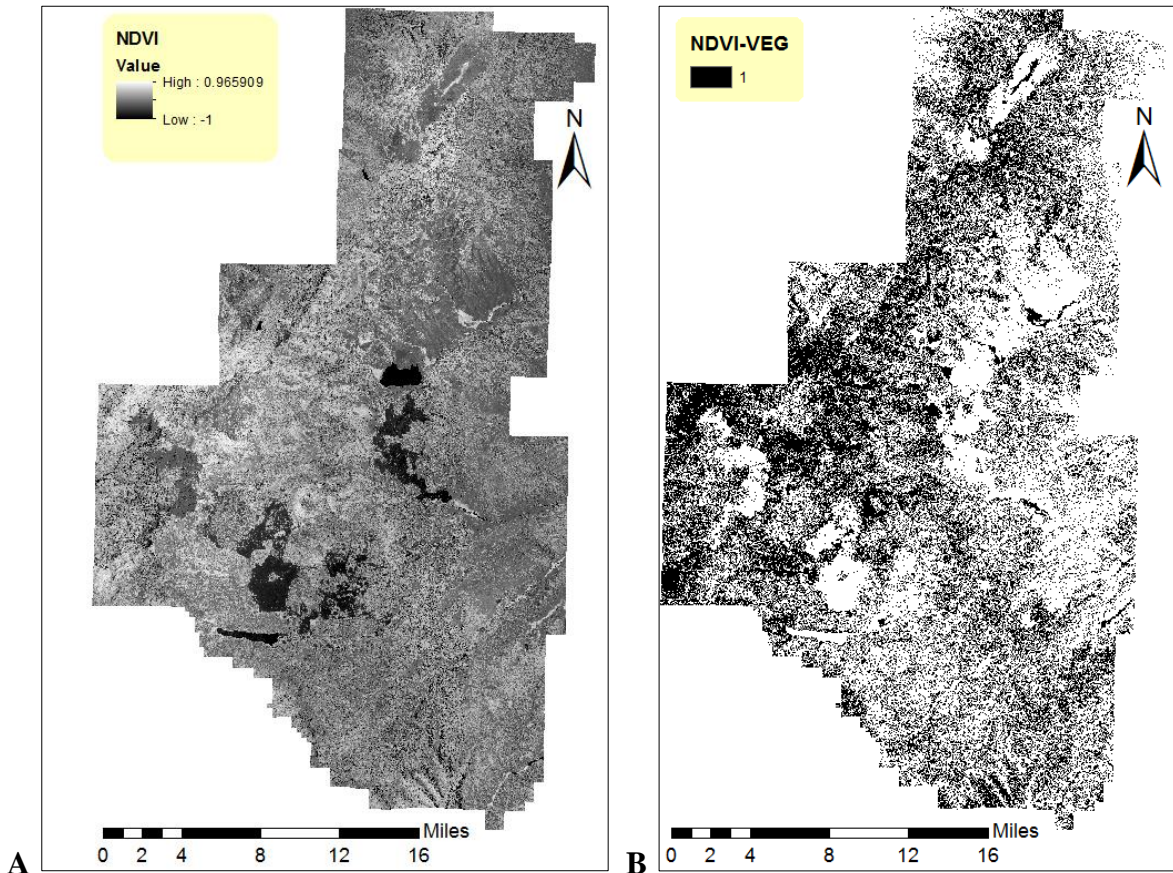


Figure 9: (A) A Normalized Difference Vegetation Index (NDVI) developed for the study. The NDVI highlights green, healthy vegetation. (B) A threshold of 0.175 was applied to the NDVI show areas with higher values as trees or other photosynthesizing vegetation.

IV.2.3 – Tree modeling

To model trees in the landscape, I used the NDVI-VEG threshold layer along with spatial land cover data and ground truth data. Figure 10 shows the data and analytical processes that were used to spatially generate ponderosa pines and associate diameters to each tree. The US Geological Survey provides land cover data through the National Land Cover Database (NLCD) and from the Gap Analysis Program (GAP). The NLCD has general land cover descriptions that include “evergreen forest”, “shrub/scrub”, and

“grassland/herbaceous” while land cover data from GAP has specific vegetation types such as “Rocky Mountain ponderosa pine woodland”, “inter-mountain basins montane sagebrush steppe”, and “Rocky Mountain subalpine mesic meadow”. Both land cover layers are 30 meter resolution but given the higher level of detail to vegetation types, the GAP land cover data was used for this study (Figure 11). GAP land cover data for the different regions of the US is made public and was downloaded from the website:

<http://gapanalysis.usgs.gov/gaplandcover/data/download/>. The ESRI grid format was downloaded and added to an ArcMap project so that it could be clipped to the boundary of the Cedar City RD.

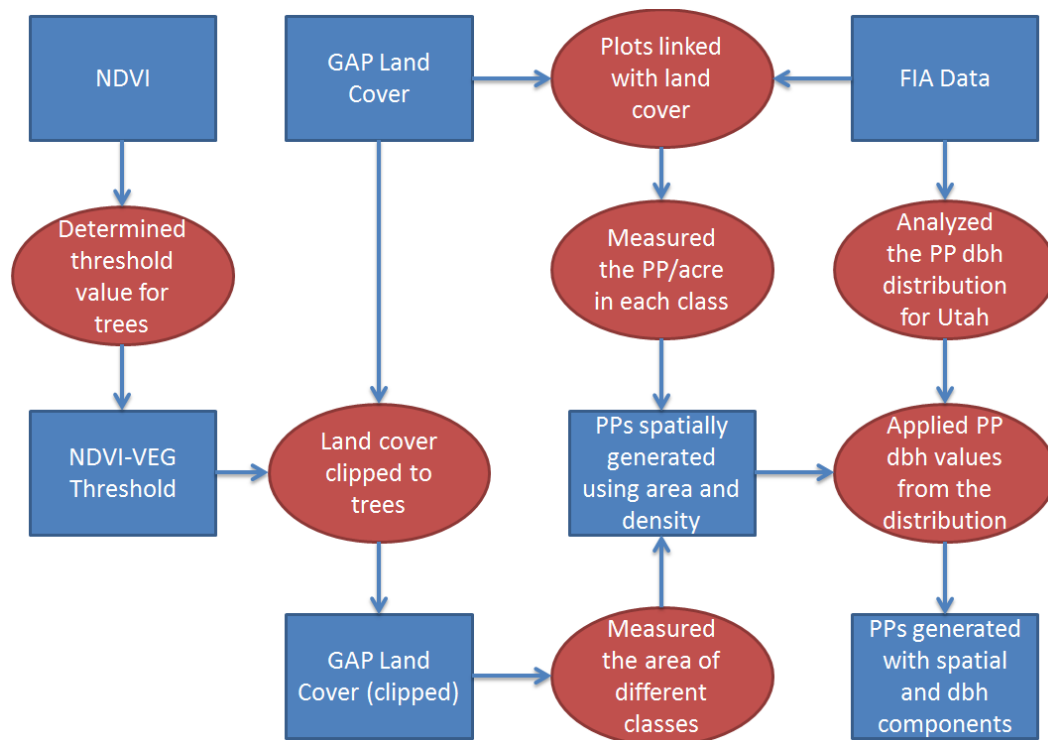


Figure 10: The ponderosa pine simulation flowchart. Ponderosa pine (PPs) densities were dependent on land cover type and diameter at breast height (dbh) was randomly generated based on the distribution as measured in FIA plots in Utah.

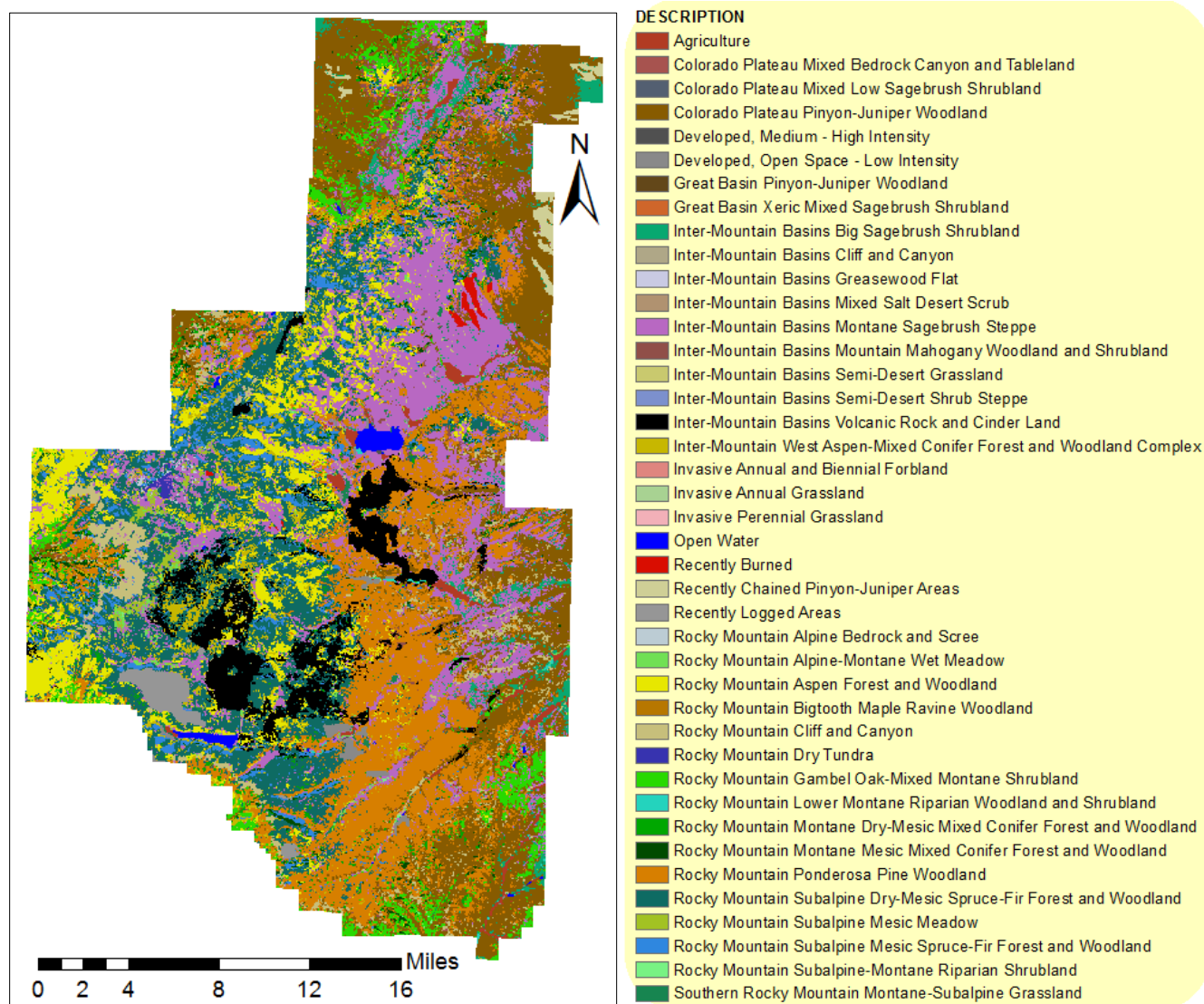


Figure 11: The GAP land cover data for the study area. This was downloaded from the US Geological Survey. Land cover types are shown in the legend as developed by Lowry et al. (2007).

The US Forest Service (USFS) established the Forest Inventory and Analysis (FIA) program which provides stand conditions for plots across the US (<http://www.fia.fs.fed.us/>) although the public plot coordinates are “fuzzed” up to a mile from their actual locations. Because of the tree-level scale used in this study, a much higher accuracy for ground truth data was needed. I was able to obtain the actual coordinates for plots within the Cedar City RD from the US Forest Service since I agreed to keep the actual plot locations private. Within the study area there was data for 55 FIA plots. All plots contained four subplots which each had a twenty-four foot radius. Within each subplot, trees with a radius of five inches or more were measured. Each subplot also contained a 6.8 foot radius microplot where trees with a radius smaller than five inches in diameter were measured.

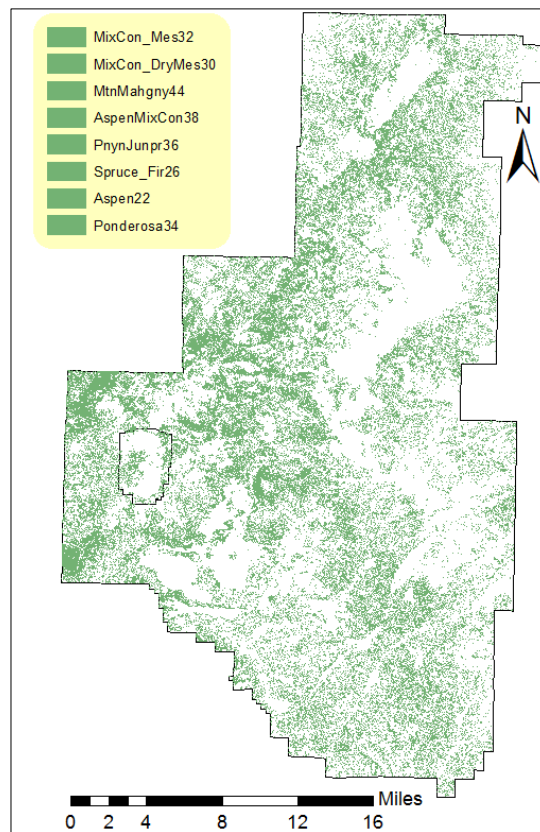


Figure 12: The GAP land cover classes clipped to the NDVI-VEG raster. Only the land cover classes that had some density of ponderosa pine were used.

The FIA data was used in combination with the GAP land cover data to gather estimates for the number of ponderosa pines per acre in each land cover type. To do this, the FIA subplots within the study area were placed in ArcMap using the actual coordinates for each plot which were provided by the US Forest Service. The GAP vegetation type that filled the majority of each subplot was linked to each subplot so that they could be queried based on the vegetation type. A table with a row for each FIA subplot and the associated GAP vegetation layer was extracted and queried using Microsoft Access. Each GAP vegetation class was then assigned the average number of ponderosa pines per acre based on the FIA data.

The next process involved developing the spatial distribution of pines throughout the landscape using the density of ponderosa pines associated with each GAP vegetation class. The vegetation classes that had some measured density of ponderosa pines were made into their own layers while other vegetation types were assumed to not contain any ponderosa pines and were therefore ignored. The vegetation types that did have a density of ponderosa pines were clipped to the 1 meter resolution NDVI-VEG layer that was based on the higher NDVI values where I assumed trees were (Figure 12). This excluded the majority of the locations where herbaceous vegetation had a higher reflectance than 0.175 since areas where those herbaceous plants had high reflectance were typically not found within the GAP vegetation classes that contained ponderosa pines. The vegetation types clipped to the NDVI-VEG grid were then converted to polygon shapefiles and the polygons within each vegetation type were dissolved into single polygons for each vegetation class. An area field was added that measured the number of acres in each vegetation layer while a field for the number of ponderosa pines was also added and was calculated based on the number of acres of the

vegetation layer and the associated average number of ponderosa pines per acre in that GAP vegetation class. Random points could then be generated within each vegetation class that was clipped to the NDVI-VEG grid (Figure 13). The number of points generated was determined by the value from the ponderosa pine field. To prevent points from being too close to each other, the points were prohibited from being closer than 1 meter from one another by specifying with the ArcMap tool.

Each coordinate representing the location of a tree was exported from ArcMap so that a dbh value could be attributed to each point. Using the FIA data, the distribution of diameters for 2049 ponderosa pines throughout Utah was analyzed. To assign dbh values from the distribution to each individual point, the frequency and probability of a tree being within one inch diameter size classes was determined. A VBA script was written for Microsoft Access that ran an acceptance-rejection algorithm to randomly generate diameters using probabilities based on the FIA distribution of ponderosa pine diameters in Utah (Figure 14). The acceptance-rejection algorithm is commonly used to generate random numbers from a probability distribution. The algorithm proceeds by selecting random numbers for the ponderosa pine diameters followed by random numbers for the probability of trees existing with those diameters based on the frequency distribution. Each time a probability was not accepted, a new diameter and probability for the associated tree was selected until the probability was accepted for each diameter. The distribution of the output was analyzed in comparison to the ideal distribution to assess the accuracy of the applied diameters. The updated point table with dbh values was imported back into ArcGIS so that the trees could be displayed in the landscape.

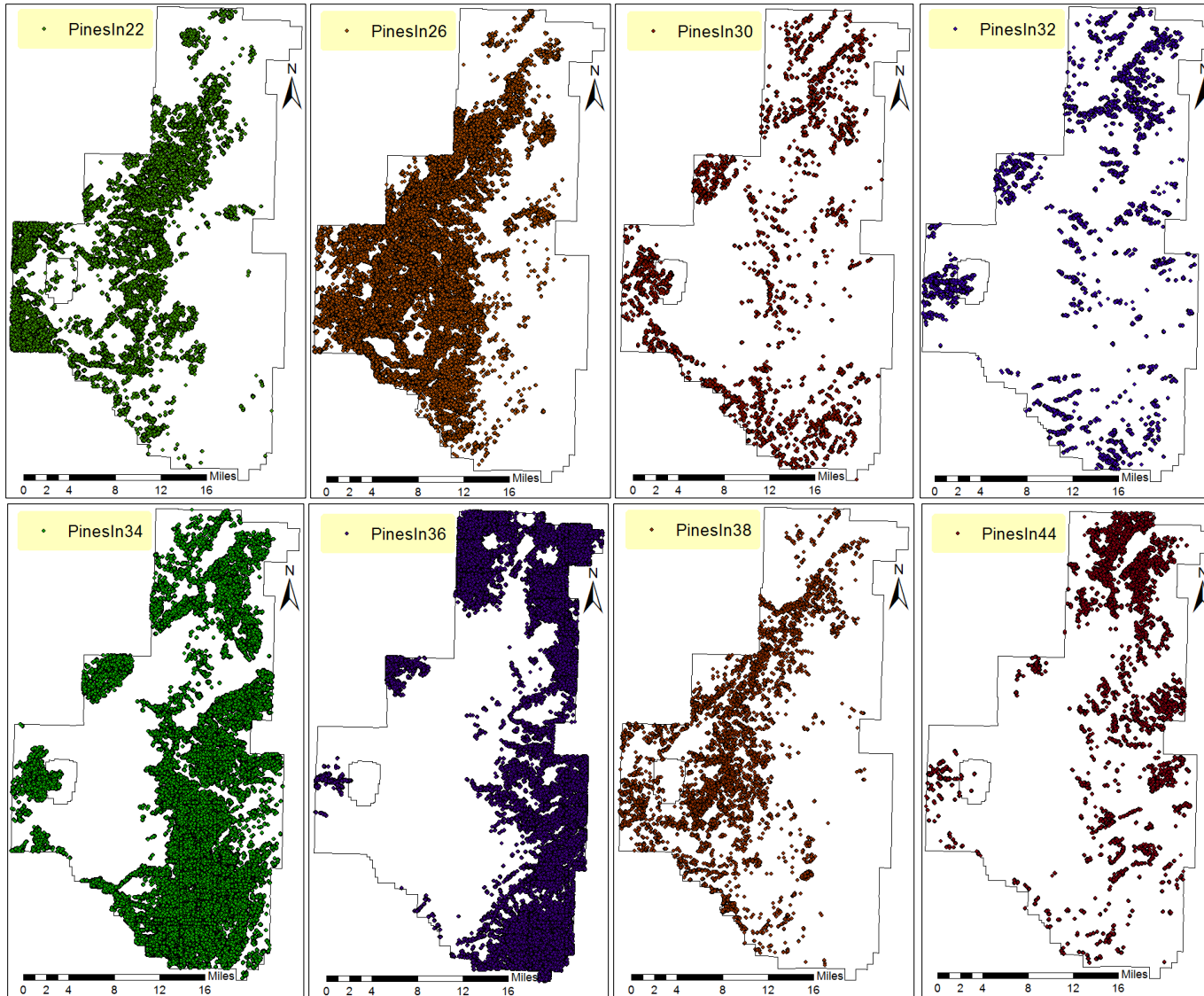


Figure 13: Ponderosa pines randomly generated for the different vegetation classes. Tree densities were dependent on the area of each class after being clipped to the NDVI-VEG raster. See Table 4 for the class code descriptions.

```
Database39 - Module1 (Code)
(General) GenerateRandomNumber
Option Compare Database

Function GenerateRandomNumber(seed As Long) As Double

    Dim accept As Boolean
    accept = False
    Dim dbhval As Double
    Dim prob As Double
    Dim dbhprobs(1 To 41) As Double
    dbhprobs(1) = 0.001464
    dbhprobs(2) = 0.012201
    dbhprobs(3) = 0.016593
    dbhprobs(4) = 0.014641
    dbhprobs(5) = 0.01757
    dbhprobs(6) = 0.061005
    dbhprobs(7) = 0.058565
    dbhprobs(8) = 0.053197
    dbhprobs(9) = 0.048316
    dbhprobs(10) = 0.04734
    dbhprobs(11) = 0.047828
    dbhprobs(12) = 0.04978
    dbhprobs(13) = 0.050756
    dbhprobs(14) = 0.043924
    dbhprobs(15) = 0.054173
    dbhprobs(16) = 0.04246
    dbhprobs(17) = 0.04978
    dbhprobs(18) = 0.037579
    dbhprobs(19) = 0.035627
    dbhprobs(20) = 0.034651
    dbhprobs(21) = 0.031235
    dbhprobs(22) = 0.02733
    dbhprobs(23) = 0.020498
    dbhprobs(24) = 0.015129
    dbhprobs(25) = 0.021474
    dbhprobs(26) = 0.015617
    dbhprobs(27) = 0.013665
    dbhprobs(28) = 0.015129
    dbhprobs(29) = 0.011713
    dbhprobs(30) = 0.012689
    dbhprobs(31) = 0.006833
    dbhprobs(32) = 0.006345
    dbhprobs(33) = 0.006345
    dbhprobs(34) = 0.002928
    dbhprobs(35) = 0.003904
    dbhprobs(36) = 0.001952
    dbhprobs(37) = 0.001464
    dbhprobs(38) = 0.002928
    dbhprobs(39) = 0.000488
    dbhprobs(40) = 0.001952
    dbhprobs(41) = 0.002928

    Do While accept = False

        dbhval = Int((41 - 1 + 1) * Rnd() + 1)
        targetprob = dbhprobs(dbhval)

        prob = Rnd()
        If prob < targetprob Then
            accept = True
        End If

    Loop
    GenerateRandomNumber = dbhval - Rnd()
End Function
```

Figure 14: VBA script of the acceptance-rejection model in Microsoft Access. The distribution of diameters of ponderosa pine was measured from FIA data in Utah.

IV.2.4 – Landscape model development

In tree inventories, some of the most useful and easily measureable information includes the tree species, locations, and dbh values. With recent advances in GIS, remote sensing, and LiDAR technologies, obtaining information about individual trees in the landscape will likely be easily attainable information in the future. With these technologies, forest scientists and managers will likely still be interested in determining the tree species, locations, and size estimates.

In the simulated landscape, estimates of the locations and dbh of ponderosa pines were developed. Tree, stand, and beetle pressure variables associated with the dbh and configuration of trees were used to model susceptibility for individual host trees within the landscape. At the tree-level, dbh was the only variable that could be used in susceptibility models for the simulated landscape. Variables that could be used at plot and site-level, include the average dbh, maximum dbh, and basal area per acre. As done in the previous section, I wanted to select a single beetle pressure variable to be used in the model. To use the model, however, a value for the beetle pressure measurement would be required when before being applied in the landscape. Correlations between variables were also examined to exclude highly correlated variables from being in the same model.

Considering the application of the model to an entire landscape, the plot and site average dbh and maximum dbh measurements would cause issues in areas of low densities. For example, isolated trees with a 2 acre area would have the same value for plot average dbh, plot maximum dbh, site average dbh, and site maximum dbh. On the other hand, basal area per acre measurements can provide more detail about the local density and sizes of trees. The variables chosen to be included in the model were the “global” number of trees killed per

acre within the previous year, tree dbh, plot ponderosa pine basal area per acre, and site ponderosa pine basal area per acre. These variables would be entered in the respective order into a stepwise multiple logistic regression analysis with the same data and methods used in the previous section.

After entering the variables into a stepwise logistic regression analysis, the following equation was developed:

$$\text{Logit} = -6.55 + (1.12 \times \text{BP}) + (.053 \times \text{dbh}) + (.005 \times \text{plot PPBA}) + (-0.1 \times \text{site PPBA})$$

Where BP is the beetle pressure variable (“global” number of beetle killed trees from the previous year), dbh is the diameter at breast height, PPBA is ponderosa pine basal area.

Before the model could be applied to the trees in the landscape, values needed to be entered into the model to represent beetle pressure. I decided to select values that would represent endemic and epidemic populations. Because the beetle pressure variable included in the model was the “global” number of trees killed per acre within the previous year, all of the values were examined. The threshold recently used in literature for epidemic sites was more than 2 trees per hectare (Carroll et al. 2006). I used the same threshold for my data so that any years with more than 0.809 trees per acre were considered epidemic years and any years below the threshold were considered endemic years. I then averaged the beetle pressure values for the epidemic and endemic years to use for the “global” number of trees killed per acre within the previous year when applying the models to the landscape.

IV.2.5 – Susceptibility mapping

To apply the susceptibility models that were developed, the variables from the models had to be attributed to each tree in the landscape. I used each of the simulated ponderosa

pinos as focal points for plot and site-level measurements. In ArcGIS, circular buffers of 0.1 acres and 2 acres were created around each tree. Variables, such as plot maximum dbh, plot ponderosa pine basal area, and site average dbh, could then be measured using those buffers. The local measurements of the model variables could then be added as attributes to each tree.

The tree data was exported from ArcGIS and imported into Access where the models were applied to the individual trees using the following equations:

$$\text{Logit}(\text{epidemic}) = -6.55 + (1.85) + (.053 \times \text{dbh}) + (.005 \times \text{plot PPBA}) + (-0.1 \times \text{site PPBA})$$

$$\text{Logit}(\text{endemic}) = -6.55 + (.15) + (.053 \times \text{dbh}) + (.005 \times \text{plot PPBA}) + (-0.1 \times \text{site PPBA})$$

All models were to be mapped with the inverse logit using the following equation so that I could display the annual probability of beetle attacks or beetle-caused mortality during endemic or epidemic conditions:

$$\text{Logit}^{-1} = \frac{\exp(\text{Logit})}{\exp(\text{Logit}) + 1}$$

The point data with the probabilities of beetle-caused mortality could then be imported back into ArcGIS so that the models could be displayed within the landscape. A two acre cell size was used to map the mean and maximum probability of attack or beetle-caused mortality for the ponderosa pines in the landscape. The maps were then visually compared to make inferences about how different population phases of bark beetles influence beetle-caused mortality in ponderosa pine forests. A random sample of the simulated ponderosa pine population was sampled to examine the relationship between host susceptibility to beetle caused mortality and the density of ponderosa pines.

IV.3 – Results

IV.3.1 – Tree modeling

Table 4 shows the vegetation types that contained subplots with ponderosa pine present and the average density of ponderosa pine within the subplots. A total of 145 subplots were analyzed for ponderosa pine densities while the overall average density of ponderosa pines within those vegetation classes was approximately 17.75 per acre. The mesic mixed conifer, dry-mesic mixed conifer, and mountain mahogany woodland vegetation types each only had three subplots to base the number ponderosa pines per acre off of while there were 39 subplots in the ponderosa pine woodland class. The ponderosa pine woodland vegetation type had an average of 55.55 ponderosa pines per acre while mountain mahogany woodland had an estimate of 40.12 ponderosa pines per acre and pinyon-juniper woodland had an average of 21.29 ponderosa pines per acre. The vegetation types with the smallest density estimates of ponderosa pine included aspen-mixed conifer forest which had an estimate of 1.09 ponderosa pines per acre and dry-mesic spruce-fir forest with an average of 2.75 ponderosa pines per acre.

The number of acres was also calculated after each vegetation type that contained ponderosa pines was clipped to the NDVI-VEG threshold (Table 6). Throughout all of the vegetation types, there was a total of 118,566.4 acres. Ponderosa pine woodland dominated the study area with about 31,706.41 acres while spruce-fir forest had 29,047.83 acres. The vegetation classes of interest with the fewest number of available acres included the dry-mesic mixed conifer forest with 2430.25 acres, the mesic mixed conifer forest with 2896.6 acres, and the mountain mahogany woodland with 3,010.32 acres.

Table 6: The vegetation types within the study area that had a density of ponderosa pines according to the FIA subplot data. The density of ponderosa pines was calculated while the number of acres of each vegetation types was measured after clipping the vegetation layers to the NDVI-VEG grid. The number of ponderosa pines generated for each vegetation type could then be calculated based on the number per acre and the area in acres.

Code	Vegetation Type	FIA Subplots	Avg PP Per Acre	Acres	PP generated
22	Rocky Mtn Aspen Forest & Woodland	14	5.16	20778.98	107185
26	Rocky Mtn Subalpine Dry-Mesic Spruce-Fir Forest & Woodland	35	2.75	29047.83	79915
30	Rocky Mtn Montane Dry-Mesic Mixed Conifer Forest & Woodland	3	8.02	2430.25	19501
32	Rocky Mtn Montane Mesic Mixed Conifer Forest & Woodland	3	8.02	2896.6	23242
34	Rocky Mtn Ponderosa Pine Woodland	39	55.55	31706.41	1761330
36	Colorado Plateau Pinyon-Juniper Woodland	26	21.29	19362.36	412313
38	Inter-Mtn W Aspen-Mixed Conifer Forest & Woodland Complex	22	1.09	9333.6	10213
44	Inter-Mtn Basins Mtn Mahogany Woodland & Shrubland	3	40.12	3010.32	120775
		SUM: 145	AVG: 17.75	SUM: 118566.4	SUM: 2534474

The result of the densities and area taken together led to a total of 2,534,474 ponderosa pines being generated. The number of ponderosa pines generated within the ponderosa pine woodland vegetation type made up nearly 70% of all the pines generated with 1,761,330 trees. The pinyon-juniper woodland vegetation class had the second highest number of ponderosa pines generated with 412,313 pines and made up approximately 16% of all the pines that were generated. There were three vegetation classes that each comprised less than 1% of the total number of pines generated which included the dry-mesic mixed conifer forest, mesic mixed conifer forest, and the aspen-mixed conifer forest.

The observed dbh distribution of ponderosa pines in FIA plots was analyzed in order to randomly generate diameters from that distribution using the acceptance-rejection method.

After running the acceptance-rejection sampling VBA script in Microsoft Access (Figure 14), the distribution of 2,534,474 pines was plotted in comparison to the distribution of what was observed from the FIA data (Figure 15). The distribution of randomly generated values was nearly identical to the observed distribution showing that the acceptance-rejection model that was designed was acceptable for my purposes.

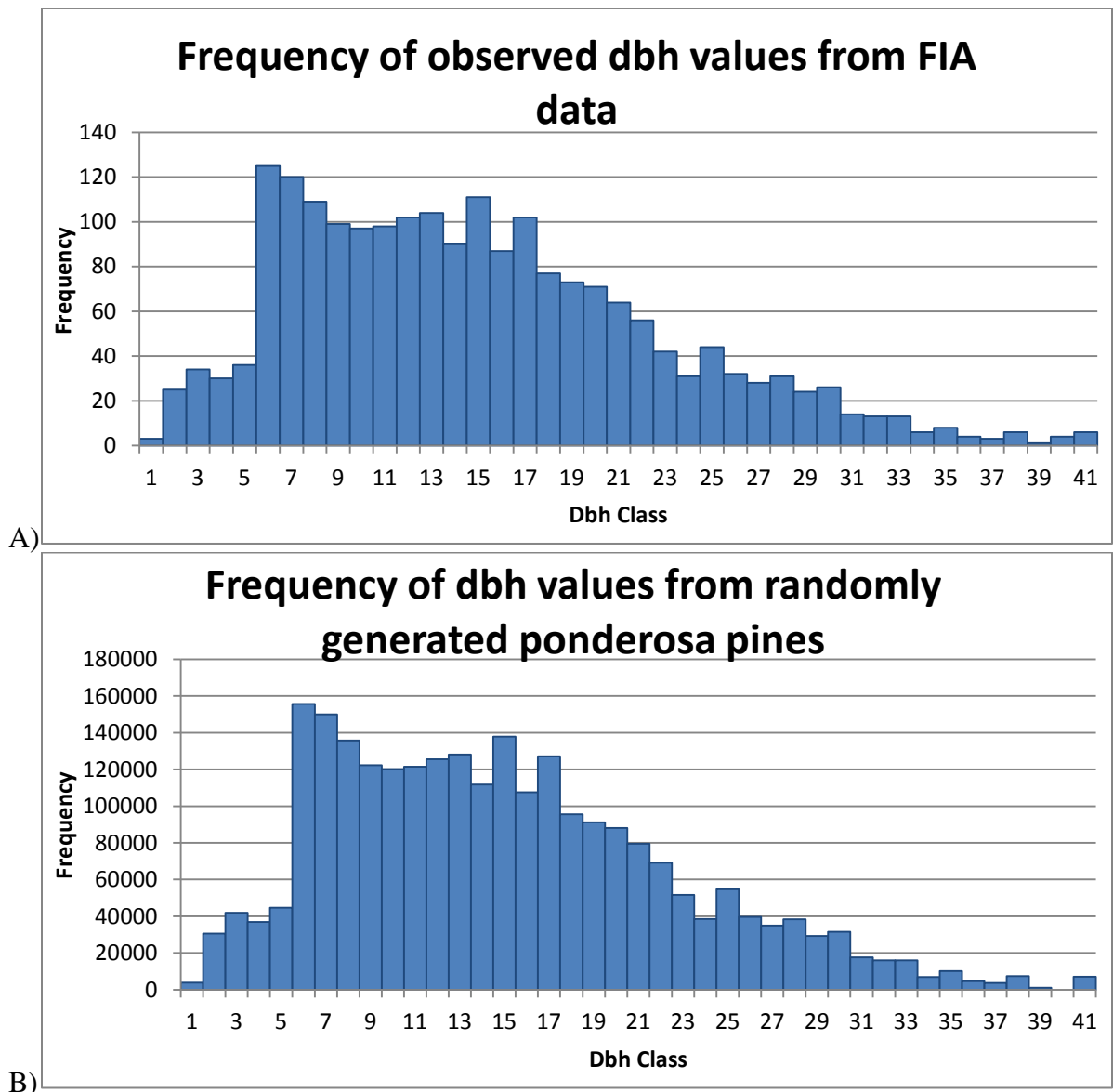


Figure 15: Frequency distributions for the dbh of sampled and generated ponderosa pines. (A) All ponderosa pines measured in FIA plots in Utah and (B) a sample of over 65,000 random generated diameters from the FIA distribution.

Table 7: The logistic regression output that was used to develop equations for applying the probability of bark beetle caused mortality per year to individual host trees in the simulated forest landscape. B is the regression coefficient, S.E. is the standard error, Sig. is the significance of each variable in the independent model

	B	S.E.	Sig.	95% C.I.for EXP(B)	
				Lower	Upper
Beetle killed trees globally (year – 1)	1.022	.036	.000	2.591	2.983
Dbh	.056	.005	.000	1.048	1.068
Plot PP BA per acre	.002	.001	.000	1.001	1.003
Constant	-7.267	.105	0.000		

Table 8: The average beetle pressure values from epidemic and endemic years. These were used in the logistic regression analyses to calculate risk under two different bark beetle population phases.

Year	Beetle killed trees per sampled acre the previous year	Population status	Average beetle pressure values
1993	1.378	Epidemic	1.653
1994	2.211		
1995	2.011		
1996	1.311		
1997	1.356		
1998	0.267	Endemic	0.132
1999	0.133		
2000	0.100		
2001	0.000		
2002	0.022		
2003	0.078		
2004	0.367		
2005	0.144		
2006	0.078		
2007	0.033		
2008	0.378		
2009	0.178		
2010	0.111		
2011	0.011		
2012	0.078		

IV.3.2 – Framework for risk mapping

To apply risk to the individual trees in the landscape, the variables were entered into stepwise multiple logistic regression analysis included the number of beetle killed trees per acre the previous year, dbh, and the plot ponderosa pine basal area per acre. All variables were significant ($P < .001$) in the logistic regression analysis (Table 7). To obtain values that could be used to represent beetle pressure, the number of beetle killed trees were averaged from epidemic and endemic years. In the model calculations for each of the individual trees, 1.653 killed trees per acre was used as the beetle pressure value to represent epidemic years and 0.132 killed trees per acre was used to represent beetle pressure in endemic years (Table 8). The calculations were applied to the individual trees in the landscape and the mean and maximum risk values per cell were mapped at a scale of two acres (Figures 16 & 17). On the map of maximum risk values for an epidemic year, the probability of bark beetle-caused mortality of individual trees within one year ranged from 0.3-6.5% while the range in an endemic year ranged from 0.08-1.5% (Figure 17).

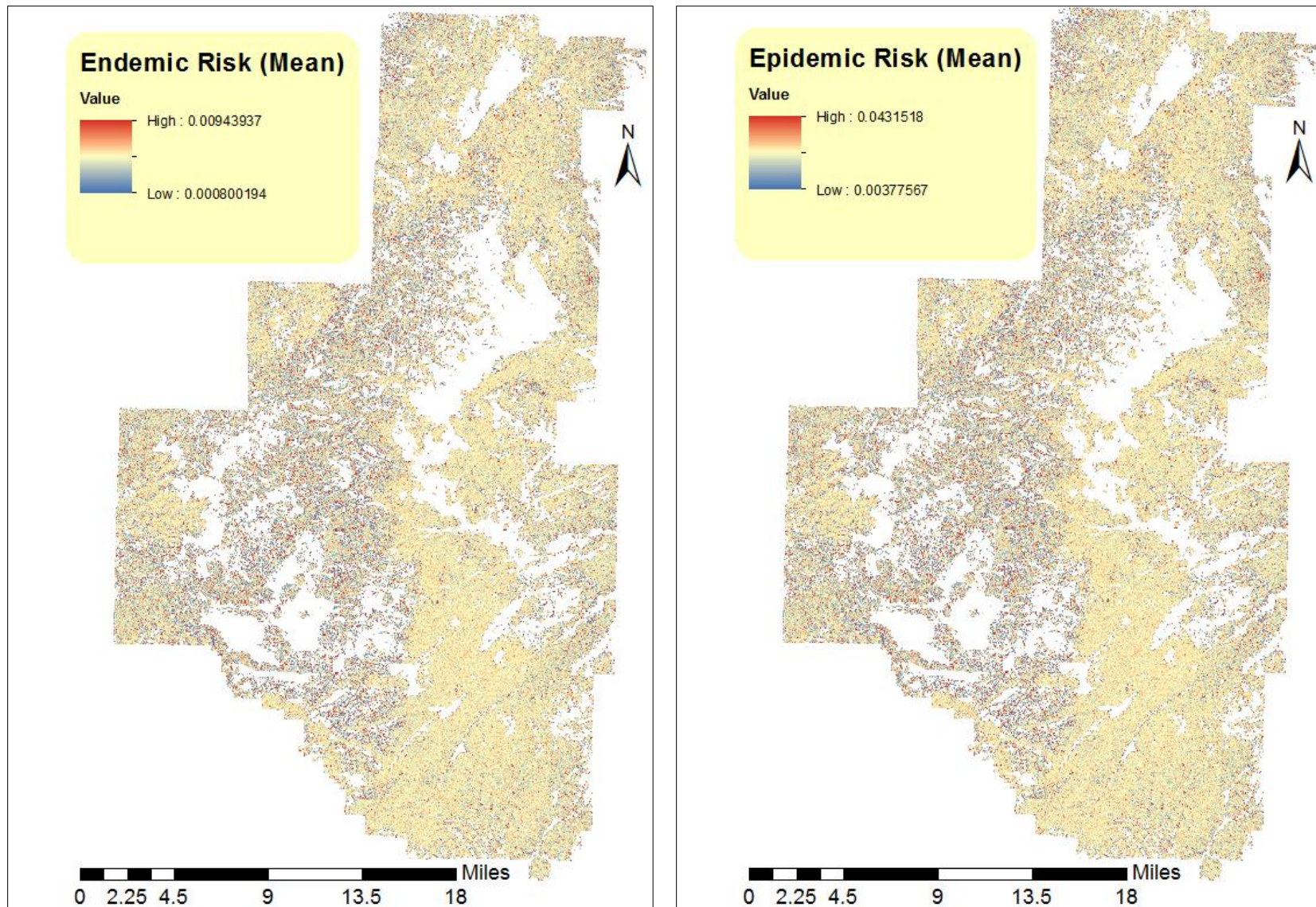


Figure 16: Mean risk maps for epidemic and endemic populations (2 acre cell size)

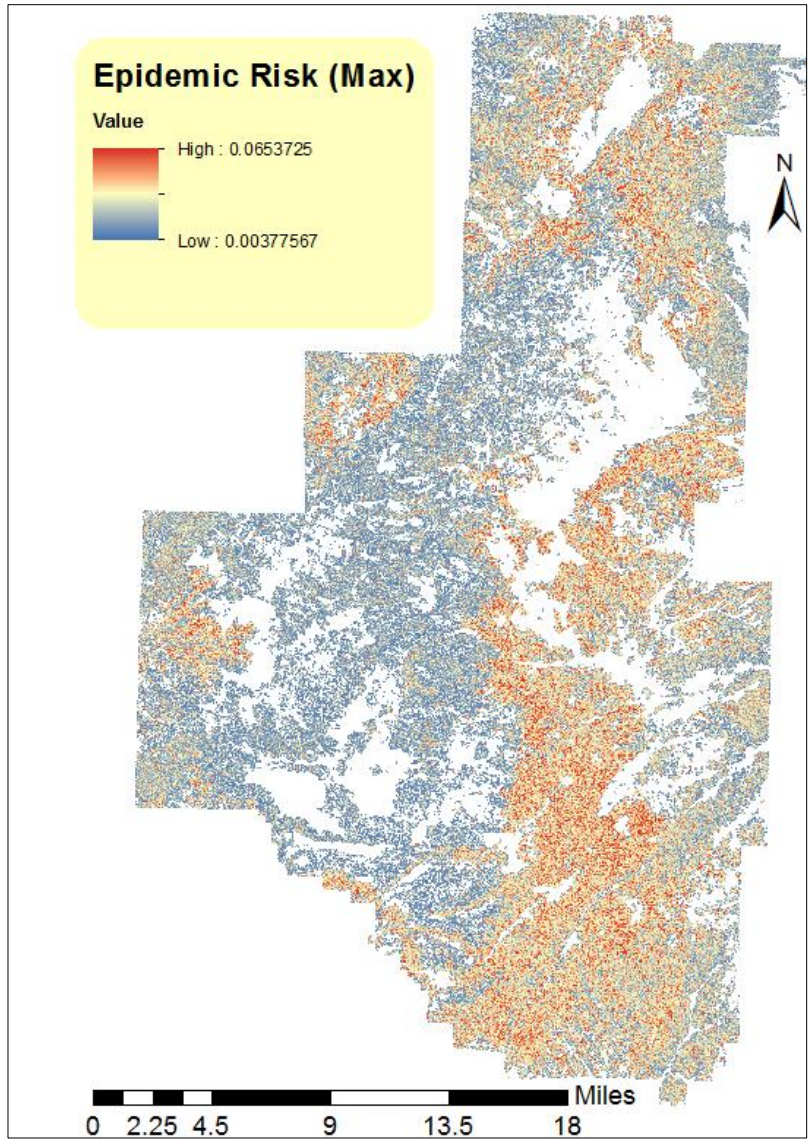
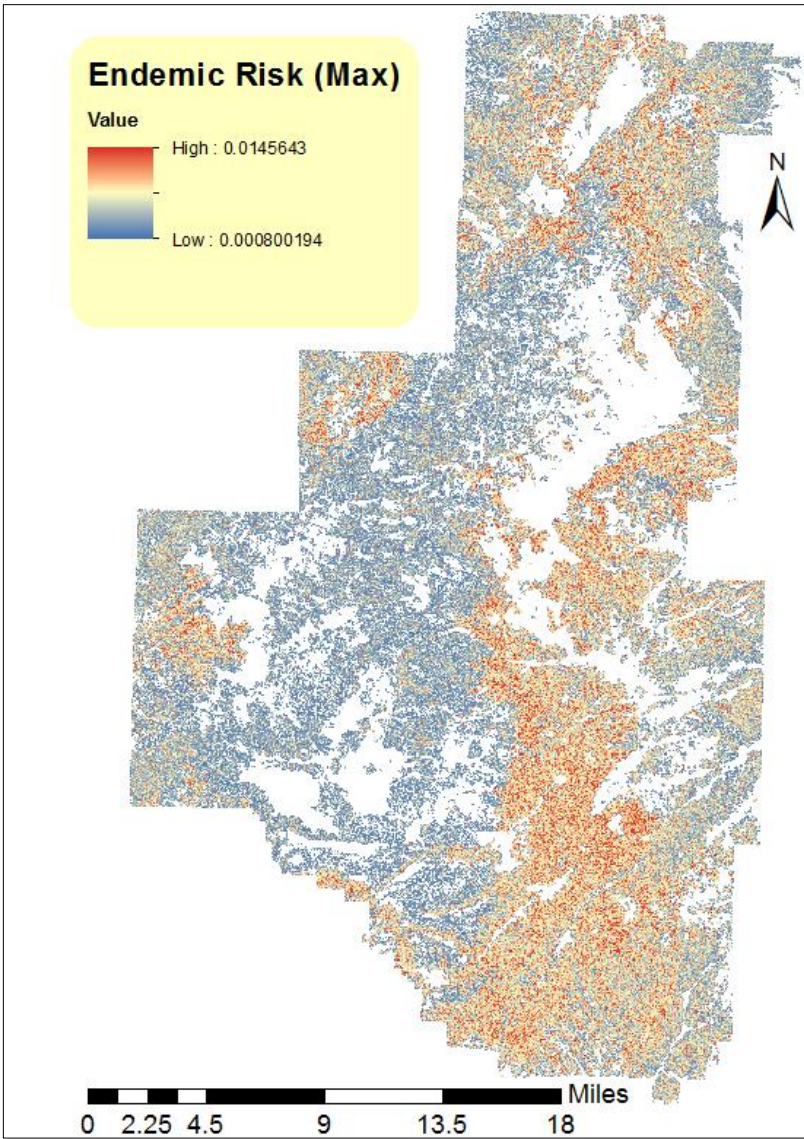


Figure 17: Maximum risk maps for epidemic and endemic populations (2 acre cell size)

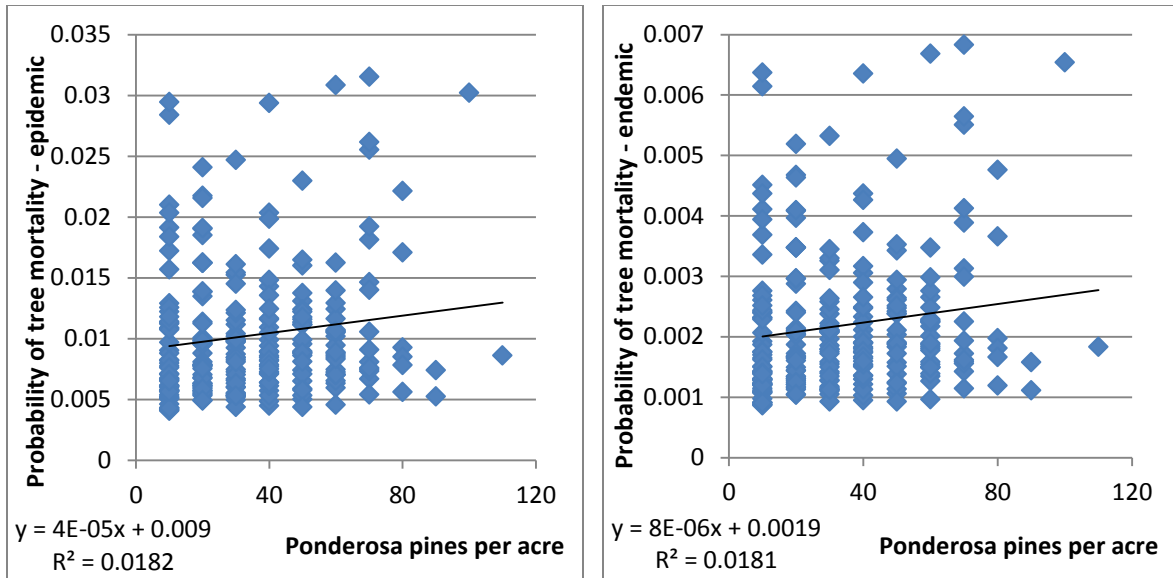


Figure 18: The relationship between tree density and tree susceptibility. A random sample of 250 trees were analyzed to examine the relationship between the number of ponderosa pines per acre and the probability of tree mortality in response to bark beetles during example epidemic and endemic conditions.

Scatter plots were made for a random sample of the simulated tree population to assess a relationship between the density of ponderosa pines and the probability of tree mortality in response to bark beetles during example epidemic and endemic conditions (Figure 18). A line was fit to the data and the slopes were near zero and the R square values were 0.0182 and 0.0181 for epidemic and endemic population densities, respectively.

IV.4 – Discussion

IV.4.1 – Tree modeling

When determining the density of ponderosa pines in each GAP vegetation class using the FIA data, the ponderosa pine woodland vegetation class had the highest density of ponderosa pines per acre (Table 4). After measuring the density of ponderosa pines in the 22 subplots within the aspen-mixed conifer forest class, I saw a very low average of about one

ponderosa pine grew per acre. It is somewhat surprising that mountain mahogany woodland had the second highest density although the sample size of three FIA subplots is likely not completely representative of the actual density of pines in that class. Similarly, the mesic mixed conifer and dry-mesic mixed conifer vegetation classes had very low densities but the same small sample size of three. The data was used to show a framework for risk mapping using information about individual trees and is not meant to be completely accurate. Improved mapping of trees and estimates of tree conditions would allow for this framework to be followed for data with higher accuracy.

After clipping each GAP vegetation class to the NDVI-VEG threshold, it was clear that ponderosa pine woodland was the dominant vegetation class in terms of area within the study area (Table 4). The ponderosa pine woodland class had the highest available area for generating ponderosa pines in while the dry-mesic mixed conifer forest, mesic mixed conifer forest, and the mountain mahogany woodland classes all made up the smallest area. The available areas in each GAP class seemed to correlate with the number of FIA subplots in each class which explains why FIA sampling in some classes was difficult.

IV.4.2 – Developing a framework for tree-level risk assessments

After simulating ponderosa pines in a realistic landscape setting, I selected variables to develop a landscape specific risk assessment model. The known information from the landscape is the coordinates for ponderosa pines and their associated dbh values. While a number of stand conditions could be assessed, average dbh and maximum dbh measurements were avoided since the dbh of individual trees were being used and in areas where ponderosa pines were at very low densities, the dbh of an individual tree would generally have the same

measurement for average or maximum dbh. On the other hand, basal area measurements provide information about the size and densities of trees which is useful data across all ponderosa pine densities. Basal area was used with the plot-level measurements instead of basal area measured at the site-level because the plot-level measurement had a higher influence on the probability of bark beetle-caused mortality. The “global” estimate of the number of bark beetle killed trees per acre from the previous year was used as a beetle pressure variable. The regression coefficients for all of the variables that were entered into the logistic regression analysis were significant ($P < .001$).

The logistic regression output was used to develop an equation for calculating the probability of bark beetle-caused mortality for individual trees. The 20 years of field data was used to estimate values for the beetle pressure variables during epidemic and endemic populations. The values for the years 1993-1997 were averaged to represent the beetle pressure under epidemic conditions and the average value from 1998-2012 was used in the model to represent endemic conditions (Table 8). The equations were applied to each of the trees in the landscape and the mean and maximum risk values were displayed at a scale of 2 acres. The epidemic and endemic maps appear very similar although the susceptibility values were higher for trees during epidemic years.

Areas with high ponderosa pine densities appeared to have higher susceptibility values. Low density areas in the landscape tended to have more variable susceptibility values since tree dbh has a stronger influence on the probability of bark beetle-caused mortality than the plot-level measure of basal area. To examine the relationship between ponderosa pine densities and host susceptibility to beetle caused mortality, a random sample of 250 simulated ponderosa pines was analyzed. There was a weak positive relationship between the

ponderosa pine densities and host susceptibility (Figure 18). The relationship is probably a response of ponderosa pine basal area being, in part, dependent on the density of ponderosa pines. The variation seen in the scatter plots around the line that was fit to the data is likely due to the influence of the other variables on host susceptibility. The actual reason that the maximum risk map shows areas of high densities tending to have high susceptibility is that there is a higher chance that one of the trees within a two acre grid cell has a relatively high dbh since dbh values were randomly attributed to the simulated trees. Dbh also has a stronger influence on tree susceptibility to bark beetle-caused mortality than the local basal area measurement.

The susceptibility of trees to endemic populations tended to be very low (Figure 16 & 17). Because of the generally low susceptibility of trees, it is possible that many endemic bark beetles are unsuccessfully finding or overwhelming host defenses. This might be a reason why populations remain low instead of increasing into epidemic levels. There are also other variables that were not included that could be playing a major role in susceptibility to endemic bark beetle populations such as climatic factors or recent growth.

The age and vigor Keen classes were shown to have a high influence on susceptibility to bark beetles although they were not included within the risk assessment. The data would also be difficult to simulate in the landscape even with increases in technology. The keen classes are based on subjective visual assessments as seen from the ground. Breaking trees into these classes would be difficult from aerial imagery so including those variables in a model to be used over a broad spatial extent is unrealistic.

Aerial detection survey data is available for the study area with shapefiles for locations affected by forest insects and pathogens. Other studies have shown the value of

using beetle pressure data to map risk (Bone et al. 2013a, Aukema 2008). Using this form of data, land managers can gather estimates for values to enter into the model to accurately represent the current beetle pressure.

As I previously mentioned, the simulated ponderosa pine forest is not supposed to be completely representative of the actual forest conditions. It provided an opportunity, however, to develop a framework for applying a susceptibility model using characteristics of individual trees. The conditions and configurations of hosts showed that high densities of ponderosa pines result in areas of relatively high susceptibility for both endemic and epidemic populations.

To create a more accurate representation of tree-based susceptibility in the landscape better methods can be used to map hosts or other trees in the landscape. LiDAR could provide data about individual tree locations and heights while allometric equations could be used to estimate the diameter of the trees. Hyper-spectral imagery could help in identifying tree species or even detecting bark beetle damage. Object-oriented classification is another method that could be used to determine the locations of individual trees in the landscape. Although accurate data on individual trees is hard to maintain, it can provide better insight for forest management. Applying susceptibility models to accurate tree data in the forest could be useful for selecting areas of the forest to thin in order to increase host vigor and decrease host susceptibility.

The goal of this section was to develop a framework for modeling and mapping host susceptibility of individual ponderosa pines to bark beetle populations in a simulated landscape. Currently, the resources are not readily available to estimate more realistic tree inventories for the earth's forests through remote sensing although the technology for

obtaining this information is rapidly becoming commonplace. With information about individual trees in the landscape, there will be new ways of assessing tree health. This thesis aimed to show that a useful way of assessing risk for forest insects and pathogens will be through developing models that focus on the susceptibility of individual trees.

V CONCLUSIONS

This thesis analyzed data from both endemic and epidemic populations of pine beetles in southwestern ponderosa pines forests within or near the Colorado Plateau. The goal of this study was to gain a better understanding of the shifts between endemic and epidemic populations and to develop tree-level risk models for predicting bark beetle-caused mortality. To do this, I (1) used extensive field data of bark beetle populations and the associated stand conditions from sites throughout the Colorado Plateau to assess what factors might contribute to a shift in the population densities of bark beetle, (2) developed the best statistical and ecological model for determining the absolute risk of bark beetle-caused mortality in ponderosa pines, and (3) used remotely sensed imagery, GIS layers, and ground truth data I estimated the spatial distribution and conditions of host trees across a large landscape setting and then used the landscape to develop a framework for applying tree-level risk assessments. I think that risk assessments for forest insects and pests would benefit from using information about the condition and configuration of individual trees as the focal point. In this section, I summarize the results of the study and discuss the implications for management and further research.

V.1 – Bark beetle population dynamics

In 1995, forty-five 2 acre sites were established within National Forests and National Parks throughout the southwestern US. The diameter at breast height of all ponderosa pines within the sites was recorded. All pines were also given a Keen class rating based on their size and vigor. If trees had been attacked by bark beetles, the trees were recorded with the year of attack. The trees that were attacked were also noted as to whether or not the attacks

were pitch-outs, strip attacks, or killed by the beetles. Sites were periodically and the data was re-measured through 2012.

From analyzing 21 years of field data on bark beetle attacks in sites throughout the southwest, I was able to determine shifts in the population dynamics over different regions. I also was able to compare stand conditions between sites with high and low beetle pressure. Site maximum dbh, ponderosa pine basal area, total basal area, and trees per acre were all significantly higher in sites with high bark beetle population densities. Multiple logistic regression analyses showed that the number of ponderosa pines per acre and the maximum dbh within sites could be used to determine whether bark beetle populations would increase beyond endemic levels.

V.2 – Modeling host susceptibility to bark beetle-caused mortality

The same field data was used to examine which tree, stand, and beetle pressure variables influenced host susceptibility to bark beetle-caused mortality and to what extent. Independent analyses of the variables showed that the diameter at breast height, Keen age and vigor, as well as a number of stand and beetle pressure variables were significant in influencing the mortality of individual host trees. Using standardized variables, the analyses could be used to assess the relative importance of each variable. Tree-level variables had a high influence on host susceptibility followed by plot and site-level stand variables. Beetle pressure variables had the highest influence at the larger scales. After performing correlation analyses, variables were entered into a multiple logistic regression analysis to develop the best statistical model for predicting the probability that trees would be killed by bark beetles within a year. Using the results of this section, I selected important variables to use to

construct multiple logistic regression models that could be applied to a modeled landscape developed in the following section.

V.3 – Developing a framework for tree-level risk assessment

To further explore the susceptibility data, I performed an analysis to relate susceptibility to the conditions and configurations of hosts in the landscape. To do this, I used remotely sensed aerial imagery for the Cedar City ranger district within the Dixie National Forest and used a Normalized Difference Vegetation Index (NDVI) to highlight trees and other healthy, green vegetation in the landscape. I used this to create a binary map to show the locations of trees which I called my NDVI-Veg layer. I then used Forest Inventory & Analysis data provided by the US Forest Service to assess the density of ponderosa pines per acre in different vegetation classes. The vegetation classes were clipped to the NDVI-Veg layer and the calculated densities of ponderosa pines were used to generate pines randomly according to the number per acres of each clipped vegetation class. I estimated a total of 2,534,474 ponderosa pines in my landscape. To display the susceptibility of pines spatially, I needed methods to estimate the diameters for these trees. The FIA data was used to measure the distribution of diameters for ponderosa pines throughout Utah. This distribution was used to create an acceptance-rejection algorithm that assigned diameters to the generated ponderosa pines.

To create susceptibility models to be mapped in the simulated ponderosa pine forest, I first had to select which variables to include in the models. Variables were limited to those that could be measured given only information about the configuration and diameter at breast height of hosts in the landscape. I also did not want to use highly correlated variables in the

same model or variables that did not accurately represent ecological relationships. I decided to use dbh, plot ponderosa pine basal area, and the “global” number of beetle killed trees per acre during the previous year as variables to include in the models. Models were developed to compare differences between susceptibility to endemic populations and epidemic populations by using field data to get possible values for the beetle pressure variable.

The models were mapped using the simulated ponderosa pine forest landscape. In areas with high pine densities, there was a higher chance of host susceptibility. The relationship between ponderosa pine density and host susceptibility was positive but weak. Ponderosa pine basal area, which was included in the model, is related to ponderosa pine density so the positive relationship makes sense. However, it seems that dbh of trees plays a larger role in host susceptibility and there is an increased chance of a tree having a higher susceptibility in areas of higher densities due to chance since dbh values were randomly attributed to the ponderosa pines. This is not directly applicable to real landscapes and thus reinforces the fact that applying the model to the simulated landscape was done as a framework for tree-level risk assessments.

V.4 – Management implications

The susceptibility data could be used to manage forests through selective thinning, for example, to reduce the number of trees that are vulnerable to endemic bark beetle populations. Older ponderosa pines with larger diameters at breast height and low vigor are vulnerable to attacks by endemic bark beetle populations. Prescribed burns can also be useful in increasing stand vigor again although the timing of the burn and the intensity should be

monitored to achieve the desired affect without making host trees vulnerable from fire damage.

Mapping trees in the forest and having estimates of their size or conditions can be valuable from a management perspective or for many other research topics. Land managers could benefit from knowing the trees on their land by having estimates of available lumber, biomass, and areas of high density or basal area. This would help land managers make decisions about where to cut, thin, burn, or leave as is. To assess susceptibility over a large spatial extent for management purposes, improved methods for mapping hosts is a requirement.

V.5 – Further work

This study has provided a foundation for further analyses to be performed. The framework provided for mapping forest susceptibility can be used with more realistic data regarding the configuration and conditions of host trees in the landscape. LiDAR and object-oriented classifications are two methods that could provide more details about ponderosa pines and other trees in the landscape. Allometric equations could be useful in estimating the dbh of trees from the canopy width or height. Imagery with higher resolutions (<1m) or hyper-spectral imagery with more bands could provide information about the species present and could help determine the vigor of hosts in the landscape by assessing slight variations in the colors of trees. Beetle pressure was also shown to influence host selection and susceptibility. Incorporating spatial information from aerial detection surveys into the models can possibly improve estimates for susceptibility within the landscape.

Information about individual trees in the landscape could benefit forest managers, forest entomologists, forest pathologists, landscape ecologists, physical geographers, and geologists. Although these tree databases would likely be large and difficult to accurately maintain over time, they can be useful in cases of ecological restoration to gather estimates of damaged trees and manage for succession of expected species after disturbances. There is a myriad of other applications that a spatial tree database can be utilized for.

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