SCIENCE DRIVEN MANAGEMENT: UNDERSTANDING THE DRIVERS OF BARK BEETLE INFESTATION IN THE STANISLAUS-TUOLMNE EXPERIMENTAL FOREST

A THESIS

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By

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Introduction

Extreme ecosystem disturbances are increasingly the result of environmental mismanagement (Bormann, 2012). While intermediate levels of disturbance can boost ecosystem health, severe disturbance can cause irreparable losses in species diversity and declines in ecosystem resilience (Bormann, 2012). Limiting the negative consequences of severe disturbance and preventing further harm requires understanding the individual drivers of stress and their interactions. Climate change and human management decisions have placed forest ecosystems across North America at heightened risk of extreme disturbances, such as widespread insect outbreak (Berry, 2007; Bentz et. al, 2010; Raffa et. al 2008). Bark beetle infestation is a focal point of many studies in forest disturbance research, but a lack of effective management response to control beetle populations points to ineffective communication between research and management communities. This study employed mainly open-source data and common-sense observations to determine drivers of beetle infestation within a section of forest in the Sierra Nevada comprising of approximately one-half kilometer. A model produced to replicate a portion of the methods presents a template that can be used to develop scientifically based, site-specific forest management plans to combat the ecosystem disturbance of beetle infestation.

Bark beetles are best able to infest stressed trees, and forests across the American West have grown increasingly stressed over the past century (Bentz, 2009; Berry, 2007). Management decisions to exploit timber resources and suppress fire have altered normal disturbance patterns and placed ecosystems at heighted risk of severe disturbance. Frequent fire and severe and long-term droughts are a natural part of ecosystem dynamics in the Sierra Nevada (Stein, 1994; Allen, 2002). With thick outer-bark, white (*p. lambertiana*) and yellow (*p.* j*efferyi, p. ponderosa*) pines have adapted a layer of protection against frequent, low-intensity fires, which clear understory and reduce competition for water (Berry, 2007; Kilgore, 1973). Historically, frequent fires in the Sierra Nevada, ignited both by lightning and by Native Americans, helped keep forest ecosystems resilient to drought stress by creating low-density forests, where trees faced minimal competition for water (Berry, 2007; Knapp et. al, 2013; Allen, 2002).

Forest management throughout the 20th century contributed to weakened forest ecosystems in the American West. Between 1850 and 1910, extensive logging efforts throughout the Sierra Nevada supplied timber for an industrializing America (Maloney et. al, 2011). Logging operations frequently targeted the largest yellow and white pines (Maloney et. al, 2011). With the largest trees in the forest gone, increased levels of sunlight and large open spaces provided an opportunity for young trees to establish in dense stands (Kilgore, 1973).

Extensive logging efforts cultivated concern over the exploitation of forest resources and, in 1905, the United States Forest Service (USFS) was established to preserve the nation's forest reserves (Marlon, 2012). A dry period in the early 1900s caused several catastrophic wildfires. As five million acres burned across the American West (Berry, 2007), it became apparent that fire was not only a potential threat to dwindling areas of land suitable for logging, but also a threat to a rapidly growing population of white settlers. In 1908, the US Forest Service adopted the policy of total fire suppression, which would last until its official abandonment in 1978 (Berry, 2007). Today, the accumulation of fuels in high density forests is considered one of the largest threats to the land of the United States Forest Service and widespread declines in tree vigor have enabled bark beetles to infest millions of acres of forested lands (Berry, 2007; Dant, 2017).

In addition to human mismanagement, climate change has a played a part in boosting the success of beetle populations. Bark beetles are constrained by colder temperatures and increased annual temperatures have spurred population growth and increased potential beetle habitat (Bentz et. al, 2010; Raffa et. al 2008). Additionally, recent droughts, accompanied by rising temperatures, have placed significant stress on tree populations (Bentz et. al, 2010). The consequences of warming temperatures and recent drought are amplified by the prevailing 20th century forest management regime of fire suppression, creating a dire situation for North American forests (Stephens, 2005).

Historically, bark beetle species (*dendroctonus*) native to the Sierra Nevada played an important role in maintaining a dynamic equilibrium of forest ecosystems (Schowalter, 2012). Bark beetles target the largest trees, which are often declining in health. By killing declining trees, bark beetles create room for younger trees to grow (Schowalter, 2012). Past logging practices, fire suppression, and changes in temperature and precipitation as a result of climate change have increased competition between trees for scarce resources and increased susceptibility to mortality from beetles (Bentz et. al, 2010). With a far greater number of weakened trees, bark beetles have infested millions of acres of forest and are currently the largest biological cause of pine death in North America (Dant, 2017; Safranyik and Wilson, 2007).

Beetle Life-Stages

Bark Beetles (*dendrotonous ponderosae*) coevolved with conifer species and utilize the chemical defense system of their host species to their reproductive advantage. Beetles are alerted to suitable hosts by the terpene composition of a host species (Chiu et. al, 2017). In defense against beetles, conifers produce a resinous pitch made up of terpenes to drown and expel burrowing beetles (Chiu et. al, 2017). Female beetles initiate mass attacks by utilizing the host's defense terpenes to produce pheromones that attract other beetles to reach a critical mass necessary to overcome the defenses of a host (Chiu et. al, 2017). Male beetles and larva release anti-aggregate pheromones, which counter the pheromones released by female beetles and help to reduce the probability of overcrowding (Pureswaran, 2000). The result of these contradicting pheromone signals is a clustering of infested trees in close proximity to one another (Pureswaran, 2000).

Excluding the few days that it takes for mature beetles to select a host to reproduce, beetles spend their entire life within a host tree. Beetles bore beneath the outer layer of bark and mate within the phloem (Gibson, 2009). They then excavate vertical holes within the phloem and lay their eggs alongside these vertical “galleries” (Gibson, 2009). Beetles generally lay eggs during warm summer months and eggs hatch after about 2 weeks (Gibson, 2009). Hatched larva feed on phloem, creating galleries at right angles to the egg laying galleries. After pupation occurs, mature beetles emerge from an exit hole and disperse to a new host (Gibson, 2009).

Bark beetles carry and spread fungal spores throughout the phloem and sapwood. Larva and young beetles gain critical nutrients from the growing fungus (Gibson, 2009). Both the galleries created by beetles and fungal spread inhibit the flow of nutrients within the phloem and can cause tree death (Gibson, 2009).

The rate at which beetle larval development occurs is temperature dependent (Bentz, 1991). In general, the life-cycle is one year, but temperature variability can change the number of life-cycles per year (Bentz, 1991). Beetles have evolved to persist in sub-freezing temperatures throughout winter months, but uncharacteristically low temperatures in the fall or spring result in extensive mortality (Bentz, 1991). Colder temperatures slow development and may mean that beetles miss the deadline of emerging from hosts during the optimal climate conditions of the warmer summer months. Warmer temperatures, on the other hand, accelerate live stages and can allow for beetle populations to undergo two or more life-cycles per year (Gibson, 2009).

Beetles have adapted the capability to disperse at a range of distances from their original host (Raffa et al., 2008). While beetles often travel short distances to attack to nearest potential host tree, they are also capable of flying further and have been recorded to travel up to 20 km from their original host location to a new infestation site (Furniss and Furniss, 1972). The result of multiple distance dispersal is infestation across a range topographic locations (Kaiser et. al, 2013).

Research Objectives

Evolutionary tactics of multiple distance dispersal and pheromone signaling have enabled beetle populations to persist and grow across various landscape positions. The objective of this study is to isolate the landscape positions most at risk for infestation. By employing topographic data as proxy variables for resource availability and growing conditions, it is possible to see locations where trees experience the most stress. In high stress locations, beetles are more capable of overcoming the weakened defense responses of their host. In isolating areas of greater susceptibility to infestation, areas most in need of management intervention are also isolated. Protecting ecosystems that have been damaged by human mismanagement will require taking preventative action against extreme ecosystem disturbance. By determining areas of high stress through employing mostly open source data, this study presents an efficient and cost-effect way to develop site specific management plans targeting areas most in need of attention.

Methods

Site Description

Located on the western slope of the Sierra Nevada, the study site occupies part of the Lower Montane mixed conifer forest. The climate is Mediterranean and characterized by warm, dry summers and cool, wet winters (Knapp et. al, 2013). While accumulation of two to three meters of snow is common in the winter, substantial precipitation in the summer is rare. These seasonally dry periods give rise to a diverse range of tree species, including: Ponderosa Pine *(pinus ponderosa*), Jeffery Pine (*pinus jeffreyi*), Sugar Pine (*pinus lambertiana*), White Fir (*abies concolor*), and Incense Cedar (*calocedrus decurrens*).

From 1600 to 1889, this area experienced fires with a median interval of 6.3 years as a result of lightning strike and because of purposeful ignition by Native Americans (Knapp et. al, 2013). The Me-Wuk tribe of Native Americans occupied this region for thousands of years before white settlers, and employed the practice of prescribed burns to manage their forest resources and increase ecosystem heterogeneity (Anderson, 2013). The study site has not burned since 1889 due to a management policy of total fire suppression (Knapp et. al, 2013).

Fire suppression significantly altered the structure and composition of tree species within the study region. Forest density has doubled since 1929, shifting forest structure, with an increase in the proportion of shade tolerant species such as firs and Incense Cedar (*Calocedrus decurrens*) and a decrease in the proportion of light limited species such as pines (Knapp et. al, 2013). Historically, fire carved gaps in the forest canopy and provided necessary light for pine seedlings, but now light limitation threatens many of the trees in this study (EA, 2010). Sugar Pines, a highly light dependent species, represent the greatest number of trees in this study (EA, 2010; Barbour, 2002).

Recent drought conditions represent a significant change from historic norms. In January of 2012, the region entered moderate drought conditions (USDM, 2017). By May of 2013, the study site was experiencing extreme drought conditions (USDM, 2017). Drought moderated each winter, but extreme drought persisted throughout the year until October of 2016, with average water year precipitation values at 27.5 inches, 13 inches below the long-term average of 40.5 inches per year (USDM, 2017; Knapp, unpublished data). In 2016 and 2017, above average total water year rainfall of 46.6 and 76.8 inches, respectively, pushed the region out of drought conditions (USDM, 2017; Knapp, unpublished data).

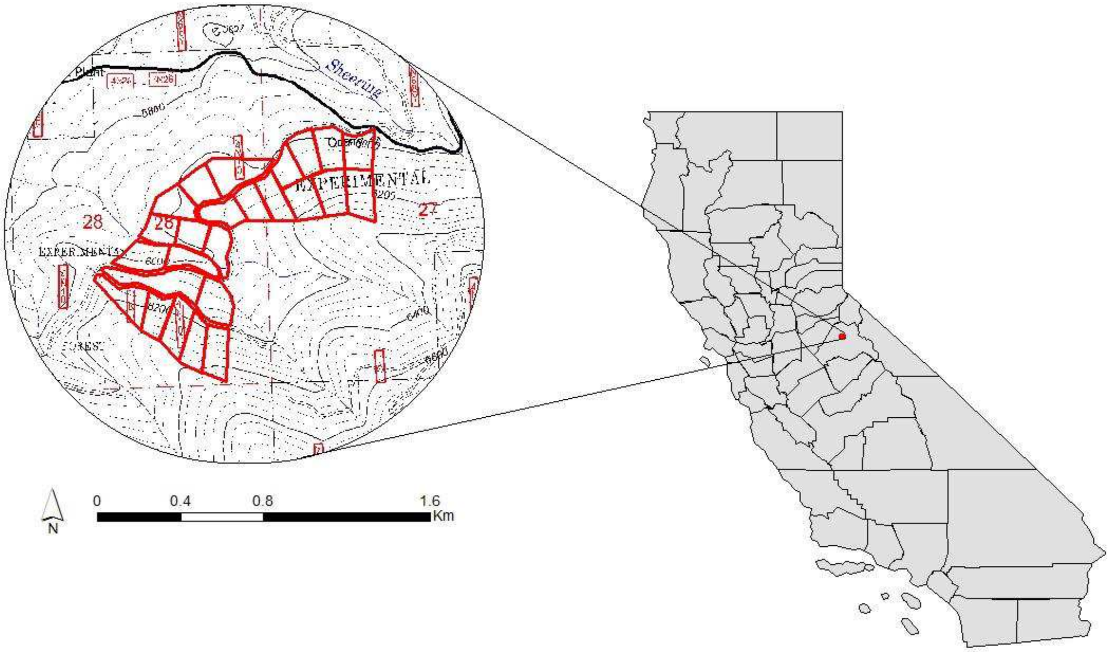

Figure 1: Map of the study site in the Stanislaus Tuolumne Experimental Forest (STEF) in Tuolumne County, Ca.

Study Site

The study site was originally designated in 2009 to examine the vigor of forest stands after prescribed burns. The study site contained 20 thinned plots, which were to be burned, and 5 control plots. Control plots were selected randomly from the pool of 25 plots, all of which were between 1.87 and 3.00 hectares (EA, 2010). The thinning treatment removed saplings and small trees (mainly White Fir and Incense Cedar with 4-10-inch diameter-at-breast- height, DBH) to establish a stand structure similar to pre-fire suppression conditions (EA, 2010). The un-thinned control plots have remained unburned and unlogged or only selectively logged since 1900 (EA, 2010).

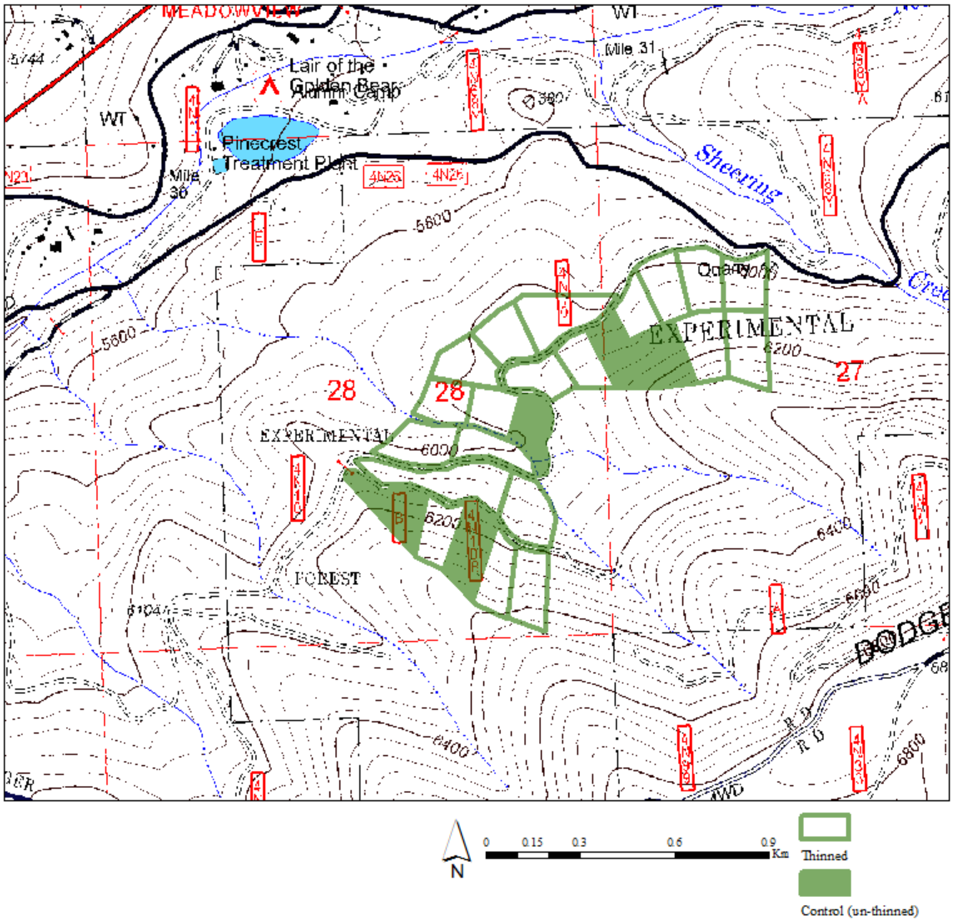

Figure 2: Control, un-thinned, plots represented by the green polygons.

Field Methods

In the summer of 2009, US Forest Service personnel identified and tagged trees that exhibited old-growth characteristics, with DBH>91.4cm. Of the 1029 trees surveyed, 78 were Ponderosa Pine (*Pinus Ponderosa*), 166 were Jeffery Pine (*Pinus Jeffreyi*), and 785 were Sugar Pine (*Pinus Lambertiana*). The location of each tree was recorded using a hand-held Garmin GPS. Diameter at breast height (DBH) and tree health observations were recorded for every tree during the summers of 2009, 2012, 2014, and 2016. In the summer of 2017, only tree health observations were recorded.

Spatial Analysis

ArcGIS was used to extract and calculate the values of several topographic variables at each tree location. Slope, aspect, and elevation were extracted from a LiDAR deduced bare earth raster with a 1-meter pixel resolution. Local geology was extracted from shapefile provided by the California Geological Survey (Jennings, 1977).

The Topographic Wetness Index (TWI) combines upslope accumulation area with local slope and served as a proxy for local water availability to each tree (Kaiser et. al, 2013). TWI was calculated for each tree point using the LiDAR deduced bare earth raster, with a 1-meter pixel resolution. The Fill Tool was used to eliminate potential error of inaccurate surface sinks and peaks caused by data-driven errors within the raster surface. Every tree in the study was assigned as a pour point and the Watershed Tool was used to extract the local upslope accumulation area for each tree. The pixel count of each watershed was designated as the area of upslope accumulation.

$$\mathrm{TWI}=\ln(\text{watershed area}/\tan(\text{local slope}))$$

Local tree density was determined using LiDAR data, by calculating the percent canopy taller than 3 meters within a 15-meter radius from each tree point. The 15-meter radius size was chosen to provide an estimation of local competitors directly surrounding the tree canopy.

Predictions for future infested areas were produced through Maxent, a modeling software designed to predict future species distribution through maximum entropy modeling (Phillips et al., 2017). Landscape variables used in Maxent included slope, aspect, elevation, percent canopy coverage, and bedrock geology. Aspect was converted to a categorical variable in order to include very high values (above 337.5 degrees) and very low values (below 22.5 degrees) within the same category. Because Maxent requires that infestation-predictor variables be in raster format, polygons for percent canopy coverage were converted to a continuous raster. In order to maintain accurate raster values within sections where 15-meter radius polygons overlapped, areas of overlap were assigned the average value of the two overlapping polygons.

Model Component

ModelBuilder was used to construct a model to extract information about topographic variables in raster format to points in a feature class. Additionally, the model was designed to transform information in a digital elevation model to express flow accumulation values for each point in a feature class.

Statistical Analysis

Excel and Minitab were used for all statistical analysis. Excel was used to perform chi-square tests comparing the distribution of infested and un-infested trees across different topographic variables, testing the null hypothesis that infested and non-infested trees would follow the same population distributions. Minitab was used to perform logistic regressions. A binary logistic regression was preformed to determine potential variables predicting infestation. A logistic regression was preformed to determine predictors of tree density in the control plots. A p-value of 0.005 was the threshold for statistical significance.

Results

In 2012, one tree of the 1029 surveyed was infested by bark beetles. By 2014, three trees were infested. In 2016, the number of infested trees rose to 58 and by 2017, 63 trees were infested. Of the infested trees, nearly half (31 trees) were in the un-thinned control plots, despite trees in the control plots accounting for only 18% of all trees in the study. The difference in the ranges of topographic variables is minimal between the control plots and un-thinned plots (appendix, Table 1).

Significant differences between observed and expected values in infested populations were found for the topographic variable of elevation (p=0.0123), but not for differences in slope (p=0.3321) or aspect (p=0.0761). In addition, chi-square tests revealed forest density (as determined by nearby canopy cover) varied significantly (p<0.00001) between infested and non-infested trees. Topographic Wetness Index did not show significant differences (p= 0.9022) between observed and expected values in infested populations.

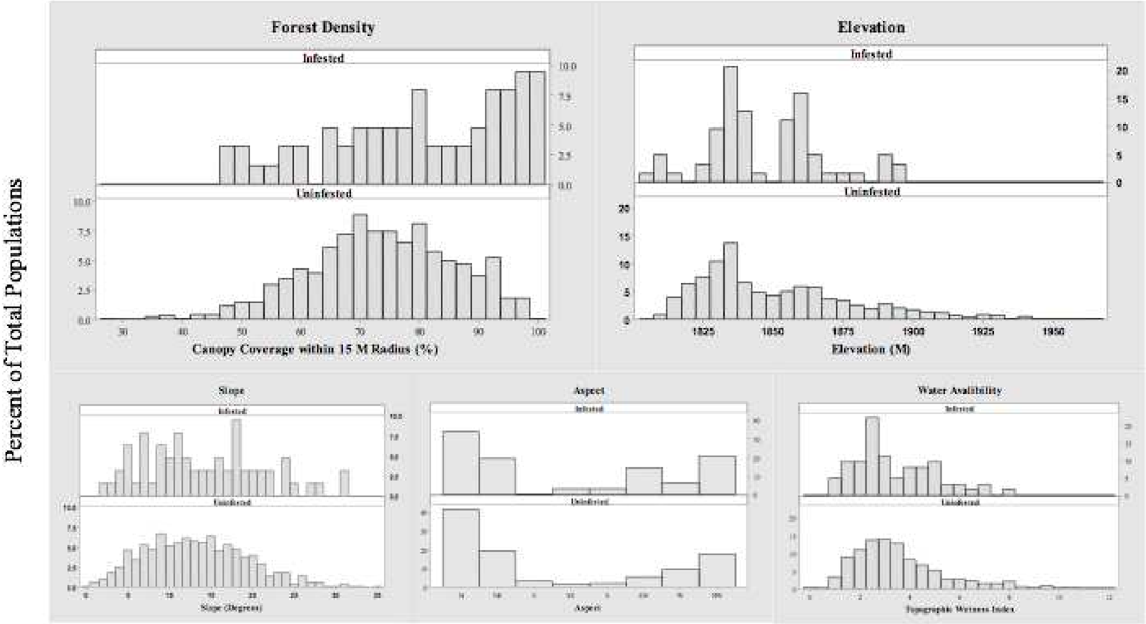

Figure 3: This figure provides a visualization of where infested and un-infested populations fall within the variables of forest density, elevation, slope, aspect, and water availability. The percent of the total infested population differs significantly the expected distribution (as denoted by the un-infested population) for the variables of forest density (p<.00001) and elevation (p=0.0123). The distribution of the infested population did not show significant differences from expected values for the variables of slope, aspect, and water availability.

Binary logistic regression calculated the predictive power of each topographic variable in determining bark beetle infestation (appendix, Table 2). Of the variables considered in the regression, tree density (percent canopy cover) and geology were the only significant predictors of infestation ($p<0.001$ for both geology and tree density). Results of the regression model indicated that the topographic variables employed did not adequately predict the observed presence of bark beetle (adj. $R^2 = 7.66\%$).

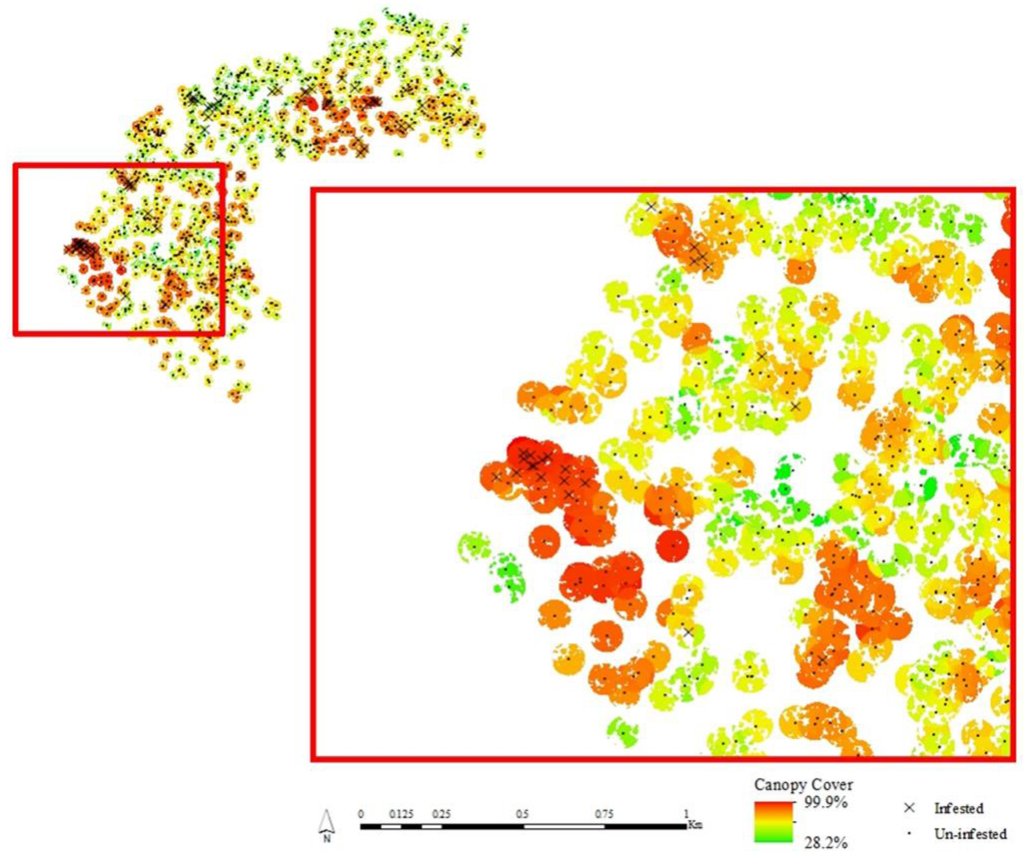

Figure 4: Each tree point (as denoted by a dot or X) is surrounded by a radius of 15-meters, where vegetation taller than 3-meters is colored. A green-to-red color scale was assigned to each radius, where tree points with the most canopy cover are red and areas with the least canopy cover are green. Canopy cover held the most predictive power in determining infestation, with more dead trees appearing in areas of higher density.

Regression analysis for the predictors of tree density was preformed using trees within the 5 un-thinned control plots, where tree density was not influenced directly by recent logging activity (appendix, table 3). The analysis did not provide a suitable model to predict tree density (R-sq adjusted 4.68%). The regression indicated water availability (topographic wetness index values) to be a potential contributor to tree density (p=0.001).

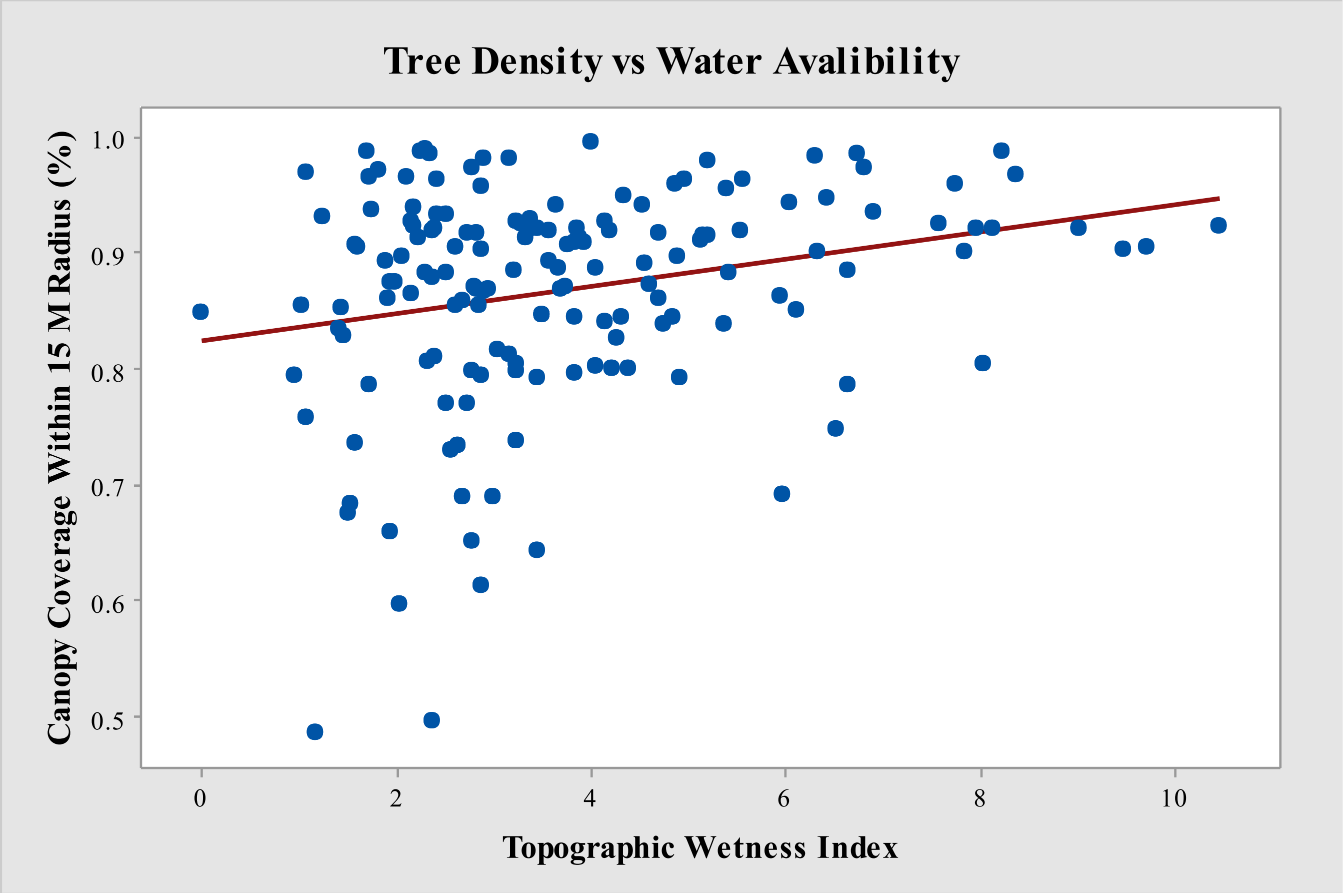

Figure 5: Tree density is positively correlated with topographic wetness Index (Pearson Correlation Value: 0.250, p=0.002). Below a TWI of 4, canopy coverage is variable. At the threshold of 4 the relationship becomes linear, indicating that wet areas above the threshold of 4 support higher tree densities.

The MaxEnt model produced an Area Under the Receiving Operating Characteristic (AUC) value of 0.756, indicating predictive power that is better than random. A random value is indicated by an AUC of 0.5 and a perfect prediction is indicated by a value of 1.0

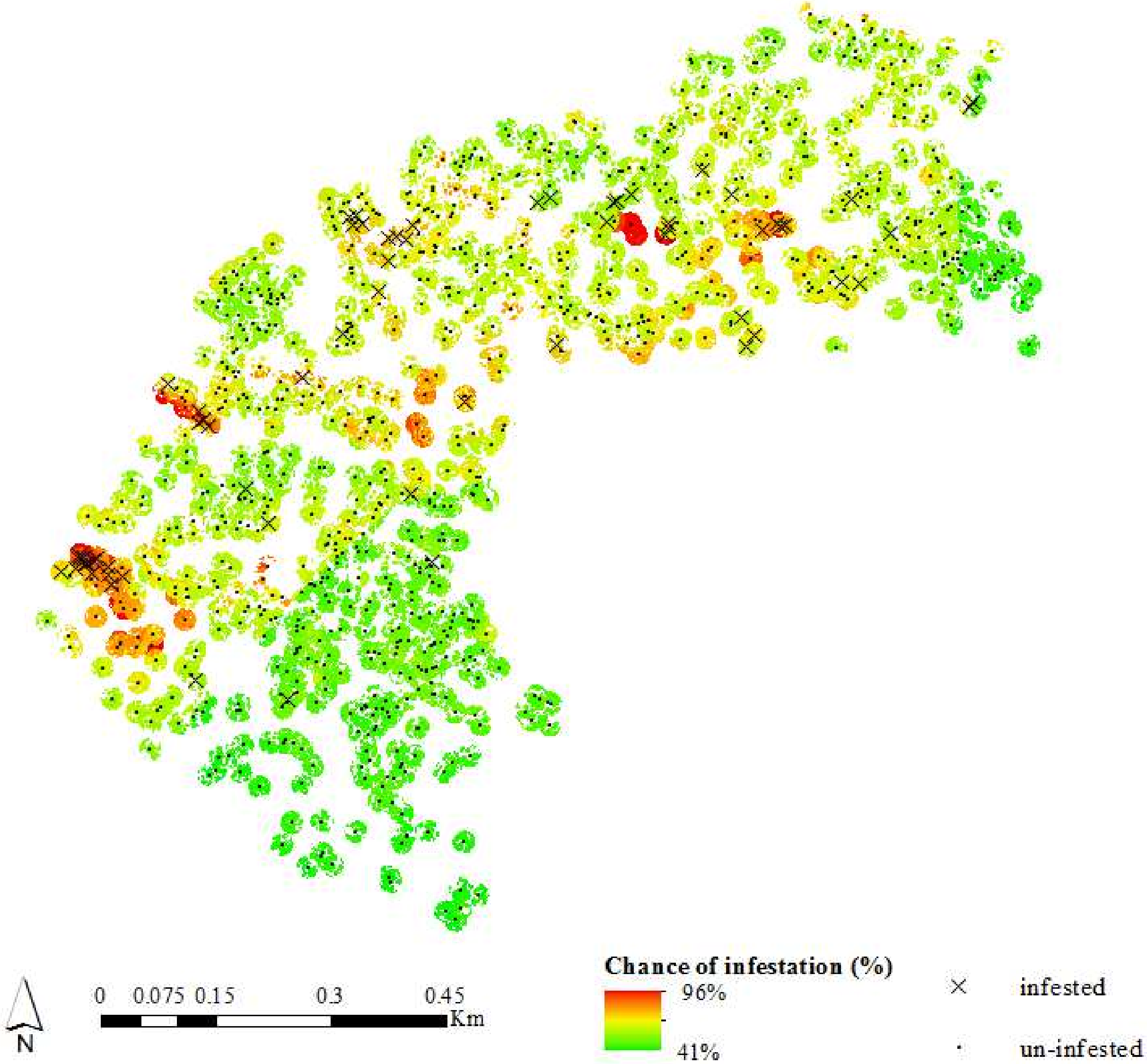

Figure 6: In many cases the Xs indicative of a dead tree coincide with regions with a higher chance of infestation, as denoted by warmer colors.

Discussion

The drivers of infestation are a complex combination of biotic and abiotic factors, appearing at different spatial and temporal scales, making them difficult to isolate. Drivers of infestation are often correlated across landscapes and it is, therefore, difficult to evaluate their relative importance. In order to minimize sources of variation, trees included in this study are within similar age classes and sampled across a relatively small and topographically homogeneous region. Even subtle changes in topography resulted in statistically significant differences in levels of infestation. The results of this study indicate that topographic and landscape scale variables can predict tree vulnerability and resilience at small spatial scales.

The Stanislaus-Tuolumne Experimental Forest is likely in a transitional period between endemic and epidemic conditions of beetle infestation. During earlier stages of infestation, the few trees targeted by bark beetles were spread out across the landscape. In subsequent years, trees infested by bark beetles exhibited more distinct clustering patterns (Figure 7). Bark beetles are capable of colonization via various modes of dispersal, thus patterns of infestation can likely be attributed to these different dispersal mechanisms (Raffa et al., 2008). In the beginning stages of infestation, beetles likely traveled via long distance dispersal from neighboring regions to infest individual trees. As the area transitioned to more epidemic conditions, short distance dispersal created the apparent clustering pattern. The abundance of large diameter pines, serving as suitable hosts, within the study area created an environment suitable for population growth to occur (Amman et al., 1985).

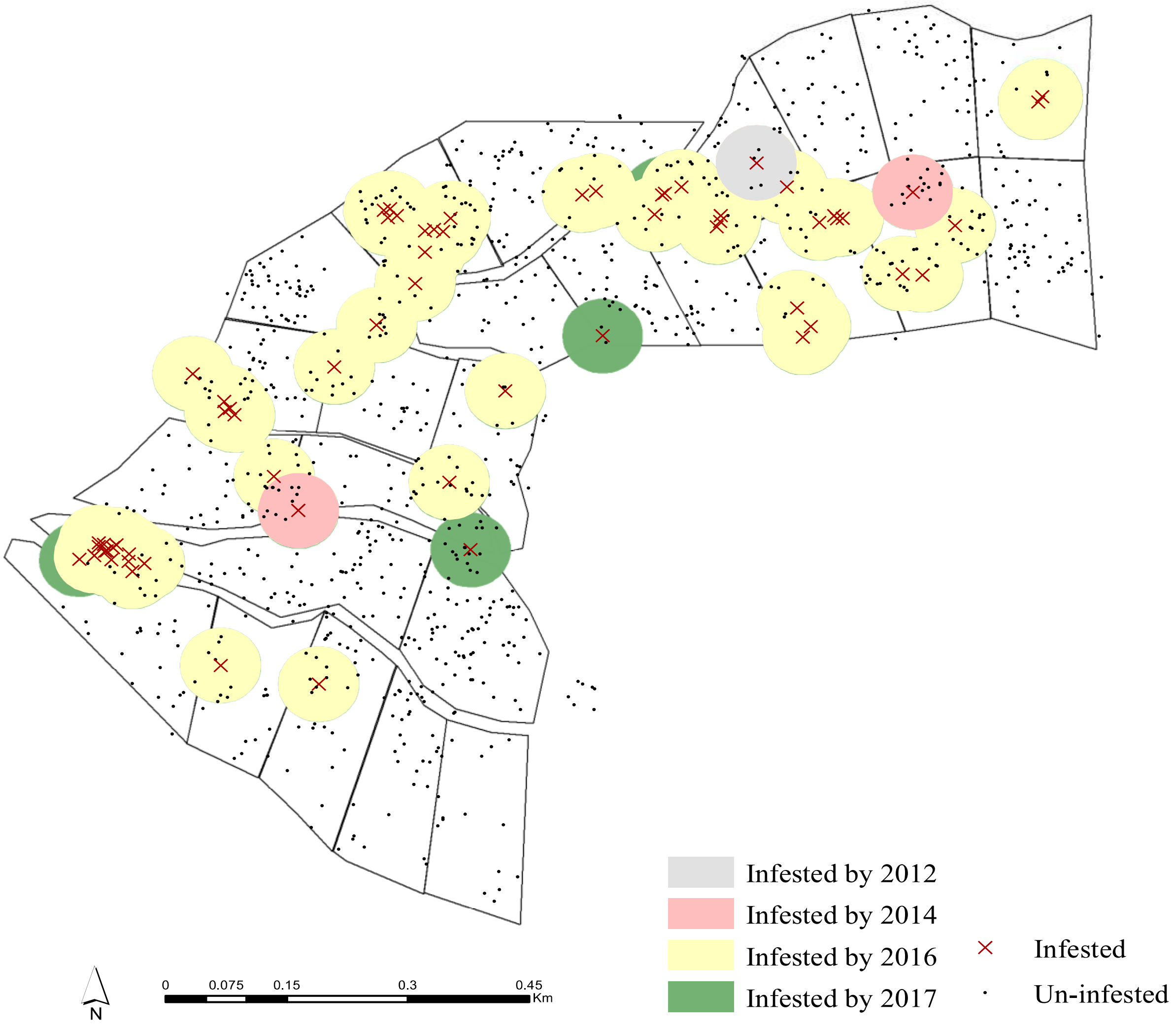

Figure 7: Clustering patterns in infestation emerge in 2016, with prior outbreaks dispersed across the study site.

Forest density was directly correlated to susceptibility to infestation. Forest density is inversely related to tree vigor, which is measured through wood production and leaf area. Trees with higher vigor have a larger proportion of photosynthetically active tissue, which is a mechanism of resistance to infestation; thus tree vigor is strongly inversely related to beetle infestation (Larsson et al. 1983; Kaiser et. al, 2013).

In the STEF experimental forest, trees in higher density areas were more likely to be infested, even when increased density did not correspond to more host trees. One potential explanation is that in dense areas, where wind is slowed by vegetation, beetles are better able to use pheromone dispersal to signal their location (Kaiser et. al, 2013).

Higher elevation sites had lower mortality rates. Beetle populations are temperature limited, with colder temperatures delaying life-stage development and increasing rates of mortality (Bentz. 1991). On the western slope of the Sierra Nevada, higher elevations experience colder temperatures and, therefore, beetles may have been limited in their ability to colonize and reproduce (Cudmore, et. al, 2010). In addition, forest density tends to decline with increasing elevation, and may have also contributed to the decreased mortality rates.

While rock type was also correlated to areas with greater infestation, it seems likely this is due to the strong correlation between geology and elevation. The rock type associated with greater levels of infestation was present only in the lower elevation ranges. Furthermore, a soil map of the study site classifies the entire area as part of the Wintoner-Inville families complex, indicating that shifts in bedrock did not have large influence on soil composition (USDA, 2014).

The heightened drought conditions that existed during most of the study carry various implications for beetle distribution patterns. Not only does water limit photosynthesis and, therefore, tree vigor, it is also a fundamental ingredient in producing resinous pitch to expel beetle populations (Christiansen, 1987). While water was limited across the study site, trees in the densest areas would be subjected to the driest conditions, as a result of greatest competition (Guarín, 2005). While areas of higher elevation are generally located in upper slope, drier positions, decreased forest density at higher elevations could have reduced competition for water.

This direct correlation between TWI and tree density, points to the significance of drought conditions in this study. Areas with high Wetness Index values had previously supported greater forest density but, with precipitation and water availability far below historic norms, trees with high TWI values were left stressed for water. In addition to lower values for tree vigor, trees in high density areas were subjected to the driest conditions as a result of increased competition throughout a historic drought.

Areas for further research

There was not a significant relationship between TWI values and infestation, which is likely due to limitations in the Index. The TWI is the relationship between the local slope and upslope accumulation area. Given the extreme drought, it would have also been useful to account for the density of upslope water users. In a water limited environment, wetness is determined, in part, by plant uptake (Guarín, 2005).

Conclusion

The direct human manipulation of forested areas and the less direct human contributions to global climate change have placed forest ecosystems at risk of extreme disturbance from beetle infestation and wildfire. One in three American households are located at the wildland-urban interface, where consequences of disturbances will continue to be direct and severe (USDA, 2015). Extreme disturbance alters wildfire patterns and wildlife habitat, both of which contribute to major shifts in ecosystem structure and function (Collins, 2011). As greater proportions of land become disturbed, humans living in urban areas will begin to face the consequences of widespread declines in timber production, watershed integrity, and recreational opportunities. Successful adaptation to a changing climate requires that preventative action be taken to curb the consequences of ecological disaster. In the case of the bark beetle epidemic, devastation is a symptom of direct human decisions to overharvest timber and suppress fire and a consequence of climate change. Action to counter those decisions must take the form of effective and efficient management.

The methods of this study and the model created present a step-by-step guide to study bark beetle infestation within similarly small areas and the findings of this study highlight potential benefits of site specific management plans. In this study, trees in the densest areas likely experienced the highest levels of stress as a result of drought conditions. Other potential drivers of stress, such location in higher slope positions, were not as amplified by drought conditions. In any site, the relative influence of each topographic driver of stress will vary depending on climatic factors, so the most effective management plans will take site-specific topographic and climate variables into account.

The present bark beetle outbreak is an amplification of natural disturbance as a result of human action. Ecosystems are resilient to small disturbances, but the current beetle outbreak exceeds historical norms. While many forested areas have already suffered the consequences infestation, vast areas of Western forest are left un-infested, but susceptible to attack. Enough is known about the causes of infestation to reduce the extent of future outbreaks. Human intervention in the form of more active forest management is necessary in curbing the cascading ecological consequences of the bark beetle outbreak. Millions of acres of forest in the American West are owned by individuals and agencies that are invested in the continued health and productivity of their forest lands. There is utility in bark beetle research, but only if science can be communicated and employed effectively. This study presents methods and a model that can be employed to develop site-specific and scientifically based forest management plans.

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Appendix

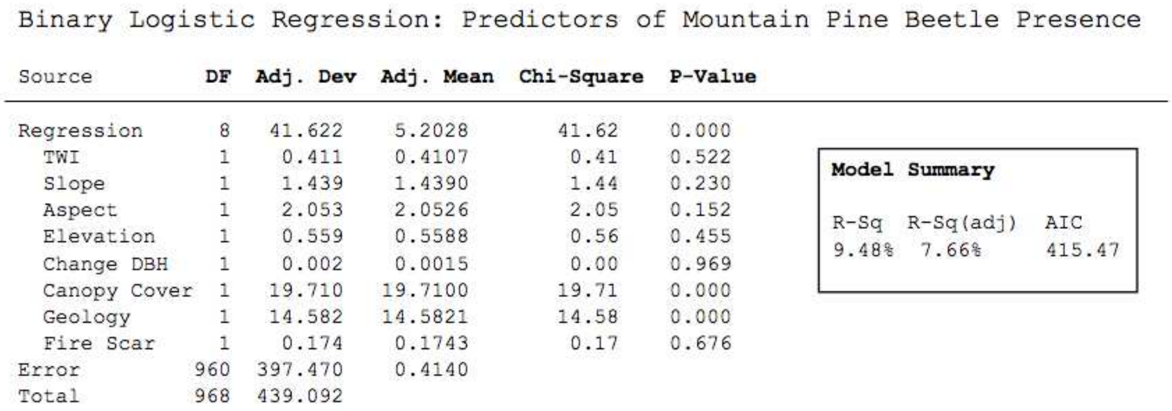
Control Plots (un-thinned)

Slope (Degrees)	Mean	14.20	Range	0.289-34.7
Elevation (Meters)	Mean	1863.72	Range	1825-1944
TWI Values	Mean	3.81	Range	0-10.4
	Median	3.28		
Canopy Cover (%)	Mean	86.90	Range	48.57-98.75
	Median	88.70		
Infested (%)		16.15	Total Trees	31
Aspect (Direction)	North	Percent of total	40.63	
	North East	Percent of total	20.84	
	East	Percent of total	1.04	
	South East	Percent of total	2.08	
	South	Percent of total	1.56	
	South West	Percent of total	2.08	
	West	Percent of total	12.5	
	North West	Percent of total	19.27	

Thinned Plots

Slope (Degrees)	Mean	13.06	Range	0.56-32.36
Elevation (Meters)	Mean	1848.59	Range	1807-1964
TWI Values	Mean	3.56	Range	0-12.1
	Median	3.16		
Canopy Cover (%)	Mean	71.62	Range	35.40-96.049
	Median	71.86		
Infested (%)		3.94	Total Trees	32
Aspect (Direction)	North	Percent of total	41.01	
	North East	Percent of total	37.68	
	East	Percent of total	9.61	
	South East	Percent of total	1.60	
	South	Percent of total	2.46	
	South West	Percent of total	6.90	
	West	Percent of total	8.25	
	North West	Percent of total	17.61	

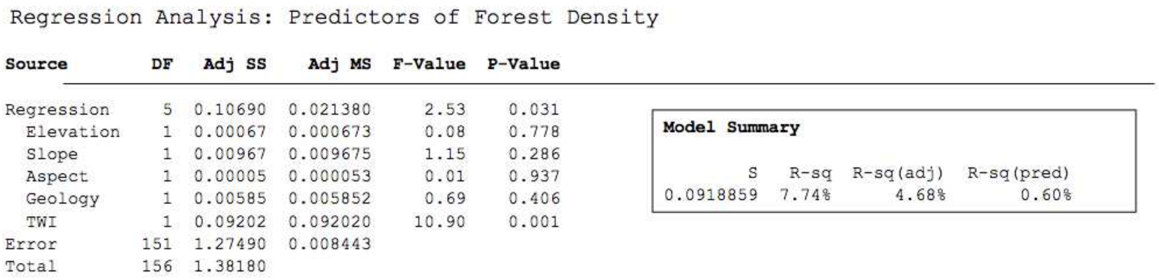
Table 1: These tables show the mean and ranges in topographic variables for the control plots and thinned plots. The difference in the ranges is minimal between the control plots and the tinned plots, indicating that differences in mortality between the two treatments could not be attributed to differences in topography.



```
Binary Logistic Regression: Predictors of Mountain Pine Beetle Presence

Source          DF  Adj. Dev  Adj. Mean  Chi-Square  P-Value
-------------------------------------------------------------------------------------
Regression       8    41.622     5.2028       41.62    0.000
  TWI            1     0.411     0.4107        0.41    0.522     Model Summary
  Slope          1     1.439     1.4390        1.44    0.230
  Aspect         1     2.053     2.0526        2.05    0.152     R-Sq   R-Sq(adj)   AIC
  Elevation      1     0.559     0.5588        0.56    0.455     9.48%   7.66%      415.47
  Change DBH     1     0.002     0.0015        0.00    0.969
  Canopy Cover   1    19.710    19.7100       19.71    0.000
  Geology        1    14.582    14.5821       14.58    0.000
  Fire Scar      1     0.174     0.1743        0.17    0.676
Error          960   397.470     0.4140
Total          968   439.092
```

Table 2: The variables used in this regression model do not provide a complete list of all contributors to bark beetle infestation (R-Sq. adjusted 7.66%). Of the variables considered in the regression, tree density (Canopy Cover) and geology are the only potential predictors of infestation (P-Values 0.000).



```
Regression Analysis: Predictors of Forest Density

Source        DF   Adj SS    Adj MS  F-Value  P-Value
-------------------------------------------------------------------------------------
Regression     5  0.10690  0.021380     2.53    0.031
  Elevation    1  0.00067  0.000673     0.08    0.778     Model Summary
  Slope        1  0.00967  0.009675     1.15    0.286
  Aspect       1  0.00005  0.000053     0.01    0.937             S   R-sq  R-sq(adj)  R-sq(pred)
  Geology      1  0.00585  0.005852     0.69    0.406     0.0918859  7.74%      4.68%       0.60%
  TWI          1  0.09202  0.092020    10.90    0.001
Error        151  1.27490  0.008443
Total        156  1.38180
```

Table 3: Regression analysis for the predictors of tree density was preformed using trees within the 5 untinned control plots, where tree density was not influenced directly by recent logging activity. The analysis did not provide a suitable model to predict tree density (R-sq adjusted 4.68%). The regression indicated water availability (topographic wetness index values) to be a potential contributor to tree density.