FINAL REPORT

Title: Effects of variable density thinning and burning treatments on the spatial patterns of drought-related tree mortality

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VDT	Variable Density Thinning

Keywords

bark beetles, prescribed fire, fuels treatments, resilience, restoration, tree vigor

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Abstract

Over recent decades, increases in substantial tree mortality events have coincided with severe drought and bark beetle outbreak. This has prompted forest managers to find treatments that enhance resistance to disturbances. Variable density thinning is an alternative management method intended to increase spatial heterogeneity, with the potential to influence levels of bark beetle-associated mortality. However, there is limited research on the ecological consequences related to the structures that characterize variable density thinning. This study evaluated how structures within variable density thinning, that were burned and unburned, affect resistance to bark beetle outbreak, whether the influence of these structures change with scale, and what spatial patterns of bark beetle-associated mortality arise in variable density thinning treatments following a drought. We conducted stand inventories of eight variable density thinning units (four prescribed burned and four unburned) within the Stanislaus-Tuolumne Experimental Forest. We collected data on all trees ≥ 25 cm diameter at breast height and recorded species, diameter at breast height, and mortality agent. We used this data to conduct spatial analysis evaluating the effects of total basal area, intraspecific host proportion, intraspecific host gaps, quadratic mean diameter, and canopy cover on tree mortality at different scales. Our results showed that bark beetle-associated mortality was relatively low in sugar pine (14 %) and equivalent to other levels of reported mortality amongst white fir (24 %) during this most recent drought and insect outbreak in the Sierra Nevada. Prescribed fire treatments did not contribute to differences in tree mortality amounts compared to unburned plots. We found that the proportion of intraspecific hosts was positively associated with white fir mortality at small scales (10 to 20 m), while quadratic mean diameter was negatively associated with mortality at larger scales (30 to 50 m). Increased canopy cover was positively related to bark beetle-associated mortality in sugar pine at 10 m, while proportion of intraspecific hosts had a stronger positive association with mortality at larger scales (20 to 50 m). Despite structural characteristics influencing proportion of bark beetle-associated mortality, spatial analyses revealed that white fir and sugar pine mortality was limited across space, with clustering of mortality occurring at scales less than 14 m. These results suggest that treatments intended to increase spatial heterogeneity and reduce fuel loads may have the positive benefit of mitigating the levels and spatial patterns of bark beetle-associated mortality during severe and prolonged drought.

Objectives

The overall objective of our study was to discern the influence of structural characteristics resulting from variable density thinning (VDT) treatments, with and without prescribed burning, affect resistance during a prolonged and severe drought. To meet this objective, we addressed the following questions:

1) Does bark beetle-associated mortality differ between variable density thinning with and without prescribed burning?

2) How do structural characteristics influence resistance to bark beetle-associated mortality?

3) At which scales do these structures have the greatest influence on tree mortality?

4) What are the spatial patterns of bark beetle-associated mortality within stands treated with VDT?

Although managers tailor plans to meet landowner objectives, increasing frequency and intensity of disturbances may prevent managers from achieving those objectives. Findings from our research can provide insight on how managers can effectively manipulate structural elements to create resistant forests in the face of climate change.

Background

Although drought is a common occurrence across the world, climate change can cause substantial tree mortality by increasing the frequency and intensity of regional droughts (Allen et al. 2015). Long-term tree mortality trends have increased over the last several decades, coinciding with above-average temperatures, high climatic water deficits, and bark beetle outbreak (van Mantgem et al. 2009, Meddens et al. 2012, Young et al. 2017). Changes in the frequency and intensity of disturbances predicted under climate change may increase the vulnerability of forest ecosystems (Allen et al. 2010), potentially altering the trajectory of forest ecosystems in unanticipated directions. Uncertainty in how forests will respond to disturbances under climate change necessitates creative ways to manage forests.

Thinning and prescribed fire are commonly used methods to reduce competition, which can potentially mitigate tree mortality to drought and bark beetles. These treatments mainly focus on reducing stand density to create sufficient resources to resist bark beetles (Coops et al. 2009, Fettig et al. 2012, Stark et al. 2013). Despite the efficacy of these treatments for enhancing tree survival during drought (van Mantgem et al. 2016) and bark beetle attack (Hood et al. 2015, Hood et al. 2016), they may lack spatial complexity that promotes forest resistance (North et al. 2009, Fettig et al. 2012) and lack other important stand structures valued by wildlife species (Carey 2003).

The effects of spatial heterogeneity on bark beetle-associated mortality can vary based on the resultant structural characteristics within a stand. Highly competitive environments can be significant drivers of tree mortality (Das et al. 2011), possibly increasing bark beetle-associated mortality if areas of greater competition increase tree stress. Bark beetles are host specific, often attacking trees of a particular genus.

Facilitation of bark beetle dispersal and colonization may occur if part of a stand contains a greater density of conspecific hosts or hosts within close proximity to each other, increasing the vulnerability of trees to mortality (Raffa and Berryman 1975). Larger trees may also be more susceptible to bark beetle-caused mortality because they tend to be more drought-stressed (Bennett et al. 2015) and are often the preferred host size of bark beetles (Raffa et al. 2008). Therefore, the size of hosts across space may also affect tree mortality. If openings increase light availability and enhance tree vigor (York et al. 2003, York et al. 2011), then decreases in canopy cover may mitigate bark beetle-associated mortality.

Spatial patterns of tree mortality may also indicate whether spatial heterogeneity can confer resistance to bark beetle-associated mortality. Because beetle dispersal is constrained by host proximity and host selection (Kautz et al. 2011, Kautz et al. 2016), movement across structures may depend on the amount of susceptible hosts. Tree mortality often occurs in clustered spatial patterns from tree to stand scales (Smith et al. 2005), possibly due to high host susceptibility within forest structures (Raffa and Berryman 1975). If greater host stocking leads to higher probability of beetle infestation (Negron and Popp 2004), then spatial variability may disrupt the continuity of available hosts and limit bark beetle-associated mortality across space (Seidl et al. 2016).

Variable density thinning (VDT) is an alternative management method that can reduce stand density, with the additional benefit of promoting spatial heterogeneity. VDT enhances forest heterogeneity by increasing variation in tree density, species composition, and size classes (Knapp et al. 2017). By mimicking the individual trees, clumps of trees, and openings that were present historically, VDT incorporates structural legacies that once helped forests evade, resist, or recover from disturbances prior to logging and fire exclusion (Perry and Amaranthus 1997). However, there is limited research on how the residual structures in VDT affect the levels and spatial patterns of bark beetle-associated mortality. A recent prolonged and severe drought in California (2012-2016) resulted in substantial levels of bark beetle mortality across a range of forest conditions (**Figure 1**), providing an opportunity to examine the effects of spatial stand structures resulting from variable density thinning and prescribed burning treatments on tree mortality.

Figure 1 Tree mortality associated with drought and bark beetle attack following variable density thinning treatments on the Stanislaus-Tuolumne Experimental Forest. Mortality was present in patches of individual trees (left), small clusters (center), and large clusters (right).

Materials and Methods

Study Site

Our study site consists of a 100 ha mixed-conifer forest located within the Stanislaus-Tuolumne Experimental Forest in the central Sierra Nevada of California (**Figure 2**). At an elevation of 1740 m to 1900 m, stands at this site are composed of white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), and incense-cedar (*Calocedrus decurrens*). Four years prior to the onset of drought (2008 – 2011), average temperature ranged from 8.7°C to 9.9 °C and precipitation ranged from 90.6 cm – 160.4 cm (PRISM, 2019). During the extended drought from 2012 to 2015, average temperature was 15 % higher than average (range = 10.6 – 11.4 °C) and precipitation was 44 % lower than average (range = 36.6 – 115.6 cm).

A combination of logging practices from the 1920s and fire exclusion increased tree densities within the Stanislaus-Tuolumne Experimental Forest and shifted dominance towards shade-tolerant species and trees of smaller-sized diameter classes (Knapp et al. 2013). In 2011, the United States Department of Agriculture Forest Service implemented a variable density thinning experiment, where eight units (4 ha each) were thinned to generate high variability stand structures similar to conditions pre-logging and fire suppression (Knapp et al. 2017). In each VDT unit, five gaps were created ranging from 0.04 – 0.2 ha within areas dominated by shade-tolerant species or with root disease present. The remainder of each VDT unit was divided into groups of similar-sized trees, with each group thinned either to a low (27.5 m^2 ha^{-1}), medium (50.5 m^2 ha^{-1}), or high (73.5 m^2 ha^{-1}) basal area target. A prescribed fire was applied to half of the units generating two different treatments, a variable density thin and burned treatment and a variable density thin and unburned treatment.

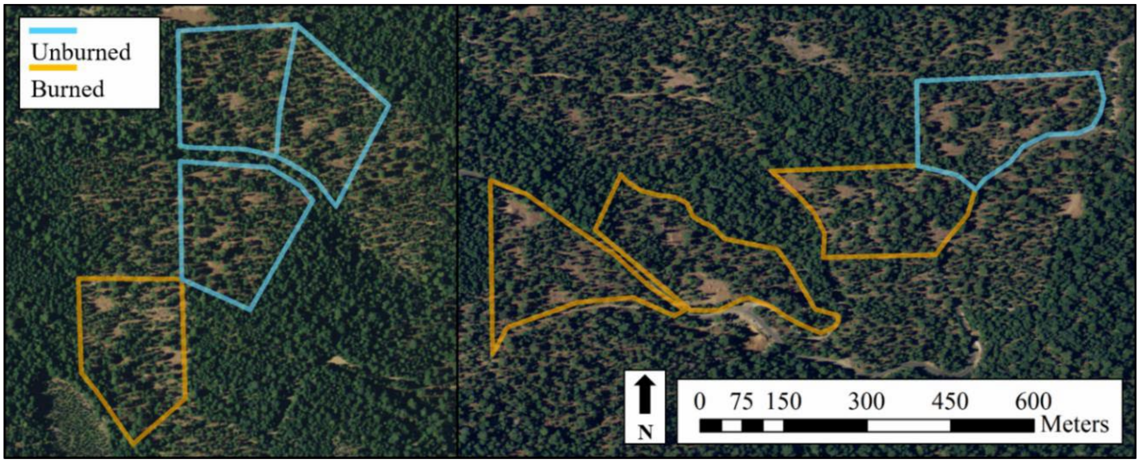

Figure 2 Locations of variable density thinning units within the Stanislaus-Tuolumne Experimental Forest. Unit boundaries superimposed on aerial photos provided by the United States Department of Agriculture National Agriculture Imagery Program, 2012.

Stand Maps

To create maps of current stand structures, we utilized light detection and ranging (LiDAR) data collected by Quantum Spatial in 2014. This dataset included each treated unit, showing a range of point densities from 14 to 20 points m^{-2}. Using this LiDAR dataset, we detected treetops with the lidR package (Roussel and Auty 2018) in R (R Core Team 2018). This package contains a function that uses local maxima filters to estimate the location of individual trees. From these estimates, we created digitized maps of tree locations for each unit that we subsequently used in the field to conduct stand inventories (**Figure 3**). The spatial reference system for all datasets used in our analyses was North American Datum 1983, Universal Transverse Mercator Zone 10 North.

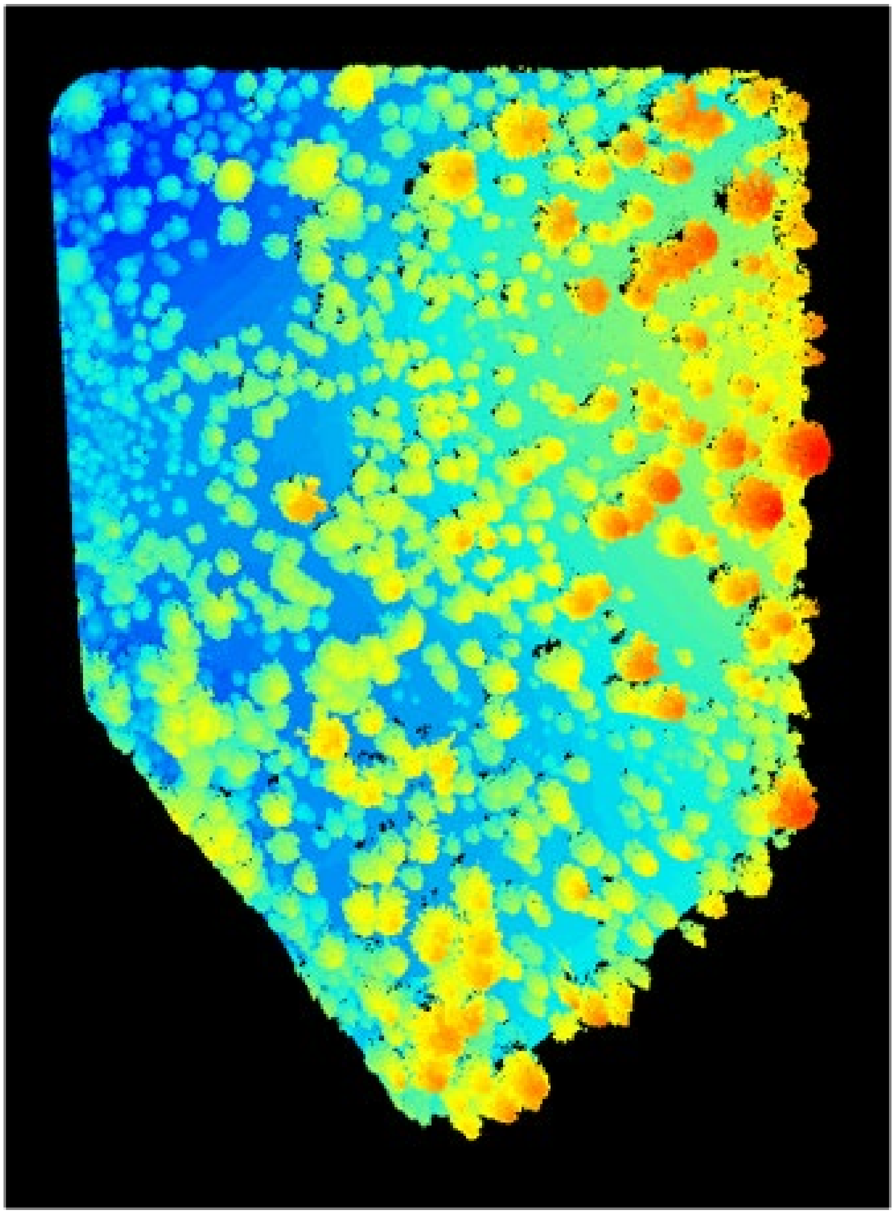

Figure 3 A stand map of a variable density thinning unit based on LiDAR generated tree locations.

Data Collection

With our digitized maps, we confirmed the location of all trees ≥ 25 cm diameter at breast height (DBH). In the field, we found that our LiDAR-generated maps did not always distinguish tree locations in areas with high canopy cover, resulting in an underestimation of trees (**Figure 4**). We added these locations to our dataset by estimating distance and bearing from the closest tree of known location. In some cases, the irregular crown structure of a single tree showed multiple tree-tops in our LiDAR- generated maps. To determine the most accurate location, we measured the distance (m) and bearing (°) from each predicted location to a tree of known location and chose the predicted point with the closest estimates. During instances where predicted points poorly reflected the actual tree location, we added new coordinates based on the distance and bearing from a tree of known location. Once a tree's location was confirmed, we recorded species, status (live or dead), and diameter at breast height (DBH, cm). If a tree was dead, we removed the bark to confirm bark beetle activity by identifying larval galleries of fir engraver (*Scolytus ventralis*) on white fir and mountain pine beetle (*Dendroctonus ponderosae*) on sugar pine.

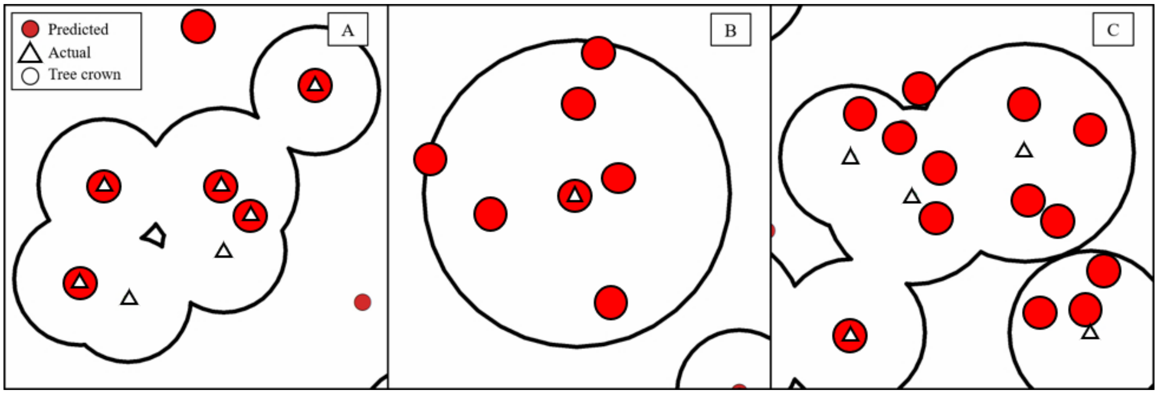

Figure 4 Map of predicted tree locations from LiDAR data and actual locations of trees. Panel A depicts underestimation of tree counts, panel B depicts overestimation of tree counts, and panel C depicts poor estimations of tree locations.

Stand Structures

Once all units were inventoried, we transferred each tree's information to the existing shapefile of tree locations using ArcMap 10.5.1 (ESRI, Redlands, CA). Our digitized maps with all tree locations also included point locations of a previously established 30 m systematic grid, which we used as plot centers to quantify proportion of tree mortality associated with fir engraver and mountain pine beetle. Using the sf package (Pebesma 2018) in R (R Core Team 2018), we delineated multi-ring buffers in intervals of 10 m, ranging from 10 to 50 m from each plot center to determine if the influence of structures change with scale. If a point had a buffer that was located outside of a unit boundary or if a plot did not contain any sugar pine or white fir, we excluded that point from further analysis. Although exclusion resulted in a reduced sample size (**Table 1**), this was a conservative approach to reduce bias in our analyses (Pommerening and Stoyan 2006). Within each buffer, we quantified structural characteristics including competition from all trees (total basal area, m^2 ha^{-1}), intraspecific host proportion (number of potential beetle hosts/total number of trees), host gap (area unoccupied by potential beetle hosts, ha), and quadratic mean diameter of potential hosts (cm). Based on allometric equations derived from Gill et al. (2000), we estimated crown radius (m) for each tree based on DBH and used these radii to estimate canopy cover (%).

Table 1 Number of plots containing bark beetle-associated mortality of white fir or sugar pine.

	10 m	20 m	30 m	40 m	50 m
White fir	120	120	81	45	28
Sugar pine	72	106	78	45	28

Data Analysis

We created separate logistic regression models to predict the proportion of white fir and sugar pine mortality across different scales. Using structural characteristics as explanatory variables, we evaluated the effect of each metric independently at a given distance from plot center. Preliminary analysis using likelihood ratio tests showed that the addition of prescribed fire as a covariate did not improve model performance. Therefore, we included all eight variable density units but excluded prescribed fire as a parameter in further analyses. We repeated these models for all distances, totaling five models for each distance and 25 models in total. We reported all models and determined the top model predicting the proportion of white fir or sugar pine mortality based on the lowest Akaike Information Criterion (AIC) values. We also assigned Akaike weights with the following formula to determine the probability that a given model was the best (Wagenmakers and Farrell 2004):

$$w_i = \frac{\exp(-\frac{1}{2}\Delta_i)}{\sum_{r=1}^{R}\exp(-\frac{1}{2}\Delta_r)}$$

The numerator represents the relative likelihood of model i, where Δ_i is the difference in AIC values between model i and the best model. The denominator represents the sum of relative likelihoods from all models being compared.

Spatial patterns of mortality

In the *spatstat* (Baddeley et al. 2015) package in R, we discerned the spatial patterns of bark beetle-associated mortality by employing the pair correlation function, which is a derivative of the Ripley's K function and is defined as:

$$g(r) = \frac{K'(r)}{2\pi r}$$

Where (r) represents the probability of observing a pair of points at an interpoint distance of r (Baddeley et al. 2015). We used the univariate form of (r) to calculate distances between trees that died from bark beetle-associated mortality, $g_{d,d}(r)$, and the bivariate form to calculate distances from trees that died from bark beetle-associated mortality and those that survived, $g_{d,l}(r)$. Within multiple distances of a dead tree, the number of neighboring dead trees and the number of trees that survived were counted. Similar to Larson et al. (2015), we generated 999 simulations of random point patterns for each distance to generate a random distribution envelope that compares the number of observed point patterns with a random distribution of trees. We pooled these Monte Carlo simulations across all individual units to assess deviations from random distributions. We then evaluated the extent of bark beetle-associated mortality by using $g_{d,d}(r) - g_{d,l}(r)$, which compares the probability of dead trees surrounding other dead trees with the probability of live trees surrounding dead trees. Positive values ($g_{d,}(r) > g_{d,l}(r)$) indicate that dead trees were clustered amongst other trees that died from bark beetle-associated mortality, while negative values ($g_{d,d}(r) < g_{d,l}(r)$) indicated that dead trees were dispersed amongst live trees.

Results

At our study site, 15 % of all trees died between 2012 and 2018. Although bark beetle galleries were present on 77 % of the white fir and 95 % of the sugar pine that died, bark beetle-associated mortality affected only 24 % of all white fir and 14 % of all sugar pine. At the plot level, white fir mortality was on average 63 to 75 % higher than sugar pine mortality across all distances. On average, 15 % of all white fir in unburned units died from bark beetle-associated mortality (range = 8 – 23 %), while 21 % of all white fir in burned units ultimately succumbed to mortality (range = 8 – 41 %). Despite higher levels of mortality present in burned units, the percentage of white fir mortality was not higher after prescribed fire was applied in 2013 ($F_{1,6}$, $p = 0.524$). Although sugar pine in unburned stands had half of the average mortality (7 % , range = 2 – 14 %) than sugar pine in units treated with prescribed fire (14 %, range = 12 – 14 %), percentage of mortality of all sugar pine was similar across both treatments ($F_{1,6}$, $p = 0.099$).

White fir mortality

Our top models predicting proportion of white fir mortality included intraspecific host proportion and quadratic mean diameter (**Table 2**). At smaller scales (10 and 20 m), proportion of intraspecific hosts was positively related to proportion of white fir mortality ($p = 0.018$ and $p < 0.001$, respectively), with plots entirely composed of white fir having 20 % mortality (**Figure 5**). At larger scales (30 to 50 m), quadratic mean diameter was negatively associated with fir mortality ($p < 0.001$, **Table 3**), with plots having 15% mortality when quadratic mean diameter of white fir was less than 40 cm. While our other models also included total basal area, canopy cover, and host gap area, these models were greater than 2 AIC points from the top models for each distance, suggesting that the quality of these models were lower relative to the top models.

Sugar pine mortality

Our top models predicting the proportion of sugar pine mortality included canopy cover and intraspecific host proportion (**Table 4**). Canopy cover at smaller scales (10 m) had a positive association with sugar pine mortality ($p = 0.026$, **Table 5**), with plots containing less than 40 % canopy cover exhibiting no sugar pine mortality (**Figure 6**). At larger scales (20 to 50 m), intraspecific host proportion was positively associated with sugar pine mortality ($p < 0.001$), with plots composed entirely of sugar pine increasing mortality up to 10 %. While our other models also included total basal area, quadratic mean diameter, and host gap area, these models were greater than 2 AIC points from the top models for each distance, suggesting that the quality of these models were lower relative to the top models.

Table 2 Summary of model inputs predicting the proportion of white fir mortality and model performance metrics. K indicates the number of parameters in the model. Δ AIC indicates the difference between AIC values from a given model and the top-rated model. AIC weight suggests the probability that a given model is the best model in comparison to all model being evaluated. Log likelihood describes the fit of estimated coefficients to observed data, with higher values suggesting a better fit.

Model inputs	**K**	**Δ AIC**	**AIC weight**	**Log likelihood**
10 meter buffers				
Host proportion	1	0.00	0.60	-104.91
Host gap	1	2.22	0.20	-106.02
Quadratic mean diameter	1	3.28	0.14	-105.51
Total BA	1	5.26	0.05	-107.54
Canopy cover	1	5.57	0.04	-107.69
20 meter buffers				
Host proportion	1	0.00	0.97	-193.89
Quadratic mean diameter	1	7.30	0.03	-192.04
Host gap	1	26.72	<0.01	-207.25
Canopy cover	1	36.36	<0.01	-212.07
Total BA	1	39.22	<0.01	-213.50
30 meter buffers				
Quadratic mean diameter	1	0.00	0.99	-178.03
Host proportion	1	25.97	<0.01	-190.51
Host gap	1	31.43	<0.01	-193.24
Canopy cover	1	31.93	<0.01	-193.49
Total BA	1	32.07	<0.01	-193.56
40 meter buffers				
Quadratic mean diameter	1	0.00	0.99	-98.42
Total BA	1	25.24	<0.01	-110.94
Host gap	1	25.48	<0.01	-111.06
Canopy cover	1	26.84	<0.01	-111.74
Host proportion	1	26.95	<0.01	-111.79
50 meter buffers				
Quadratic mean diameter	1	0.00	0.98	-61.70
Host proportion	1	9.05	0.01	-66.22
Host gap	1	10.11	<0.01	-66.75
Total BA	1	17.17	<0.01	-70.29
Canopy cover	1	20.79	<0.01	-72.10

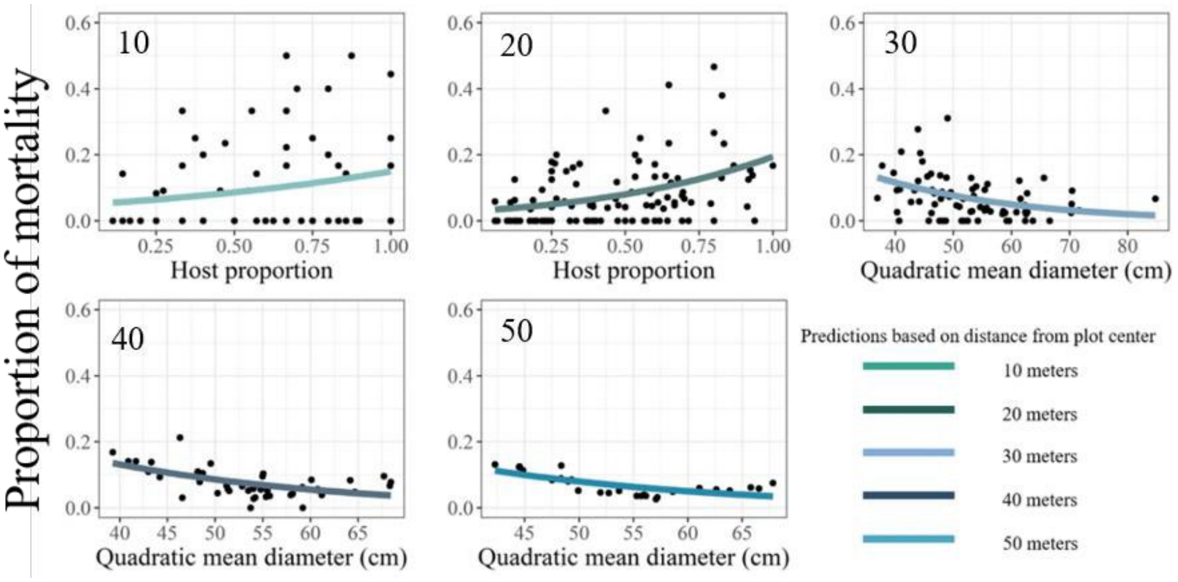

Figure 5 Response curves from top logistic regression models predicting the proportion of white fir mortality across different scales, with black dots representing observed values. Numbers in top left corner indicate distance (m) from plot center.

Table 3 Summary of effect size for top logistic regression models predicting proportion of white fir mortality across different scales.

Model inputs	**Coefficient estimate (β)**	**Standard error**	**p-value**
10 meters			
Intercept	0.08	0.54	<0.001
Conspecific density	1.00	0.98	**0.018**
20 meters			
Intercept	0.07	0.52	<0.001
Conspecific density	1.00	0.92	**<0.001**
30 meters			
Intercept	0.01	0.52	<0.001
Quadratic mean diameter	0.50	0.50	**<0.001**
40 meters			
Intercept	0.01	0.52	<0.001
Quadratic mean diameter	0.50	0.50	**<0.001**
50 meters			
Intercept	0.01	0.52	<0.001
Quadratic mean diameter	0.50	0.50	**<0.001**

Table 4 Summary of model inputs predicting the proportion of sugar pine mortality and model performance metrics. K indicates the number of parameters in the model. Δ AIC indicates the difference between AIC values from a given model and the top-rated model. AIC weight suggests the probability that a given model is the best model in comparison to all model models evaluated. Log likelihood describes the fit of estimated coefficients to observed data, with higher values suggesting a better fit.

Model inputs	**K**	**Δ AIC**	**AIC weight**	**Log likelihood**
10 meter buffers				
Canopy cover	1	0.00	0.75	-25.78
Host proportion	1	4.71	0.07	-28.13
Host gap	1	4.95	0.06	-28.25
Total BA	1	5.10	0.06	-28.33
Quadratic mean diameter	1	5.26	0.05	-28.41
20 meter buffers				
Host proportion	1	0.00	0.96	-81.88
Host gap	1	6.90	0.03	-85.34
Total BA	1	11.30	<0.01	-87.53
Quadratic mean diameter	1	11.55	<0.01	-87.66
Canopy cover	1	11.86	<0.01	-87.81
30 meter buffers				
Host proportion	1	0.00	0.99	-90.05
Host gap	1	8.66	0.01	-94.38
Canopy cover	1	20.41	<0.01	-100.25
Total BA	1	20.78	<0.01	-100.44
Quadratic mean diameter	1	22.66	<0.01	-101.38
40 meter buffers				
Host proportion	1	0.00	0.96	-64.65
Quadratic mean diameter	1	6.57	0.04	-67.94
Host gap	1	11.36	<0.01	-70.32
Canopy cover	1	13.93	<0.01	-71.62
Total BA	1	14.08	<0.01	-71.70
50 meter buffers				
Host proportion	1	0.00	0.99	-45.69
Quadratic mean diameter	1	17.78	<0.01	-49.57
Host gap	1	18.22	<0.01	-49.80
Total BA	1	21.40	<0.01	-51.38
Canopy cover	1	21.49	<0.01	-51.43

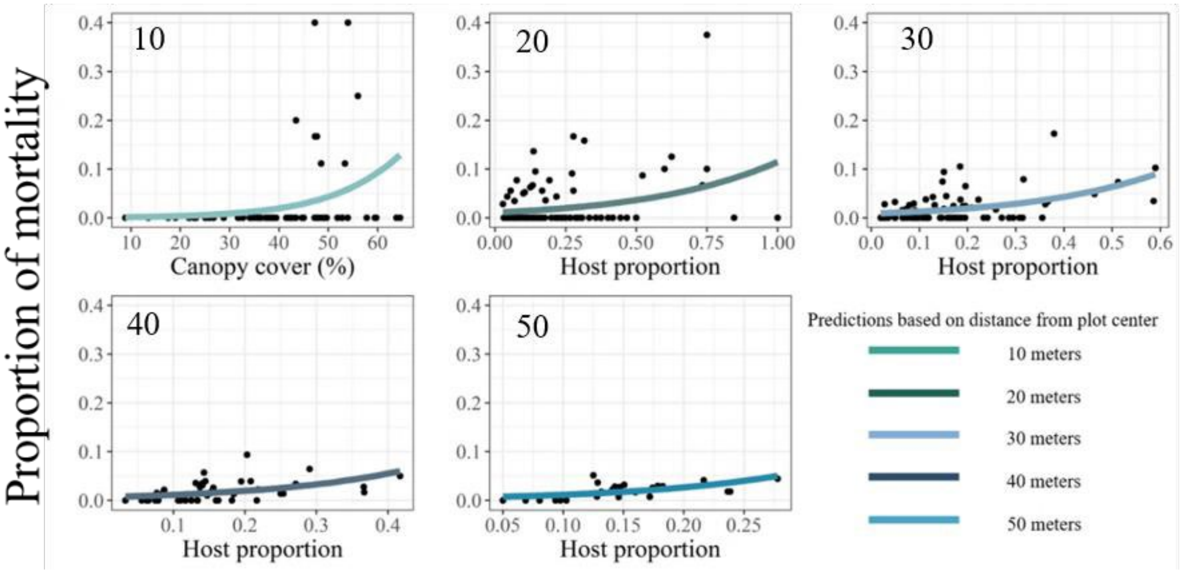

Figure 6 Response curves from top logistic regression models predicting the proportion of sugar pine mortality across different scales, with black dots representing observed values. Numbers in top left corner indicate distance (m) from plot center.

Table 5 Summary of effect size for top logistic regression models predicting proportion of sugar pine mortality across different scales.

Model inputs	**Coefficient estimate (β)**	**Standard error**	**p-value**
10 meters			
Intercept	1.00	1.00	0.028
Canopy cover	0.54	0.52	**0.026**
20 meters			
Intercept	0.55	0.55	<0.001
Conspecific density	1.00	1.00	**<0.001**
30 meters			
Intercept	0.02	0.54	<0.001
Conspecific density	1.00	1.00	**<0.001**
40 meters			
Intercept	0.02	0.54	<0.001
Conspecific density	1.00	1.00	**<0.001**
50 meters			
Intercept	0.02	0.53	<0.001
Conspecific density	1.00	1.00	**<0.001**

Spatial patterns of mortality

Our spatial analysis suggested that patterns of bark beetle-associated mortality were similar for white fir and sugar pine. While individual units showed clustered patterns of white fir mortality across varying distances (**Figure 7**), pooled estimates indicated a clustered mortality pattern at scales less than 12 m (**Figure 8**). At scales greater than 12 m, observed patterns of white fir mortality did not deviate from mortality patterns generated by complete spatial randomness, suggesting that mortality was randomly distributed at these larger scales. Additionally, pooled estimates from a paired correlation function analysis suggested that patterns of bark beetle-associated mortality differed between burn and unburned treatments. Clustering of bark beetle-associated mortality occurred at scales less than 10 m for white fir within unburned units, while clustering of mortality across units treated with prescribed fire did not show patterns of clustering across any scale.

Due to a small sample size of sugar pine that died from bark beetle-associated mortality within individual units, we were unable to generate (r) estimates of random patterns of mortality for all units. Therefore, we excluded six units from further analysis (**Figure 9**). However, pooled estimates of the patterns across two units with sufficient sample size showed observations of sugar pine mortality clustered at scales less than 14 m (**Figure 10**). At scales greater than 14 m, patterns of sugar pine mortality did not deviate from mortality patterns generated by complete spatial randomness, suggesting that mortality was also randomly distributed at larger scales. Sugar pine mortality showed a lack of significant clustering across any scale in units treated with prescribed fire, but there was an insufficient sample size of bark beetle-associated mortality in unburned units to compare spatial patterns of mortality.

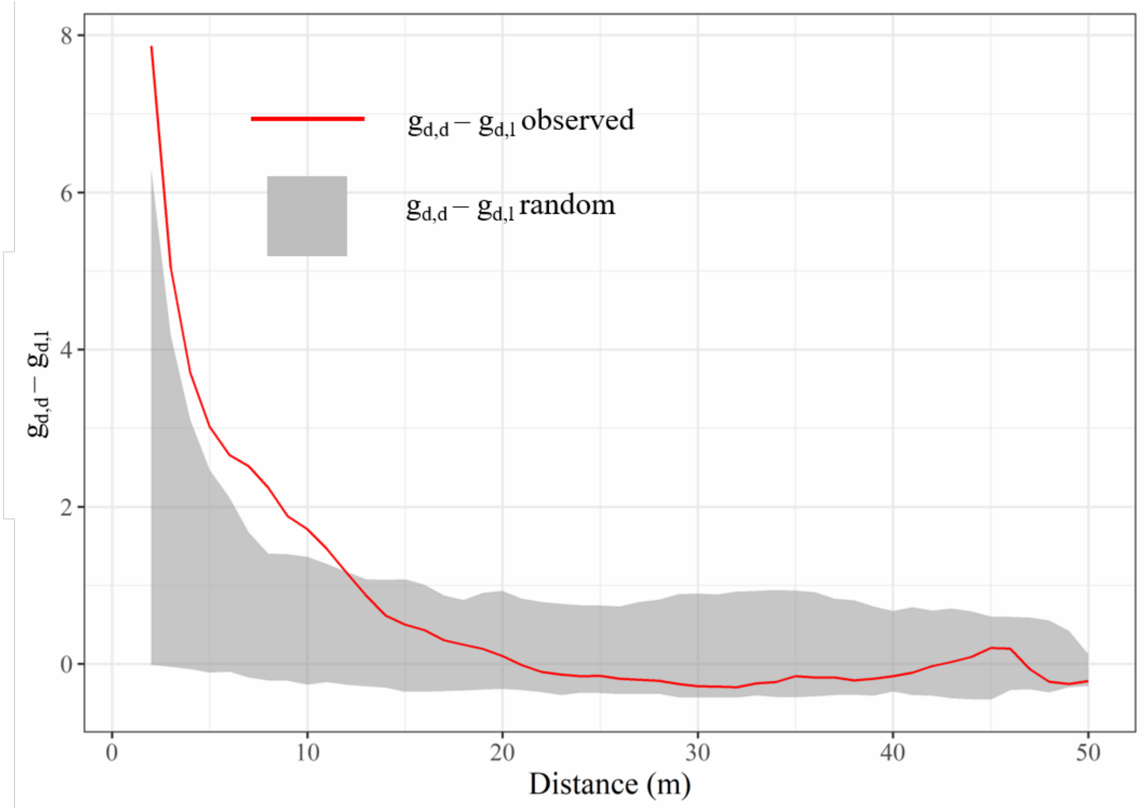

Figure 7 Pooled estimates of spatial patterns of bark beetle-associated mortality between observed dead white fir (red line) and mortality patterns generated by complete spatial randomness (gray). Deviations of observed values above the gray area ($g_{d,} - g_{d,l}{}_{observed} > g_{d,d} - g_{d,l}{}_{random}$) indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality.

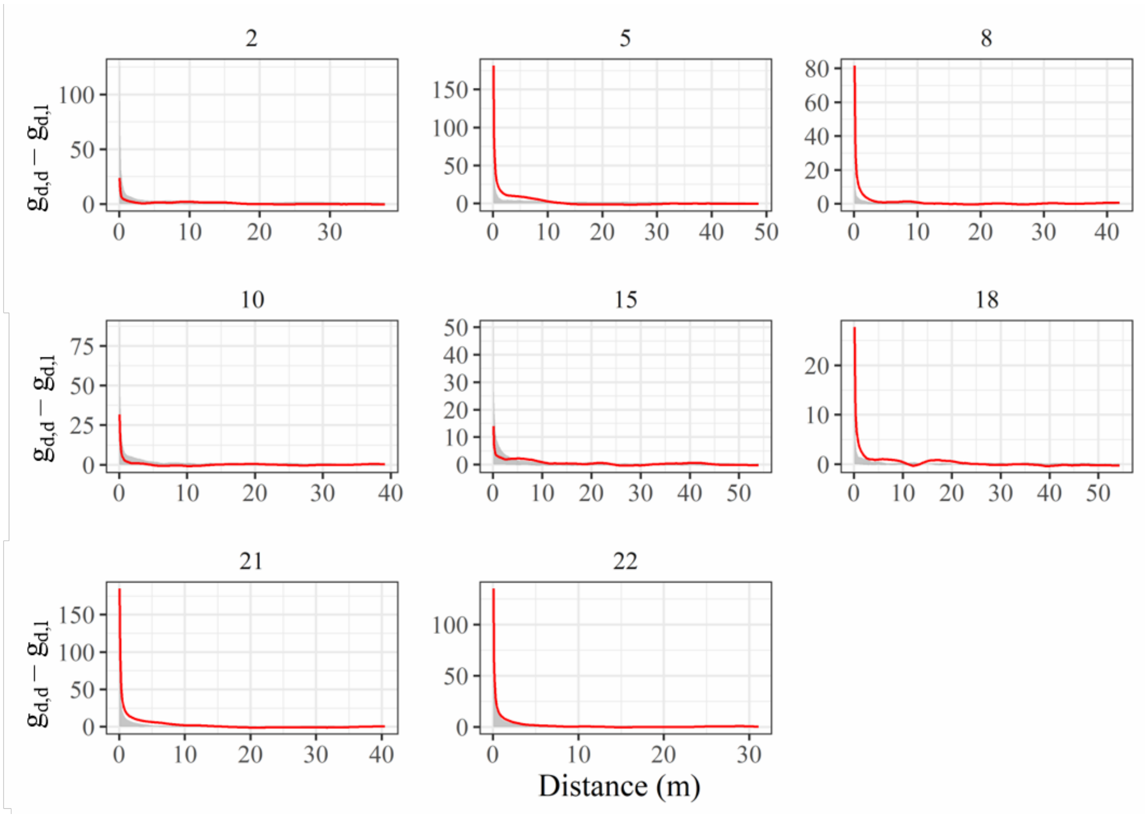

Figure 8 Individual unit estimates of spatial patterns of bark beetle-associated mortality between observed dead white fir (red line) and mortality patterns generated by complete spatial randomness (gray). Deviations of observed values above the gray area ($g_{d,} - g_{d,l}{}_{observed} >$ $g_{d,d} - g_{d,l}{}_{random}$) indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality. Plots without patterns of random mortality did not contain an adequate sample of dead trees to generate simulation envelopes and were removed from the pooled estimate of (r).

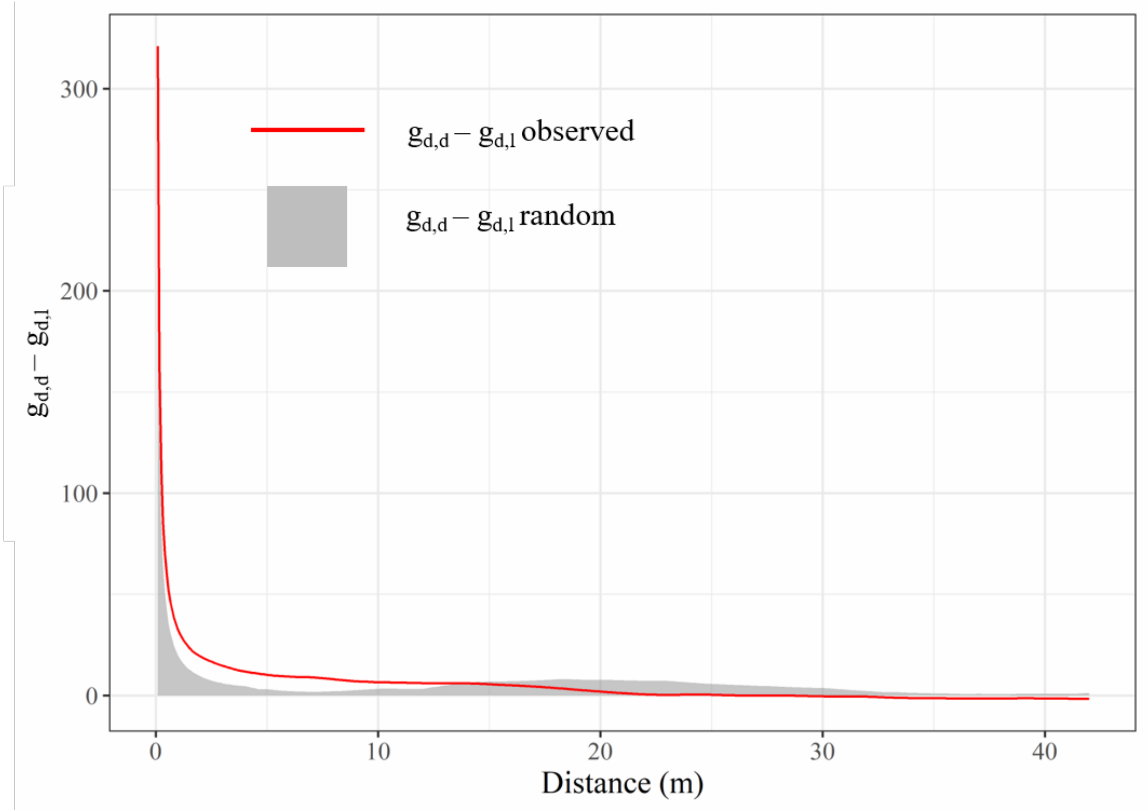

Figure 9 Pooled estimates of spatial patterns of bark beetle-associated mortality between observed dead sugar pine (red line) and mortality patterns generated by complete spatial randomness (gray). Deviations of observed values above the gray area ($g_{d,} - g_{d,l_{observed}} > g_{d,d} - g_{d,l_{random}}$) indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality.

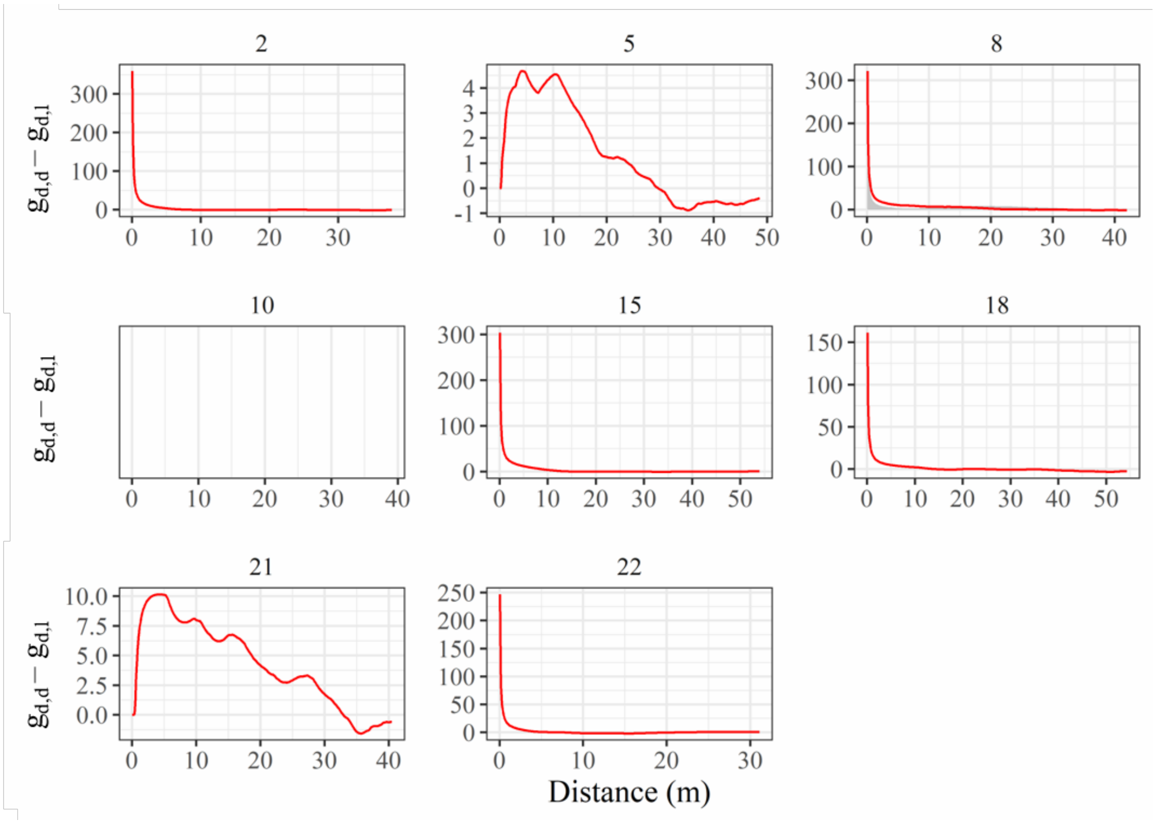

Figure 10 Individual unit estimates of spatial patterns of bark beetle-associated mortality between observed dead sugar pine (red line) and mortality patterns generated by complete spatial randomness (gray). Deviations of observed values above the gray area ($g_{d,d} - g_{d,l_{observed}} > g_{d,d} - g_{d,l_{random}}$) indicates clustering of trees that died from bark beetle-associated mortality, while deviations of observed values below the gray area indicate dispersed patterns of mortality. If observed values are within the gray area, spatial analysis suggests no difference from a random distribution of mortality. Plots without patterns of random mortality did not contain an adequate sample of dead trees to generate simulation envelopes and were removed from the pooled estimate of (r).

Discussion

While VDT is a management method that increases spatial heterogeneity (Knapp et al. 2017), there is limited research on how residual structures influence mortality during drought and bark beetle outbreak. By observing patterns of bark beetle-associated mortality during an unprecedented drought (Griffin and Anchukaitis 2014), we found higher levels of mortality for both sugar pine and white fir than the 2 % annual rate of tree mortality generally caused by bark beetles under endemic levels (Samman and Logan 2000). Despite increased mortality, our observations of sugar pine mortality were less than the 48 % mortality levels reported in untreated stands within the same region (Fettig et al. 2019). However, our observations of white fir mortality were equivalent to the 26 % also reported in untreated stands within the Sierra Nevada (Fettig et al. 2019). Although we found elevated levels of bark beetle-associated mortality, the spatial patterning of dead sugar pine and white fir was randomly distributed at scales greater than 14 m, suggesting that structures within variable density thinning treatments may be manipulated to limit tree mortality across space.

Our results indicate that the proportion of intraspecific hosts was the primary driver of fir mortality. Bark beetle attack and white fir basal area have been positively related to tree mortality in mixed conifer forests of Arizona, with substantial tree mortality (>30 %) during extended drought conditions (Kane et al. 2014). Percentage of white fir mortality may be directly proportional to the density of available hosts (Egan et al. 2010), with our findings showing greater mortality of white fir at smaller scales (10 to 20 m) when white fir were the only species present. Density-dependent mortality is influenced by the increased presence of conspecific neighbors (Fangliang and Duncan 2000), possibly increasing mortality risk due to competition for similar niches when resources are limited (Duncan 1991) during the drought. However, the importance of conspecific density at these localized scales may also arise from interactions between host selection and host abundance. Fir engraver shows strong host selection for trees infected with root rot (Hertert et al. 1975, Macias-Samano et al. 1998), with root pathogens concentrating in clustered disease centers (Hansen and Goheen 2000).

Therefore, mortality attributed to fir engraver may be associated with the abundance of stressed hosts within close proximity to each other. VDT may have created dispersed clumps of infected hosts across space, possibly diminishing the importance of conspecific density at larger scales. We also found that white fir mortality was negatively associated with tree size at larger scales (30 to 50 m), with other studies finding an inverse relationship between tree size and the probability of bark beetle-associated mortality during drought conditions (Negron et al. 2009). Evidence suggests that larger trees tend to be more drought-stressed (Bennet et al. 2015), possibly due to the greater radiation exposure and evaporative demand or larger crowns (Roberts et al. 1990). However, physiological performance can be related to suitable microsite conditions (Carter and Smith 1988). White fir establish in sites with greater soil moisture, with basal area positively associated with soil thickness (Meyer et al. 2007). It is possible that larger white fir already existed in suitable sites with greater water resources, rendering them more vigorous and less susceptible to bark beetle-associated mortality. Other studies have found that white fir that died from bark beetle-associated mortality had shorter crowns and lower tree vigor than trees that survived (Ferrell et al. 1994). Because prescriptions for VDT preferentially chose large and vigorous trees (Knapp et al. 2017), smaller trees with high vigor may have been less prominent across these treatments and limited host availability at larger scales.

While sugar pine mortality was also primarily driven by the proportion of conspecific hosts, this effect was stronger at larger scales (20 to 50 m). While disrupting the continuity of hosts prevents bark beetle-associated mortality from clustering at smaller scales (Smith et al. 2005), mortality at larger scales may still occur if susceptible hosts remain on the landscape. Because sugar pine are relatively shade intolerant (Franklin and Dyrness 1973), increases in canopy cover may decrease light availability and tree vigor (York et al. 2003). If sugar pine were further away from other hosts, mountain pine beetle would need to be more efficient at host detection to make long- range dispersal less risky (Kautz et al. 2016). Therefore, the negative effects of host proportion at larger scales may be a combination of lower tree vigor and more efficient host detection by bark beetles.

Contrary to expectations, total competition alone was not the predominant factor explaining the variation in proportion of sugar pine and white fir mortality at any of the scales we investigated. Competition may be a significant driver of tree mortality (Das et al. 2011, Ruiz-Benito et al. 2013), especially under severe drought conditions (Young et al. 2017). However, other studies have found that mortality rates are not always attributed to competition (van Mantgem et al. 2009), possibly due to the effect of climatic stress superseding the effects of competitive stress under prolonged drought (Floyd et al. 2009). Although trees avoid drought-induced mortality by restricting transpiration, doing so weakens host defenses (McDowell et al. 2011) and creates opportunities for bark beetles to colonize and kill host trees (Bentz et al. 2010). If severe drought leads to insufficient resources for all trees, then increased stomatal control during drought may have predisposed trees to bark beetle-associated mortality (Plaut et al. 2012) regardless of competition. If all preferred beetle hosts are susceptible to attack due to severe climatic stress, then mortality may be more influenced by the number of available hosts that can facilitate beetle dispersal rather than the influence of stand density on tree vigor.

Although rates of bark beetle-associated mortality can increase following drought (Dobbertin et al. 2007), our results indicate mortality was limited across VDT treatments. Bark beetle dispersal distances can range from 30 to 50 m, suggesting that infestations stay relatively localized during the initial stages of an outbreak (Robertson et al. 2007). As outbreak conditions progress, mortality generally occurs in clustered patterns (Grodzki et al. 2003, Robertson et al. 2007) and radiates outwards from multiple epicenters of beetle activity until clusters coalesce across larger landscapes (Chapman et al. 2012). Generally, our findings show that spatial patterns of bark beetle-associated mortality in VDT were apparent at scales less than 14 m, but were not different than mortality patterns generated by complete spatial randomness at larger scales. Beetles are host-specific and often attack trees with weakened defense systems (Raffa et al. 2008), suggesting that structural characteristics created by VDT may have inhibited beetle detection or dispersal by limiting host availability through variable species composition or increasing the amount of resistant hosts.

Our results show that structural elements within treatments intended to increase spatial heterogeneity may influence bark beetle-associated mortality during unprecedented drought conditions. Although treatments that increase spatial complexity have been proposed as a way to enhance forest resistance (North et al. 2009), valid concerns exist about using the historical range of variation to guide treatments for future disturbances. Historical disturbance regimes may not serve as an appropriate analogue for due to on-going and projected increases in the frequency and intensity of many disturbances (O’Hara 2016). In anticipation of novel ecosystems under climate change, some argue for more proactive approaches that focus less on returning to past conditions and focus more on creating desirable states for the future (Seastedt et al. 2008). Although our results found that bark beetle-associated mortality can be influenced by structural elements indicative of historical reference conditions, mortality patterns did not coalesce into larger patches of tree mortality indicative of outbreak conditions. Our findings also suggest that prescriptions designed to increase species diversity and increase variation in tree size may complement reductions in competition when climatic water stress overrides competitive stress.

While these findings do not imply that recreating historical structures is optimal relative to other thinning methods, it does suggest treatments intended to increase spatial heterogeneity on the scale that was present historically may have the added benefit of mitigating tree mortality to disturbances.

Conclusions and Implications

Overview

The results from our study provides valuable information regarding the spatial patterns of bark beetle-associated mortality during severe drought conditions following variable density thinning and prescribed burning treatments. While tree mortality in white fir and sugar pine following treatment was elevated above reported background mortality levels, mortality was equivalent or lower than those reported in similar forests that were untreated during the same drought. The addition of prescribed fire did not increase bark beetle-associated tree mortality compared to variable density treatments alone, suggesting that low intensity burns did not predispose trees to additional mortality. Mortality in white fir and sugar pine was clustered and most associated with a greater proportion of hosts, indicating that less diverse clusters were more likely to be attacked by bark beetles.

Implication of results to management and policy

Variable density thinning treatments can be an effective means of increasing forest health and limiting mortality in mixed-conifer stands during an extended and severe drought. The addition of prescribed burning did not change the amount or of tree mortality compared to unburned areas. Thus, managers looking to enhance the spatial variability of forests and reducing fuel loads could confidently employ variable density thinning treatments to increase the resistance of forests to drought and bark-beetle associated mortality. Our findings indicate that further gains could be made if the composition of retained clusters is considered. For both white fir and sugar pine, bark beetle-associated mortality in these forests was associated with clusters that contained a higher proportion of host species.

Literature Cited

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., Mcdowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalex, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.H., Allard, G., Running, S.W., Semerci, A., and N. Cobb. 2010. A global overview of drought and heat- induced treemortality reveals emerging climate change risks for forests. Forest Ecology and Management 259:660-684.

Allen, C.D., Breshears, D.D., and N.G. McDowell. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:1-55.

Baddeley, A., Rubak, E., and R. Turner. 2015 Spatial Point Patterns: Methodology and

Applications with R. CRC Press: Boca Raton, FL.

Bennett, A.C., McDowell, N.G., Allen, C.D., and K.J. Anderson-Teixeira. 2015. Larger trees suffer most during drought in forests worldwide. Nature Plants 15139.

Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., and S.J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60:602-613.

Carey, A.B. 2003. Bioclompexity and restoration of biodiversity in temperate coniferous forest: inducing spatial heterogeneity with variable-density thinning. Forestry 76:127-136.

Carter, G.A. and W.K. Smith. 1988. Microhabitat comparisons of transpiration and photosynthesis in three subalpine conifers. Canadian Journal of Botany 66:963-969.

Chapman, T.B., Veblen, T.T., and T. Schoennagel. 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. Ecology 93:2175- 2185.

Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, M.C., Hessburg, P.F., and J.A. Lutz. 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. Forest Ecology and Management 291:442-457.

Coops, N.C., Waring, R.H., Wulder, M.A., and J.C. White. 2009. Prediction and assessment of bark beetle-induced mortality of lodgepole pine using estimates of stand vigor derived from remotely sensed data. Remote Sensing of Environment 113:1058-1066.

Das, A., Battles, J., Stephenson, N.L., and P.J. van Mantgem. 2011. The contribution of competition to tree mortality in old-growth coniferous forests. Forest Ecology and Management 261:1203-1213.

Dobbertin, M., Wemeliner, B., Bigler, C., Burgi, M., Carron, M., Forster, B., Gimmi, U., and A. Rigling. 2007. Linking increasing drought stress to Scots pine mortality and bark beetle infestations. The Scientific World Journal 7:231-239.

Duncan, R.P. 1991. Competition and the coexistence of species in a mixed podocarp stand. Journal of Ecology 79:1073-1084.

Egan, J.M., Jacobi, W.R., Negrón, J.F., Smith, S.L, and D.R. Cluck. 2010. Forest thinning and subsequent bark beetle-caused mortality in Northeastern California. Forest Ecology and Management 260:1832-1842.

Fangliang, H. and R.P. Duncan. 2000. Density-dependent effects on tree survival in an old-growth Douglas-fir forest. Journal of Ecology 88:676-688.

Ferrell, G.T., Otrosina, W.J., and C.J. Demars Jr. 1994. Predicting susceptibility of white fir during a drought-associated outbreak of the fir engraver, *Scolytus ventralis*, in California. Canadian Journal of Forest Research 24:302-305.

Fettig, C.J., Hayes, C.J., Jones, K.J., Mckelvey S.R., Mori S.L., and S.L. Smith. 2012. Thinning Jeffrey pine stands to reduce susceptibility to bark beetle infestation in California, U.S.A. Agricultural and Forest Entomology 14:111-117.

Fettig, C.J., Mortense, L.A., Bulaon, B.M., and P.B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. Forest Ecology and Management 432:164-178.

Floyd, M.L., Clifford, M., Cobb, N.S., Hanna, D., Delph, R., Ford, P., and D. Turner. 2009. Relationship of stand characteristics to drought-induced mortality in three Southwestern pinyon-juniper woodlands. Ecological Applications 19:1223-1230.

Franklin, J.F. and C.T. Dyrness. 1973. Natural vegetation of Oregon and Washington. United States Department of Agriculture Forest Service. GTR PNW-8. Pacific Northwest Forest and Range Experiment station: Portland, Oregon.

Gill, S.J., Biging, G.S., and E.C. Murphy. 2000. Modeling conifer tree crown radius and estimating canopy cover. Forest Ecology and Management 126:405-416.

Griffin, D. and K.J. Anchukaitis. 2014. How unusual is the 2012-2014 California drought? Geophysical Research Letters 41:9017-9023.

Grodzki, W. Jakus, R. and M. Gazda. 2003. Patterns of bark beetle occurrence in Norway spruce stands of national parks in Tatra Mountains in Poland and Slovakia. Journal of Pest Science 76:78-82.

Hansen, E.M. and E.M. Goheen. 2000. *Phellinus weirii* and other native root pathogens as determinants of forest structure and process in Western North America. Annual Review of Phytopathology 38:515-539.

Hertert, H.D., Miller, D.L., and A.D. Partridge. 1975. Interaction of bark beetles (Coleoptera: Scolytidae) and root-rot pathogens in grand fir in northern Idaho. Canadian Entomology 107:829-904.

Hood, S., Sala, A., Heyerdahl, E.K., and M. Boutin. 2015. Low-severity fire increases tree defense against bark beetles. Ecology 96:1846-1855.

Hood, S., Baker, S., and A. Sala. 2016. Fortifying the forest: thinning and burning increase resistance to bark beetle outbreak and promote forest resilience. Ecological Applications 26:1984-2000.

Kane, J.M., Kolb, T.E., and J.D. McMillin. 2014. Stand-scale tree mortality factors differ by site and species following drought in southwestern mixed conifer forests.
Forest Ecology and Management 330:171-182.

Kautz, M., Dworschak, K., Gruppe, A., and R. Schopf. 2011. Quantifying spatio- temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. Forest Ecology and Management 262:598-608.

Kautz, M., Imron, M.A., Dworschak, K., and R. Schopf. 2016. Dispersal variability and associated population-level consequences in tree-killing bark beetles. Movement Ecology 4:1-12.

Knapp, E.E., Skinner, C.N., North, M.P., and B.L. Estes. 2013. Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. Forest Ecology and Management 310:903-914.

Knapp, E. E., Lydersen, J.M., North, M.P., and B.M. Collins. 2017. Efficacy of variable density thinning and prescribed fire for restoring heterogeneity to mixed-conifer forest in the central Sierra Nevada, CA. Forest Ecology and Management 406:228-241.

Larson, A.J. and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. Forest Ecology and Management 267:74-92.

Larson, A.J., Lutz, J.A., Donato, D.C., Freund, J.A. Swanson, M.E., HilleRisLambers, J., Sprugel D.G., and J.F. Franklin. 2015. Spatial aspects of tree mortality strongly differ between young and old-growth forests. Ecology 96:2855-2861.

Macias-Samano, J.E., Bordern, J.H., Gries, R., Pierce, H.D., Gries, G., and G.G.S. King. 1998. Primary attraction of the fir engraver, *Scolytus ventralis*. Journal of Chemical Ecology 25:1049-1075.

McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F., and M. Stitt. 2011. The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends in Ecology & Evolution 26:523-532.

Meddens, A.J., Hicke, J.A., and C.A. Ferguson. 2012. Spatiotemporal patterns of observed bark beetle-cause tree mortality in British Columbia and the western United States. Ecological Applications 22:1876-1891.

Meyer, M.D., North, M.P., Gray, A.N., and H.S.J. Zald. 2007. Influence of soil thickness on stand characteristics in a Sierra Nevada mixed-conifer forest. Plant and Soil 294:113-123.

Negron, J.F. and J.B. Popp. 2004. Probability of ponderosa pine infestation by mountain pine beetle in the Colorado Front Range. Forest Ecology and Management 191:17-27.

Negron, J.F., McMillin, J.D., Anhold, J.A., and D. Coulson. 2009. Bark beetle-caused mortality in drought-affected ponderosa pine landscape in Arizona, USA. Forest Ecology & Management 257:1353-1362.

North, M., Stine, P., O'Hara, K., Zielinski, W., and S. Stephens. 2009. An ecosystem management strategy for Sierran mixed-conifer forests. United States Department of Agriculture, Forest Service, Pacific Southwest Research Station, General Technical Report 220.

O’Hara, K.L. 2016. What is close-to-nature silviculture in a changing world? Forestry 89:1-6.

Pebesma, E. 2018. Simple features for R: Standardized support for spatial vector data. The R Journal 10:439-446.

Perry, D.A. and M.P. Amaranthus. 1997. Disturbance, recovery, and stability. P. 31-56 in Creating a forestry for the twenty-first century: The science of ecosystem management, Kohm, K.A., and J.F. Franklin (eds.). Island Press: Washington, D.C.

Plaut, J.A., Yepez, E.A., Hill, J., Pangle, R., Sperry, J.S., Pockman, W.T., and N.G. McDowell. 2012. Hydraulic limits preceding mortality in a piñon-juniper woodland under experimental drought. Plant, Cell, and Environment 35:1601- 1617.

Pommerening A. and D. Stoyan. 2006. Edge-correction needs in estimating indices of spatial forest structure. Canadian Journal of Forest Research 36:1723-1739.

PRISM Climate Group, Oregon State University, http://prism.oregonstate.edu, created on March, 2019.

R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffa, K.F. and A.A. Berryman. 1975. Flight responses and host selection by bark beetles. In: Dispersal of forest insects: Evaluation, theory and management implications (A.A. Berryman and L. Safranyik, eds.). Proceedings of the second IUFRO Conference. Canadian and United States Department of Agriculture Forest Service, Washington State University.

Raffa, K.F., Aukema, B.H., Bentz, B.J., Carroll, A.L., Hicke, J.A., Turner, M.G., and W.H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. BioScience 58:501-517.

Roberts, J., Cabra, O.M.R., and L. Ferreira de Aguiar. 1990. Stomatal and boundary-layer conductances in an Amazonian terra firme rain forest. Journal of Applied Ecology 27:336-353.

Robertson, C., Nelson, T.A., and B. Boots. 2007. Mountain pine beetle dispersal: The spatial-temporal interaction of infestation. Forest Science 53:395-405.

Roussel, J. and D. Auty. 2018. lidR: airborne LiDAR data manipulation and visualization for forestry applications. R package version 1.4.2.

Ruiz-Benito, P., Lines, E.R., Gomez-Aparicio, L., Zavala, M.A., and D.A. Coomes. 2013. Patterns and drivers of tree mortality in Iberian forests: Climatic effects are modified by competition. PLoS ONE 8:e56843.

Samman, S. and J. Logan (eds.). 2000. Assessment and response to bark beetle outbreaks in the Rocky Mountain area. Report to Congress from Forest Health Protection, Washington Office. United States Department of Agriculture Forest Service, Rocky Mountain Research Station. RMRS-GTR-62, Fort Collins, Colorado.

Seastedt, T.R., Hobbs, J.R., and K.N. Suding. 2008. Management of novel ecosystems: are novel approaches required? Frontiers in Ecology and the Environment 6:547- 553.

Seidl, R., Donato, D.C., Raffa, K.F., and M.G. Turner. 2016. Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks. Proceedings of the National Academy of Sciences 113:13075-13080.

Smith, T.F., Rizzo, D.M., and M. North. 2005. Patterns of mortality in an old-growth mixed-conifer forest of the Southern Sierra Nevada, California. Forest Science 51:266-275.

Stark, D.T., Wood, D.L., Storer, A.J., and S.L. Stephens. 2013. Prescribed fire and mechanical thinning effects on bark beetle caused tree mortality in a mid- elevation Sierran mixed-conifer forest. Forest Ecology and Management 306:61- 67.

Turner, M.G., Gardern, R.H., Dale, V.H., and R.V. O'Neill. 1989. Predicting the spread of disturbances across heterogeneous landscapes. Oikos 55:121-129.

United States Department of Agriculture. NAIP 2012 aerial imagery, 1-meter resolution, in natural color [imagery]. Obtained from California Department of Fish and Wildlife, February 9, 2019.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., and T.T. Veblen. 2009. Widespread increase of tree mortality rates in the Western United States. Science 323: 521-524.

van Mantgem, P.J., Caprio, A.C., Stephenson, N.L., and A.J. Das. 2016. Does prescribed fire promote resistance to drought in low elevation forests of the Sierra Nevada, California, USA? Fire Ecology 12:13-24.

Wagenmakers, E. and S. Farrell. Notes and comment: AIC model selection using Akaike weights. Psychnomic Bulletin & Review 11:192-196.

York, R.A., Battles, J.J., and R.C. Heald. 2003. Edge effects in mixed conifer group selection openings: tree height response to resource gradients. Forest Ecology and Management 179:107-121.

York, R.A., Battles, J.J., Wenk, R.C., and D. Saah. 2011. A gap-based approach for regenerating pine species and reducing surface fuels in multi-aged mixed conifer stands in the Sierra Nevada, California. Forestry 85:203-213.

Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., and A.M. Latimer. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. Ecology Letters 20:78-86.

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Appendix B: List of Deliverables

Publications in Peer-reviewed Journals		
Status	**Title**	**Journal**
In preparation	Effects of thinning and burning on resistance to drought and bark beetle-associated mortality in a mixed-conifer forest	Forest Ecology and Management
In preparation	Mechanisms and spatial patterns of bark beetle-associated mortality following variable density thinning treatments in a Sierra mixed-conifer forest	Ecological Applications
In preparation	Mortality and growth of mixed conifer stands experimentally treated with different thinning approaches and prescribed fire in response to a severe drought	Forest Ecology and Management

Master's Thesis		
Status	**Title**	**Academic Institution**
Completed	Mechanisms and spatial patterns of bark beetle-associated mortality following variable density thinning treatments in a Sierra Nevada mixed-conifer forest	Humboldt State University

Other Deliverables		
Type	**Status**	**Title**
Presentation	Completed	Mechanisms of bark beetle caused mortality following variable density thinning and prescribed fire treatments in a central Sierra mixed conifer forest
Presentation	Completed	Spatial patterns and mechanisms of bark beetle-caused mortality following variable density thinning and prescribed fire treatments in a central Sierra mixed-conifer forest
Presentation	Completed	The effectiveness of variable density thinning and prescribed fire in promoting resistance to drought- induced bark beetle mortality
Presentation	Accepted	Restoring heterogeneity: A comparison of variable density thinning and historical reference conditions in the central Sierra Nevada
Presentation	Accepted	Effects of thinning on tree resistance to drought and bark beetle-associated mortality in a Sierra Nevada mixed-conifer forest
Science Brief	In preparation	The effectiveness of variable density thinning and prescribed fire in promoting resistance to drought- induced bark beetle mortality
Field Tour	Summer 2020	Field tour of variable density thinning study site at Stanislaus Toulumne Experimental Forest

Appendix C: Metadata

Tree mortality and location data associated with the project were digitally recorded using Microsoft Excel and these data are provided as an .xlsx file. Shapefiles of the unit boundaries are also provided (.dbf, .shp, .shx, etc.). All data underwent quality control measures to assure correct entry. All data and metadata have been submitted to the United States Department of Agriculture Forest Service Research Data Archive. The format of the submitted metadata follows the FGCD-STD guidelines.