

<sup>1</sup> Local host tree density increases forest insect disturbance severity,  
<sup>2</sup> but host size effect depends on climatic water deficit

<sup>3</sup> Michael J. Koontz<sup>1,2,\*</sup>, Andrew M. Latimer<sup>1,2</sup>, Leif A. Mortenson<sup>3</sup>, Christopher J. Fettig<sup>3</sup>, Malcolm P.  
<sup>4</sup> North<sup>1,2,4</sup>

<sup>5</sup> <sup>1</sup>Graduate Group in Ecology, University of California, Davis, CA, USA

<sup>6</sup> <sup>2</sup>Department of Plant Sciences, University of California, Davis, CA, USA

<sup>7</sup> <sup>3</sup>USDA Forest Service, Pacific Southwest Research Station, Placerville, CA, USA

<sup>8</sup> <sup>4</sup>USDA Forest Service, Pacific Southwest Research Station, Davis, CA, USA

<sup>9</sup> \*Correspondence: michael.koontz@colorado.edu

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<sup>11</sup> Executive Summary (to eventually become abstract)

<sup>12</sup> Framing: environmental drivers of insect severity, forest structure drivers of insect severity, but *complex* forest  
<sup>13</sup> structure is key as is relevant scale of local ecological process; little information on how the complex forest  
<sup>14</sup> structure interacts with environmental drivers because these data are challenging to capture simultaneously...

<sup>15</sup> Bark beetles are a primary mortality agent of trees in western U.S. forests, and the recent Californian hot  
<sup>16</sup> drought of 2012 to 2015 created favorable conditions for bark beetle-induced tree mortality throughout the  
<sup>17</sup> yellow pine/mixed-conifer forest system in the Sierra Nevada mountain range. The western pine beetle,  
<sup>18</sup> *Dendroctonus brevicomis*, is the forest insect that is largely responsible for the especially common deaths of its  
<sup>19</sup> main host in California, the ponderosa pine tree (*Pinus ponderosa*). While previous work has demonstrated a  
<sup>20</sup> link between climate conditions related to tree water stress and forest density on the severity of the western  
<sup>21</sup> pine beetle disturbance, it remains challenging to disentangle the relative effects of these variables. Further,  
<sup>22</sup> forest density can affect western pine beetle behavior in a number of ways, which creates a need for more  
<sup>23</sup> information on complex forest structure (including local density, tree size, and the heterogeneity of these  
<sup>24</sup> variables across a forest stand) to uncover the most likely mechanism.

<sup>25</sup> We conducted aerial surveys over an established network of 32 permanent vegetation monitoring plots along  
<sup>26</sup> a 350km and 1000m elevation gradient in the Sierra Nevada mountain range of California using a small,  
<sup>27</sup> unhumanned aerial system (sUAS aka drone) equipped with a narrow-band multispectral camera. Using  
<sup>28</sup> Structure from Motion (SfM) processing on over 450,000 images, we reconstructed the complex vegetation  
<sup>29</sup> structure of over 9 square kilometers of forest that experienced ponderosa pine mortality as a result of

western pine beetle activity. Using this dataset, we built a model to predict the probability of ponderosa pine mortality as a function of forest structure variables (including ponderosa pine density and mean size, as well as all tree density and mean size), an environmental gradient of climatic water deficit, and a Gaussian process to capture spatial covariance in the response.

Data from small, unhummaned aerial systems (sUAS) can provide important context surrounding ground plots, which enables inference and generates new insights into ecological processes. sUAS are best-suited to enhancing ground data, which implies that we need not abandon lessons learned from sound experimental design (i.e., a network of plots along a gradient is still a powerful way to use sUAS as an ecological tool).

Host availability for aggressive bark beetles appears to have played the dominant role in increasing the probability of ponderosa pine mortality in the most hard-hit forest stands during the cumulative mortality event of 2012 to 2018. Host size played a role in its interaction with environmental condition— climatic water deficit— such that numerous and smaller host trees increased the probability of ponderosa mortality at cool/wet sites, while numerous and larger host trees increased the probability of ponderosa mortality at hot/dry sites.

Our results corroborate the role of host tree density and regional climate conditions on the severity of forest insect disturbance, but also highlight the importance of complex forest structure (i.e., both host density and average host size) in its interaction with regional climate. Thus, the future forest structure may be affected differently by a large-scale forest insect disturbance for the same host tree/forest insect pairing, and during the same extreme drought, but across a gradient of regional climate conditions.

## Introduction

Aggressive bark beetles dealt the final blow to many of the nearly 150 million trees killed in the California drought of 2012 to 2015 and its aftermath (USDAFS 2019). A harbinger of climate change effects to come, record high temperatures exacerbating the drought (Griffin and Anchukaitis 2014) increased water stress on trees, which increases their susceptibility to attacking bark beetles (Fettig 2012, Kolb et al. 2016). A century of fire suppression policy has enabled forests to grow into dense stands, which also makes them more vulnerable to bark beetle attack (Fettig 2012, North et al. 2015). This combination of environmental conditions and forest structural characteristics led to tree mortality events of unprecedented size in the driest, densest forests across the state (Young et al. 2017). The mechanisms underlying the link between tree susceptibility to insect attack and hot, dry conditions are often directly attributed to tree physiology (Bentz et al. 2010), but the link to forest density is multifaceted (Fettig 2012). Because forest density is a coarse metric

60 of the complex forest structure to which bark beetles respond (Raffa et al. 2008), our understanding of the  
61 connection between forest density and insect disturbance severity may be enhanced with more finely-resolved  
62 measures of forest structure (Stephenson et al. 2019). Further, the interaction between local-scale complex  
63 forest structure and broad-scale environmental conditions as they affect forest insect disturbance remains  
64 underexplored (Seidl et al. 2016).

65 The yellow pine/mixed-conifer forests in California's Sierra Nevada region are characterized by regular bark  
66 beetle disturbances, primarily by the western pine beetle (*Dendroctonus brevicomis*) and its main host in  
67 the system, ponderosa pine (*Pinus ponderosa*) (Fettig et al. 2019). The western pine beetle is a "primary"  
68 or "aggressive" bark beetle, with reproductive success contingent upon host tree mortality (???, Fettig et  
69 al. 2019). This strong Allee effect creates a dynamic between beetle host selection behavior and host tree  
70 susceptibility to attack (???, Logan et al. 1998). Under normal conditions, primary bark beetles like the  
71 western pine beetle will sporadically kill weakened trees, but under outbreak conditions, wide swaths of even  
72 healthy trees may be killed (Bentz et al. 2010, Raffa et al. 2015). A key defense mechanism of trees to  
73 bark beetle attack is to flood beetle bore holes with resin, which physically expels beetles and may interrupt  
74 beetle communication (Raffa et al. 2015). Under severe water stress, trees may no longer have the resources  
75 available to mount this defense (Kolb et al. 2016) and thus prolonged drought can often trigger increased  
76 bark beetle-induced tree mortality as average tree vigor declines (Bentz et al. 2010).

77 Forest structure— the spatial distribution, size, and species composition of trees— also strongly influences  
78 western pine beetle activity. For instance, high-density forests are more prone to bark beetle attacks, and  
79 several mechanism likely underlie this phenomenon (Fettig 2012). A high-density forest may experience  
80 greater bark beetle-induced tree mortality because host availability is high and shorter dispersal distances  
81 facilitate successful colonization of those hosts (Miller and Keen 1960, Berryman 1982, Fettig et al. 2007),  
82 because high host availability reduces the chance of landing on a non-host and imposing an energy cost to  
83 individual beetles (???, Evenden et al. 2014), because crowded trees experience greater competition for water  
84 resources and thus average tree resistance is lower (Hayes et al. 2009), or because smaller gaps between trees  
85 protect pheromone plumes from dissipation by the wind and thus enhance intraspecific beetle communication  
86 (Thistle et al. 2004). Additionally, tree size affects bark beetle host selection behavior as smaller trees tend to  
87 have less capacity for resisting attack, but larger trees represent a more desirable target because their thicker  
88 phloem provides greater nutritional value (Chubaty et al. 2009, Graf et al. 2012). Tree density thus provides  
89 limited insight into the mechanism by which forest structure affects bark beetle disturbance, and *complex*  
90 forest structure— with explicit recognition of local variability tree density, tree size, and species composition  
91 (i.e., host versus non-host composition)— may be a more useful in explaining

92 Climate change mitigation strategies emphasize reducing tree densities (North et al. 2015, Young et al. 2017),  
93 but understanding the optimal scale and pattern of tree distribution that can mitigate bark beetle outbreaks  
94 will be vital for predicting how California forests may respond to these interventions. Recent research has  
95 shown a strong link between complex forest structure and forest resilience, but measuring this complexity  
96 generally requires expensive equipment or labor-intensive field surveys (Larson and Churchill 2012, Kane et al.  
97 2014). These barriers restrict survey extent, which limits insights into phenomena like bark beetle disturbance  
98 that rapidly emerge over weeks to months but have long-lasting effects on forest conditions.

99 Further, the vast spatial extent and environmental gradient of mortality (Young et al. 2017, USDAFS 2019)  
100 challenges our ability to simultaneously consider how environmental conditions may interact with local forest  
101 structure to produce patterns of insect activity.

102 Small, unhumanned aerial systems (sUAS) enable fast and relatively cheap remote imaging over dozens of  
103 hectares of forest, which can be used to determine both forest structure and tree condition at the individual  
104 tree scale (Morris et al. 2017, Shiklomanov et al. 2019).

105 We used ultra-high resolution remote sensing data from a small, unhumanned aerial system over a network of  
106 32 sites in the Sierra Nevada spanning 1000m of elevation and 350km of latitude and covering a total of 9  
107 square kilometers of forest to ask how fine-scale forest structure affected the probability of tree mortality  
108 during the cumulative mortality event of 2012 to 2018. We asked:

- 109 1. How does local host tree density and size affect the severity of western pine beetle disturbance?
- 110 2. How does total tree density and size affect the severity of western pine beetle disturbance?
- 111 3. How does environmentally-driven tree moisture stress affect the severity of western pine beetle distur-  
112 bance?
- 113 4. Do the effects of forest structure and environmental condition on western pine beetle disturbance  
114 interact?

## 115 Methods

### 116 Study system

117 The study sites comprise mostly ponderosa pine trees, *Pinus ponderosa*, whose primary bark beetle predator  
118 in California is the western pine beetle (WPB), *Dendroctonus brevicomis*. The WPB is an aggressive bark  
119 beetle, meaning it must attack and kill live trees in order to successfully reproduce (Raffa et al. 2008).  
120 Pioneer WPBs disperse to a new host tree, determine the host's susceptibility to attack, and use pheromone

121 signals to attract other WPBs. The attracted WPBs mass attack the tree by boring into its inner bark,  
122 laying eggs, and dying, leaving their offspring to develop inside the doomed tree before themselves dispersing  
123 (Raffa et al. 2008). Small WPB populations prefer weakened trees but large populations can overwhelm  
124 the defense mechanisms of even healthy trees. Successful attacks on large, healthy trees are boons to bark  
125 beetle fecundity and trigger outbreaks in which populations explode and massive tree mortality occurs. In  
126 California, the WPB can have 3 generations in a single year giving it a greater potential to spread rapidly  
127 through forests than its more infamous congener, the mountain pine beetle, *Dendroctonus ponderosa* (MPB).

128 We built our study on 180 vegetation/forest insect monitoring plots at 36 sites established between 2016 and  
129 2017 (Fettig et al. 2019). These established plots were located in beetle-attacked, mixed-conifer forests across  
130 the Eldorado, Stanislaus, Sierra and Sequoia National Forests and were stratified by elevation (914-1219  
131 meters [3000-4000 feet], 1219-1524 meters [4000-5000 feet], 1524-1828 meters [5000-6000 feet] above sea level).  
132 In the Sequoia National Forest, the National Forest that is furthest south, plots were stratified with the lowest  
133 elevation band between 1219 and 1524 (4000-5000 feet) and extended to an upper elevation band of 1828-2133  
134 (6000-7000 feet) to capture a more similar forest community composition as at the more northern National  
135 Forests. The sites have variable forest structure and disturbance history and plot locations were selected  
136 specifically in areas with >40% ponderosa pine basal area and >10% ponderosa pine mortality. The 0.04ha  
137 circular plots are clustered along transects in groups of 5, with between 80 and 200m between each plot. All  
138 trees within the plot were assessed as dead or alive. The stem location of all trees was mapped relative to the  
139 center of each plot using azimuth/distance measurements. Tree identity to species and diameter at breast  
140 height (dbh) were recorded if dbh was greater than 6.35cm. During the spring and early summer of 2018, all  
141 field plots were revisited to assess whether dead trees had fallen (Fettig et al. 2019).

## 142 **Instrumentation**

143 Imagery was captured using a DJI Zenmuse X3 RGB camera (DJI 2015a) and a Micasense RedEdge3 5-band  
144 multispectral camera (Micasense 2015). We mounted both of these instruments simultaneously on a DJI  
145 Matrice 100 aircraft (DJI 2015b) using the DJI 3-axis stabilized gimbal for the Zenmuse X3 camera and a  
146 Micasense angled fixed mount for the RedEdge3 camera. The gimbal and the angled fixed mount ensured  
147 both instruments were nadir-facing during image capture. Just prior or after image capture at each site, we  
148 calibrated the RedEdge3 camera by taking an image of a calibration panel on the ground in full sun with  
149 known reflectance values for each of the 5 narrow bands.

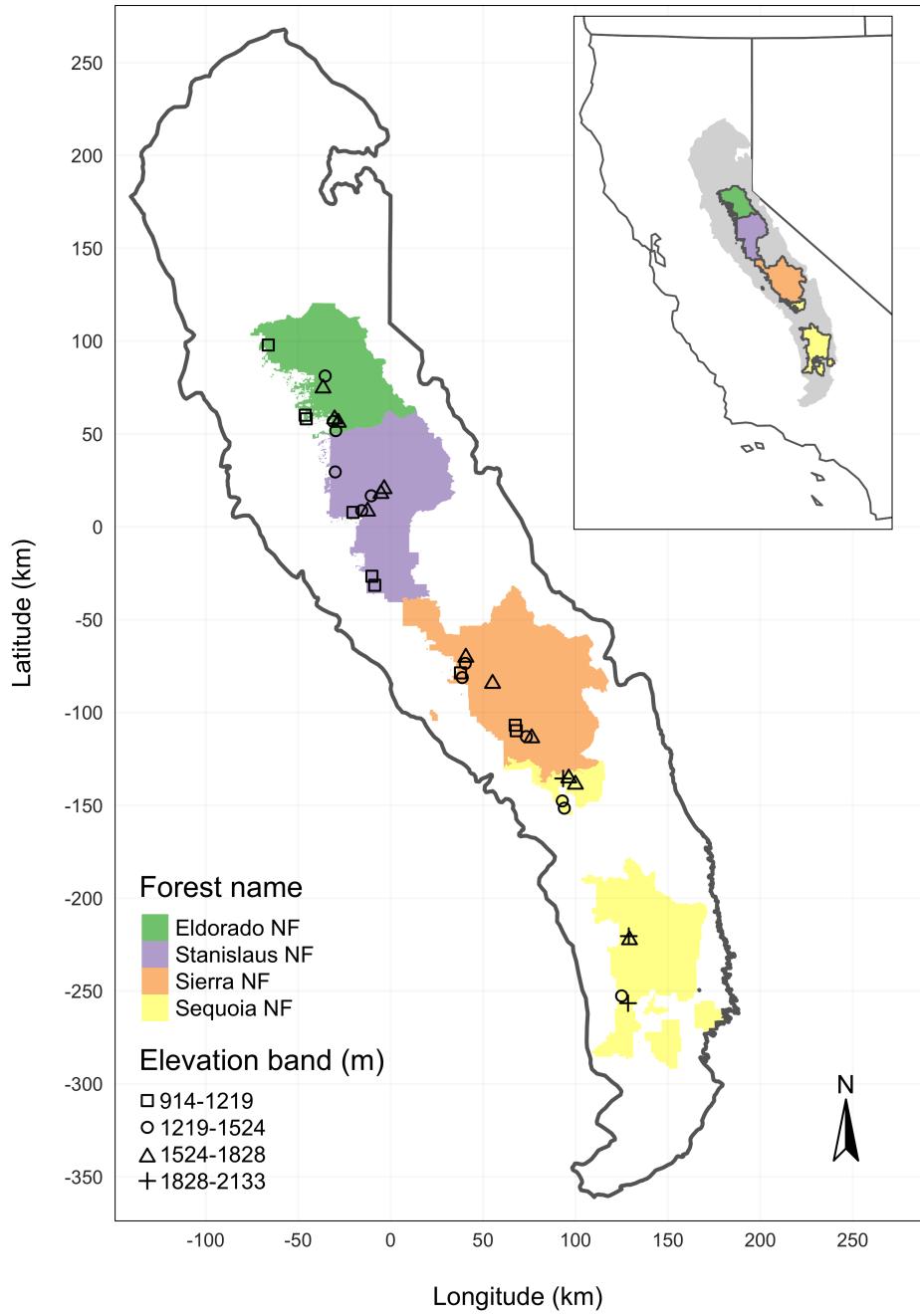


Figure 1: The network of field plots spanned a 350 km latitudinal gradient from the Eldorado National Forest in the north to the Sequoia National Forest in the south. Plots were stratified by three elevation bands in each forest, with the plots in the Sequoia National Forest (the southern-most National Forest) occupying elevation bands 305m above the three bands in the other National Forests in order to capture a similar community composition.

Table 1: Reflectance sensitivity of the Micasense Rededge3 camera. The calibration panel value represents the reflectance of the calibration panel for the given wavelength.

Band number	Band name	Center wavelength	Band width	Wavelength range	Panel reflectance
1	blue (b)	475	20	465-485	0.64
2	green (g)	560	20	550-570	0.64
3	red (r)	668	10	663-673	0.64
4	near infrared (nir)	840	40	820-860	0.6
5	red edge (re)	717	10	712-722	0.63

## 150 Flight protocol

151 Image capture was conducted as close to solar noon as possible to minimize shadow effects (always within 4  
 152 hours; usually within 2 hours). Prior to the aerial survey, two strips of bright orange drop cloth (~100cm x  
 153 15cm) were positioned as an “X” over the permanent monuments marking the center of the 5 field plots from  
 154 Fettig et al. (2019).

155 For each of the 36 sites (containing 5 plots each), we captured imagery over the surrounding ~40 hectares of  
 156 forested area using north-south aerial transects. For three sites, we surveyed less surrounding area in order to  
 157 maintain visual and radio communication with the aircraft during flight which can be obstructed by steep  
 158 terrain or non-centrally available takeoff locations. (Table 3; as a supplement, I think; Columns: Site, forest,  
 159 elevation, rep, CWD, surveyed area, survey date).

160 We preprogrammed transect paths using Map Pilot for DJI on iOS (hereafter Map Pilot) (Easy 2018). All  
 161 transects tracked the terrain and their altitude remained approximately constant at 120 meters above ground  
 162 level in order to maintain consistent ground sampling distance in the imagery. Ground level was based on a

163 1-arc-second digital elevation model (Farr et al. 2007) and we implemented terrain following using Map Pilot.

164 For this analysis, we dropped 4 sites whose imagery was of insufficient quality to process.

165 Structure from motion (SfM) processing requires highly overlapping images, especially in densely vegetated  
 166 areas. We planned transects with 90% forward overlap and 90% side overlap at 100 meters below the lens.

167 Thus, with flights being at 120 meters above ground level, we achieved slightly higher than 90/90 overlap for  
 168 objects 20 meters tall or shorter (91.6/91.6 overlap at the ground). Overlap values were based on focal length

169 (3.6mm), sensor width (6.2mm), and image dimension (4000x3000 pixels) parameters of the Zenmuse X3  
170 camera. Images were captured at a constant rate of 1 image every 2 seconds for both cameras. A forward  
171 overlap of 90% at 100 meters translates to a flight speed of approximately 6.45 m/s and a side overlap of 90%  
172 at 100 meters translates to transects approximately 17.2 meters apart. The Rededge camera has a different  
173 focal length (5.4mm), sensor width (4.8mm), and image dimension (1280x960 pixels), which translates to  
174 image overlap of 80.7/80.7 at 100m below the lens and 83.9/83.9 at ground level. Approximately 1900 photos  
175 were captured over each 40 hectare survey area for each camera.

## 176 Structure from motion/Photogrammetric processing

177 We used structure from motion (SfM), aka photogrammetry, to generate orthorectified reflectance maps,  
178 digital surface models, and dense point clouds for each field site. We used Pix4Dmapper Cloud to process  
179 imagery using parameters ideal for images of a densely vegetated area taken by a multispectral camera.  
180 For three sites, we processed the RGB and the multispectral imagery in the same project to enhance the  
181 resolution of the dense point cloud. All SfM projects resulted in a single processing “block,” indicating that  
182 all images in the project were optimized and processed together.

## 183 Creating canopy height models

184 We classified each survey area’s dense point cloud into “ground” and “non-ground” points using a cloth  
185 simulation filter algorithm (Zhang et al. 2016) implemented in the **lidR** (Roussel et al. 2019) package. We  
186 rasterized the ground points using the **raster** package (Hijmans et al. 2019) to create a digital terrain model  
187 representing the ground underneath the vegetation at 1 meter resolution. We created a canopy height model  
188 by subtracting the digital terrain model from the digital surface model created in Pix4Dmapper.

## 189 Tree detection

190 We tested a total of 7 automatic tree detection algorithms and a total of 177 parameter sets on the canopy  
191 height model or the dense point cloud to locate trees within each site (Table 2). We used 3 parameter sets of  
192 a variable window filter implemented in **ForestTools** (Plowright 2018) including the default variable window  
193 filter function in **ForestTools** as well as the “pines” and “combined” functions from Popescu and Wynne  
194 (2004). We used 6 parameter sets of a local maximum filter implemented in **lidR**. We used 131 parameter  
195 sets of the algorithm from Li et al. (2012), which operates on the original point cloud. These parameter  
196 sets included those from Shin et al. (2018) and Jakubowski et al. (2013). We used 3 parameter sets of the  
197 **watershed** algorithm implemented in **lidR**, which is a wrapper for a function in the **EBImage** package (Pau  
198 et al. 2010). We used 3 parameter sets of **ptrees** (Vega et al. 2014) implemented in **lidR** (Roussel et al.

199 2019) and `lidRplugins` (Roussel 2019) and which operates on the raw point cloud, without first normalizing  
 200 it to height above ground level (i.e.. subtracting the ground elevation from the dense point cloud). We used  
 201 the default parameter set of the `multichm` (Eysn et al. 2015) algorithm implmented in `lidR` (Roussel et  
 202 al. 2019) and `lidRplugins` (Roussel 2019). We used 30 parameter sets of the experimental algorithm `lmfx`  
 203 (Roussel 2019).

Table 2: Algorithm name, number of parameter sets tested for each algorithm, and references.

Algorithm	Parameter sets tested	Reference(s)
li2012	131	Li et al. (2012); Jakubowski et al. (2013); Shin et al. (2018)
lmfx	30	Roussel (2019)
localMaxima	6	Roussel et al. (2019)
multichm	1	Eysn et al. (2015)
ptrees	3	Vega et al. (2014)
vwf	3	Plowright (2018)
watershed	3	Pau et al. (2010)

## 204 Map ground data

205 Each orthorectified reflectance map was inspected to locate the 5 orange “X”s marking the center of the  
 206 field plots. We were able to locate 110 out of 180 field plots and were then able to use these plots for  
 207 validation of automated tree detection algorithms. We used the `sf` package (Pebesma et al. 2019) to convert  
 208 distance-from-center and azimuth measurements of each tree in the ground plots to an x-y position on the  
 209 SfM-derived reflectance map using the x-y position of the orange X visible in the reflectance map as the  
 210 center.

## 211 Correspondence of automatic tree detection with ground data

212 We calculated 7 forest structure metrics for each field plot using the ground data collected by Fettig et al.  
 213 (2019): total number of trees, number of trees greater than 15 meters, mean height of trees, 25<sup>th</sup> percentile  
 214 tree height, 75<sup>th</sup> percentile tree height, mean distance to nearest tree neighbor, mean distance to 2<sup>nd</sup> nearest  
 215 neighbor.

216 For each tree detection algorithm and parameter set described above, we calculated the same set of 7 structure  
217 metrics within the footprint of the validation field plots. We calculated the Pearson's correlation and root  
218 mean square error (RMSE) between the ground data and the aerial data for each of the 7 structure metrics  
219 for each of the 177 automatic tree detection algorithms/parameter sets.

220 For each algorithm and parameter set, we calculated its performance relative to other algorithms as whether  
221 its Pearson's correlation was within 5% of the highest Pearson's correlation as well as whether its RMSE was  
222 within 5% of the lowest RMSE. For each algorithm/parameter set, we summed the number of forest structure  
223 metrics for which it reached these 5% thresholds. For automatically detecting trees across the whole study,  
224 we selected the algorithm/parameter set that performed well across the most number of forest metrics.

225 **Segmentation of crowns**

226 We delineated individual tree crowns with a marker controlled watershed segmentation algorithm (Meyer and  
227 Beucher 1990) using the detected treetops as markers implemented in the **ForestTools** package (Plowright  
228 2018). If the automatic segmentation algorithm failed to generate a crown segment for a detected tree (e.g.,  
229 often snags with a very small crown footprint), a circular crown was generated with a radius of 0.5 meters. If  
230 the segmentation generated multiple polygons for a single detected tree, only the polygon containing the  
231 detected tree was retained. Image overlap decreases near the edges of the overall flight path, which reduces  
232 the quality of the SfM processing in those areas. Thus, we excluded segmented crowns within 35 meters of  
233 the edge of the survey area. Given the narrower field of view of the RedEdge multispectral camera versus  
234 the X3 RGB camera whose optical parameters were used to define the ~40 hectare survey area around each  
235 site, as well as the 35 meter additional buffering, the survey area at each site was approximately 30 hectares  
236 (Table 3).

237 We used the **velox** package (Hunziker 2017) to extract all the pixel values from the orthorectified reflectance  
238 map for each of the 5 narrow bands within each segmented crown polygon. Per pixel, we additionally  
239 calculated the normalized difference vegetation index (NDVI; Rouse et al. (1973)), the normalized difference  
240 red edge (NDRE; Gitelson and Merzlyak (1994)), the red-green index (RGI; Coops et al. (2006)), the red  
241 edge chlorophyll index (CI[red edge]; Clevers and Gitelson (2013)), and the green chlorophyll index (CI[green];  
242 Clevers and Gitelson (2013)). For each crown polygon, we calculated the mean value for each raw and derived  
243 reflectance band (5 raw; 5 derived).

<sup>244</sup> **Classification of trees**

<sup>245</sup> We overlaid the segmented crowns on the reflectance maps from 20 sites spanning the latitudinal and  
<sup>246</sup> elevational gradient in the study. Using QGIS, we hand classified 564 trees as live/dead and as one of 5  
<sup>247</sup> dominant species in the study area (*Pinus ponderosa*, *Pinus lambertiana*, *Abies concolor*, *Calocedrus decurrens*,  
<sup>248</sup> or *Quercus kelloggii*) using the mapped ground data as a guide.

<sup>249</sup> We used all 10 mean values of the reflectance bands for each tree crown polygon to predict whether the hand  
<sup>250</sup> classified trees were alive or dead using a boosted logistic regression model implemented in the **caret** package  
<sup>251</sup> (accuracy of live/dead classification on a withheld test dataset: 97.3%) (Kuhn 2008). For just the living trees,  
<sup>252</sup> we similarly used all 10 reflectance values to predict the tree species using regularized discriminant analysis  
<sup>253</sup> implemented in the **caret** package (accuracy of species classification on a withheld testing dataset: 66.7%;  
<sup>254</sup> accuracy of WPB host/non-WPB-host (i.e., ponderosa pine versus other tree species) on a withheld testing  
<sup>255</sup> dataset: 74.4%).

<sup>256</sup> Finally, we used these models to classify all tree crowns in the data set as alive or dead as well as the species  
<sup>257</sup> of living trees.

<sup>258</sup> **Allometric scaling of height to basal area**

<sup>259</sup> We converted the height of each tree determined using the canopy height model to its basal area. Using  
<sup>260</sup> the tree height and diameter at breast height (DBH; breast height = 1.37m) ground data from Fettig et al.  
<sup>261</sup> (2019), we fit a simple linear regression to predict DBH from height for each of the 5 dominant species. Using  
<sup>262</sup> the model-classified tree species of each segmented tree, we used the corresponding linear relationship for  
<sup>263</sup> that species to estimate the DBH given the tree's height. We then calculated each tree's basal area, assuming  
<sup>264</sup> no tapering from breast height.

<sup>265</sup> **Note on assumptions about dead trees**

<sup>266</sup> For the purposes of this study, we assumed that all dead trees were ponderosa pine and were thus host trees  
<sup>267</sup> for the western pine beetle. This is a reasonably good assumption, given that Fettig et al. (2019) found that  
<sup>268</sup> 73.4% of the dead trees in the coincident ground plots were ponderosa pine. The species contributing to  
<sup>269</sup> the next highest proportion of dead trees was incense cedar which represented 18.72% of the dead trees in  
<sup>270</sup> the ground plots. Incense cedar is not a potential host of the western pine beetle, and we expand on the  
<sup>271</sup> limitations of this study given the assumption of dead trees being ponderosa pine in the Discussion.

272 **Rasterizing individual tree data**

273 Because the tree detection algorithms were validated against ground data at the plot level, we rasterized the  
274 classified trees at a spatial resolution similar to that of the ground plots (rasterized to 20m x 20m equalling  
275 400 m<sup>2</sup>; circular ground plots with 11.35m radius equalling 404 m<sup>2</sup>). In each raster cell, we calculated the:  
276 number of live trees, number of dead trees, number of ponderosa pine trees, total number of trees (of all  
277 species, including ponderosa pine), quadratic mean diameter (QMD) of ponderosa pine trees, and QMD of all  
278 trees of any species (overall QMD). We converted the count of ponderosa pine trees and the total tree count  
279 to a density measurement of trees per hectare (tpha) by multiplying the counts in each 20m x 20m cell by 25  
280 to create a “host density” and an “overall density” variable per cell.

281 **Environmental data**

282 We used climatic water deficit (CWD) (Stephenson 1998) from the 1980-2010 mean value of the basin  
283 characterization model (Flint et al. 2013) as an integrated measure of temperature and moisture conditions  
284 for each cell. Higher values of CWD correspond to hotter, drier conditions and lower values correspond  
285 to cooler, wetter conditions CWD has been shown to correlate well with broad patterns of tree mortality  
286 in the Sierra Nevada (Young et al. 2017). We resampled the climatic water deficit product using bilinear  
287 interpolation implemented in the `raster` package to match the 20m x 20m spatial scale of the other variables.  
288 We converted the CWD value for each cell into a z-score representing that cell’s deviation from the mean  
289 CWD across the climatic range of Sierra Nevada ponderosa pine as determined from 179 herbarium records  
290 described in Baldwin et al. (2017). Thus, a CWD z-score of one would indicate that the CWD at that  
291 cell is one standard deviation hotter/drier than the mean CWD across all geolocated herbarium records for  
292 ponderosa pine in the Sierra Nevada.

293 **Statistical model**

294 We used a generalized linear model with a zero-inflated binomial response and a logit link to predict the  
295 probability of ponderosa pine mortality within each raster cell as a function of the crossed effects of ponderosa  
296 pine quadratic mean diameter and density added to the crossed effect of overall quadratic mean diameter and  
297 density as well as the interaction of each summand with climatic water deficit at each site.  
298 To measure and account for spatial autocorrelation of the bark beetle behavioral processes underlying  
299 ponderosa mortality, we first subsampled the data at each site to a random selection of 200, 20m x 20m  
300 cells representing approximately 27.5% of the surveyed area. With these subsampled data, we included a  
301 separate exact Gaussian process term per site of the interaction between the x- and y-position of each cell

302 using the `gp()` function in the `brms` package (Bürkner 2017). The Gaussian process accounts for spatial  
 303 autocorrelation in the model by jointly estimating the spatial covariance of the response variable with the  
 304 effects of the other covariates.

$$y_{i,j} \sim \begin{cases} 0, & p \\ Binom(n_i, \pi_i), & 1 - p \end{cases}$$

$$\text{logit}(\pi_i) = \beta_0 +$$

$$\beta_1 X_{cwd,j} +$$

$$\beta_1 X_{cwd,j} (\beta_2 X_{\text{pip}oQMD,i} + \beta_3 X_{\text{pip}o\text{Density},i} + \beta_4 X_{\text{pip}oQMD,i} X_{\text{pip}o\text{Density},i}) +$$

$$\beta_1 X_{cwd,j} (\beta_5 X_{\text{overall}QMD,i} + \beta_6 X_{\text{overall}\text{Density},i} + \beta_7 X_{\text{overall}QMD,i} X_{\text{overall}\text{Density},i}) +$$

$$\mathcal{GP}_j(x_i, y_i)$$

305 Where  $y_i$  is the number of dead trees in cell  $i$ ,  $n_i$  is the sum of the dead trees and live ponderosa pine trees  
 306 in cell  $i$ ,  $\pi_i$  is the probability of ponderosa pine tree mortality in cell  $i$ ,  $p$  is the probability of there being  
 307 zero dead trees in a cell arising as a result of an unmodeled process,  $X_{cwd,j}$  is the z-score of climatic water  
 308 deficit for site  $j$ ,  $X_{\text{pip}oQMD,i}$  is the scaled quadratic mean diameter of ponderosa pine in cell  $i$ ,  $X_{\text{pip}o\text{Density},i}$   
 309 is the scaled density of ponderosa pine trees in cell  $i$ ,  $X_{\text{overall}QMD,i}$  is the scaled quadratic mean diameter  
 310 of all trees in cell  $i$ ,  $X_{\text{overall}\text{Density},i}$  is the scaled density of all trees in cell  $i$ ,  $x_i$  and  $y_i$  are the x- and y-  
 311 coordinates of the centroid of the cell in an EPSG3310 coordinate reference system, and  $\mathcal{GP}_j$  represents the  
 312 exact Gaussian process describing the spatial covariance between cells at site  $j$ .

313 We used 4 chains with 2000 iterations each (1000 warmup, 1000 samples), and confirmed chain convergence  
 314 by ensuring all `Rhat` values were less than 1.1 (Brooks and Gelman 1998). We used posterior predictive  
 315 checks to visually confirm model performance by overlaying the density curves of the predicted number of  
 316 dead trees per cell over the observed number (Gabry et al. 2019). For the posterior predictive checks, we  
 317 used 50 random samples from the model fit to generate 50 density curves and ensured curves were centered  
 318 on the observed distribution, paying special attention to model performance at capturing counts of zero.

### 319 Software and data availability

320 All data are available via the Open Science Framework. Statistical analyses were performed using the `brms`  
 321 packages. With the exception of the SfM software (Pix4Dmapper Cloud) and the GIS software QGIS, all  
 322 data carpentry and analyses were performed using R (R Core Team 2018).

## 323 Results

Table 3: Site characteristics for each of the 32 sites. The site name consists of the forest name, elevation band, and rep separated by an underscore. The Eldorado National Forest is ‘eldo’, the Stanislaus National Forest is ‘stan’, the Sierra National Forest is ‘sier’, and the Sequoia National Forest is ‘sequ’. The elevation band represents the lower bounds of the 305 meter (1000 foot) elevation bands in feet. Thus ‘3k’ implies that site was located between 3,000 and 4,000 feet (914-1219 meters). Aerially detected mortality and density of the whole site is presented along with the mortality and density calculated from the ground data (aerial / ground). The density is measured in trees per hectare (tpha).

Site	CWD (mm)	CWD (z-score)	Survey area (ha)	Mortality (aerial/ground)	Density (tpha; aerial/ground)
eldo_3k_1	678	0.319	31.02	0.11/0.61	630.01/410.19
eldo_3k_2	706	0.501	30.61	0.12/0.36	444.26/647.42
eldo_3k_3	655	0.163	30.95	0.22/0.36	492.63/410.19
eldo_4k_1	570	-0.383	28.04	0.09/0.39	632.82/588.11
eldo_4k_2	642	0.0831	28.41	0.15/0.78	338.20/271.82
eldo_5k_1	663	0.219	28.44	0.11/0.44	661.80/543.63
eldo_5k_2	627	-0.0132	30.02	0.12/0.36	584.89/968.65
eldo_5k_3	599	-0.2	29.73	0.07/0.32	488.66/622.71
stan_3k_1	638	0.059	31.04	0.10/0.52	739.45/1037.84
stan_3k_2	739	0.713	18.78	0.40/0.78	433.53/405.25
stan_3k_3	762	0.859	30.1	0.22/0.41	558.43/326.18
stan_4k_1	540	-0.58	29.62	0.29/0.63	507.61/711.66
stan_4k_2	528	-0.658	30.54	0.18/0.56	481.85/256.99
stan_5k_1	524	-0.688	30.94	0.19/0.54	388.89/336.06
stan_5k_2	524	-0.685	29.94	0.21/0.44	399.33/622.71
sier_3k_1	764	0.871	30.42	0.19/0.48	651.46/850.04
sier_3k_2	768	0.898	30.05	0.20/0.77	438.84/153.21

Site	CWD (mm)	CWD (z-score)	Survey area (ha)	Mortality (aerial/ground)	Density (tpha; aerial/ground)
sier_3k_3	773	0.932	29.77	0.32/0.77	511.26/459.62
sier_4k_1	841	1.38	30.43	0.54/0.51	576.15/538.69
sier_4k_2	764	0.877	29.3	0.33/0.57	499.43/854.98
sier_4k_3	688	0.383	26.39	0.48/0.59	454.23/499.15
sier_5k_1	722	0.599	14.59	0.41/0.43	631.30/716.60
sier_5k_2	710	0.523	27.53	0.53/0.74	477.29/454.67
sier_5k_3	779	0.968	28.93	0.33/0.43	569.44/484.33
sequ_4k_1	767	0.891	29.59	0.50/0.56	365.81/607.88
sequ_4k_3	816	1.21	29.69	0.35/0.71	433.35/306.41
sequ_5k_1	718	0.577	27.12	0.35/0.52	364.01/444.79
sequ_5k_2	587	-0.274	29.1	0.45/0.43	478.31/499.15
sequ_5k_3	611	-0.117	31.34	0.42/0.48	348.68/494.21
sequ_6k_1	731	0.657	27.78	0.30/0.70	433.43/360.77
sequ_6k_2	690	0.39	11.83	0.26/0.43	699.04/934.06
sequ_6k_3	603	-0.174	26.51	0.36/0.32	535.54/691.89

324 **Tree detection**

325 We found that the experimental `lmfx` algorithm with parameter values of `dist2d = 1` and `ws = 2.5` (Roussel  
 326 et al. 2019) performed the best across 7 measures of forest structure as measured by Pearson's correlation  
 327 with ground data (Table 3).

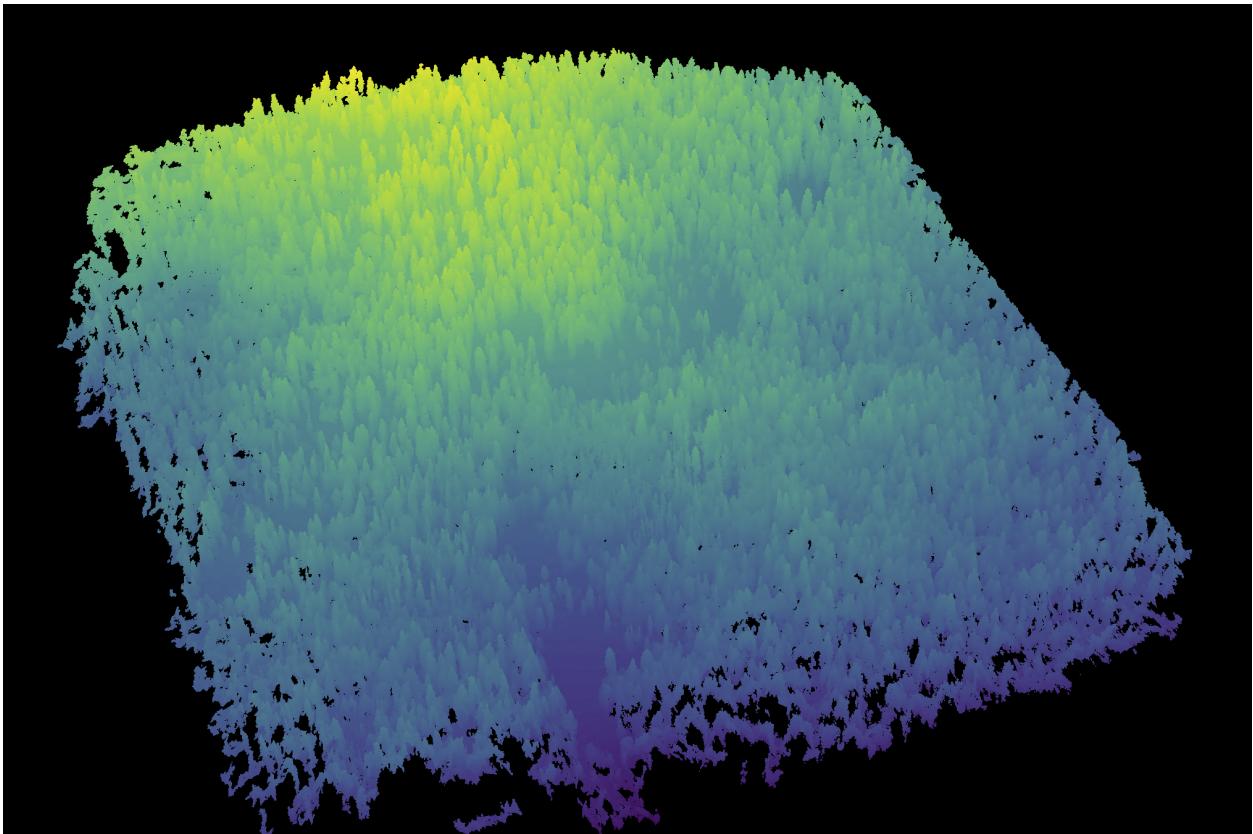


Figure 2: A dense point cloud representing ~40 hectares of forest is generated using Structure from Motion (SfM) processing of ~1900 images. The dense point cloud z- position represents the ground elevation plus the vegetation height.

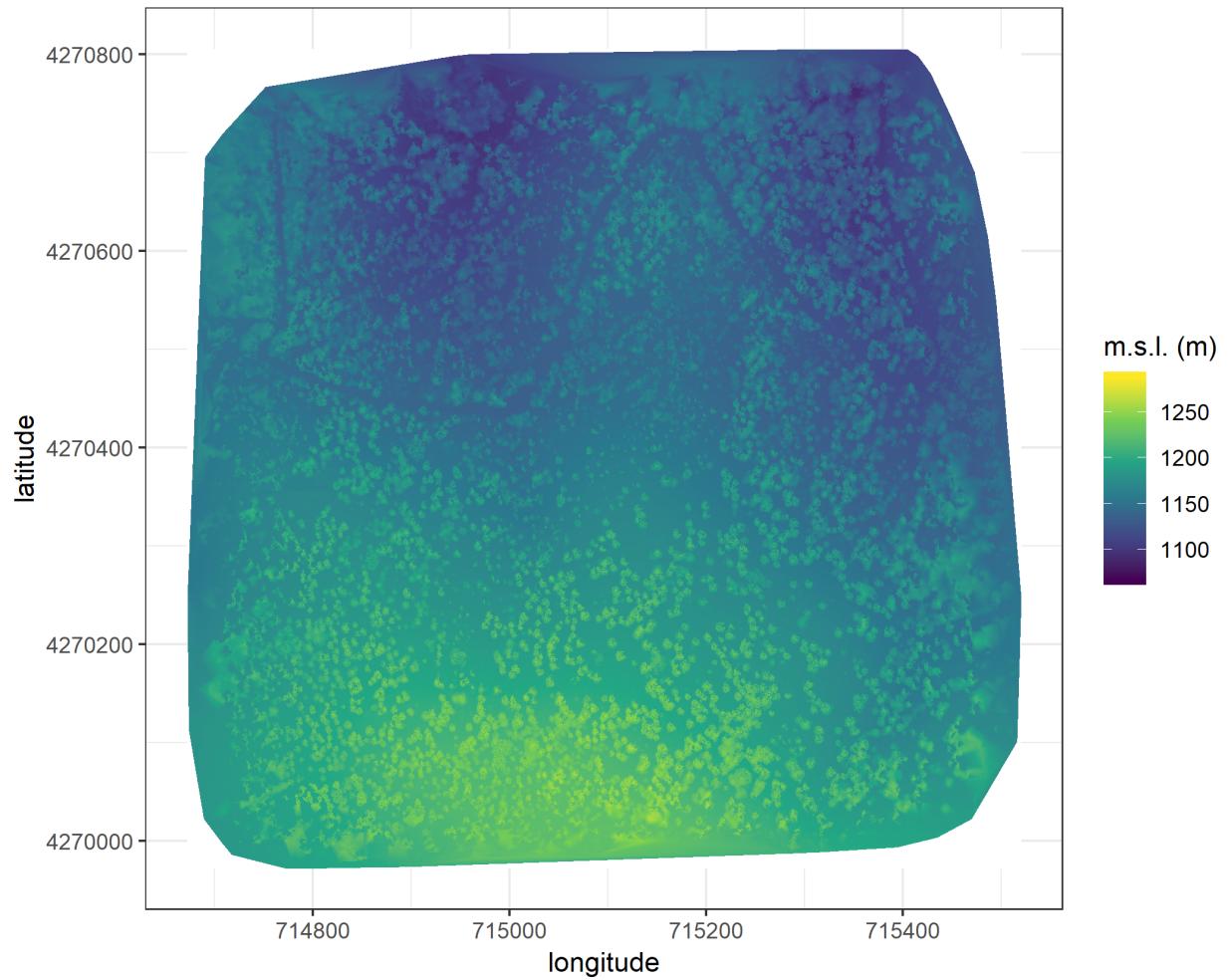


Figure 3: The digital surface model (DSM) is a 2-dimensional representation of the dense point cloud generated using structure from motion (SfM) processing. The DSM represents the ground elevation plus the vegetation height.

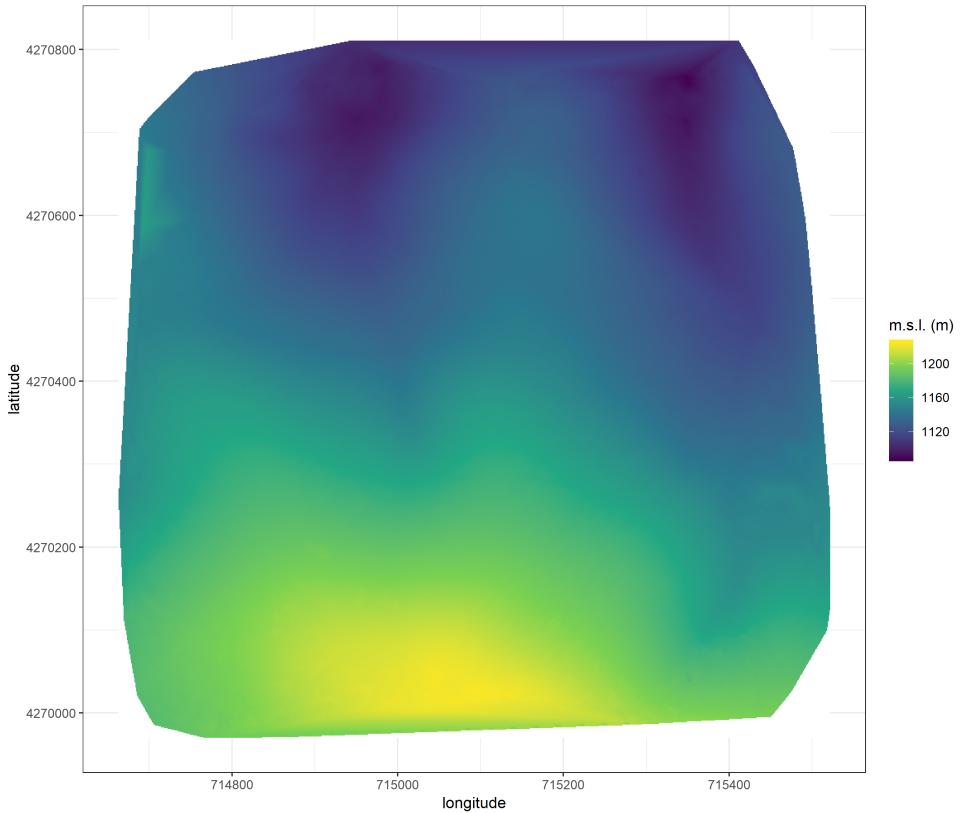


Figure 4: The digital terrain model (DTM) is generated by processing the dense point cloud using the cloth simulation filter algorithm (Zhang et al. 2016), which classifies points as “ground” or “not-ground” and then interpolates the “ground” elevation using Delaunay triangulation for the rest of the dense point cloud footprint. The DTM represents the ground elevation without any vegetation.

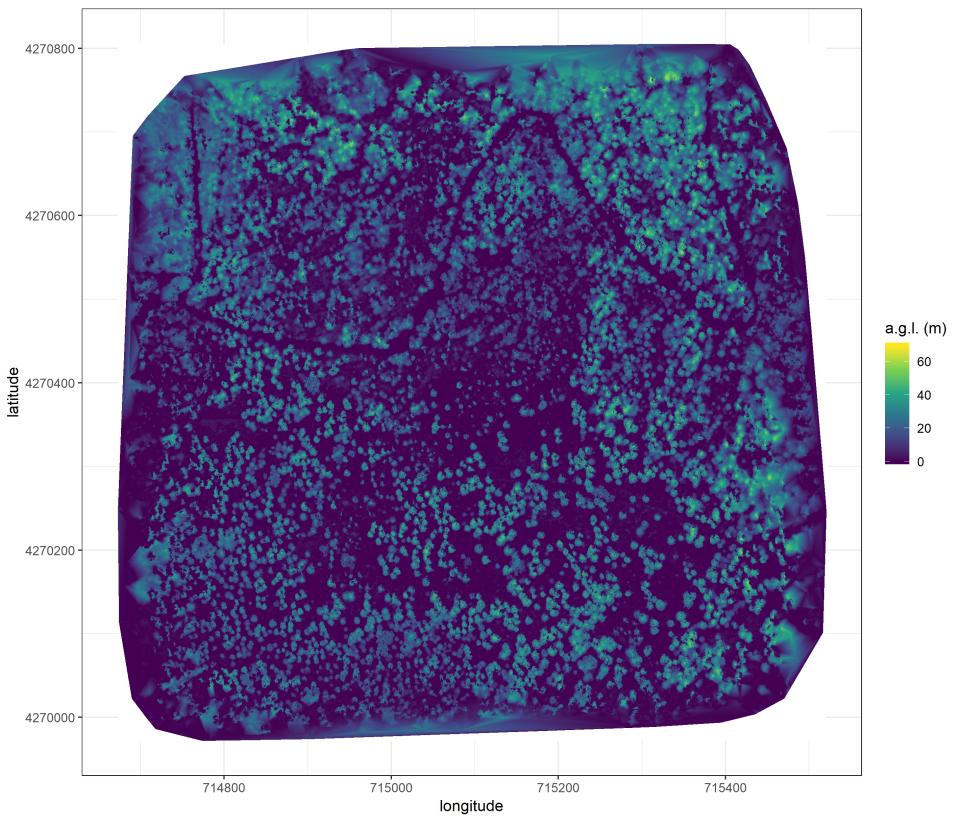


Figure 5: The canopy height model (CHM) is generated by subtracting the digital terrain model from the digital surface model. The CHM represents the height of all of the elevation above ground level.

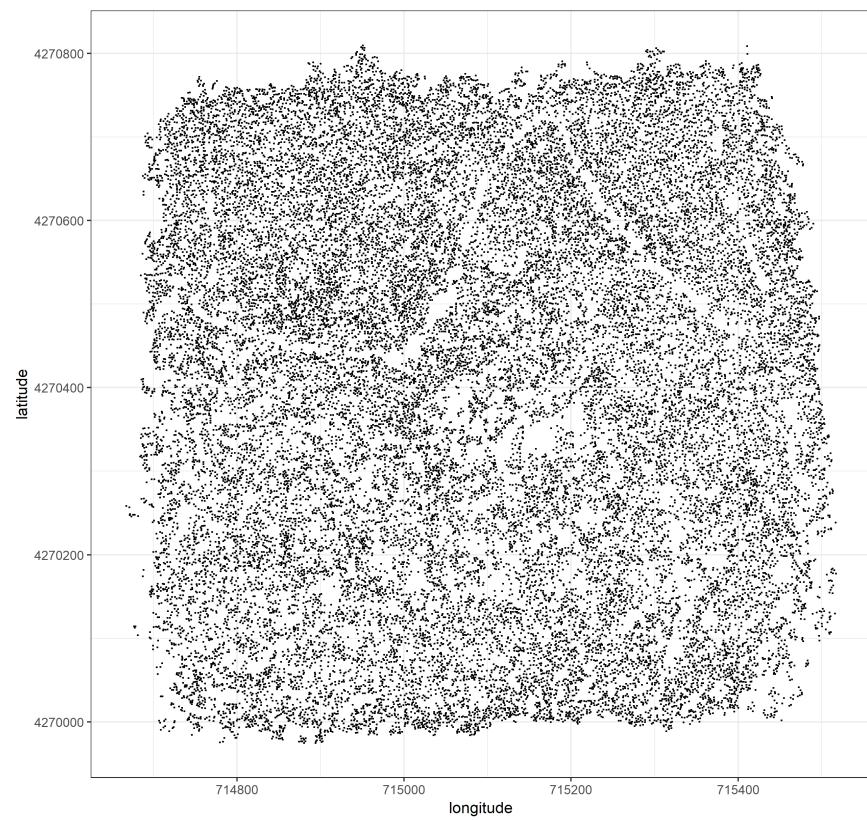


Figure 6: Tree locations are detected using the `lmfx` (Roussel et al. 2019) treetop detection algorithm on the dense point cloud.

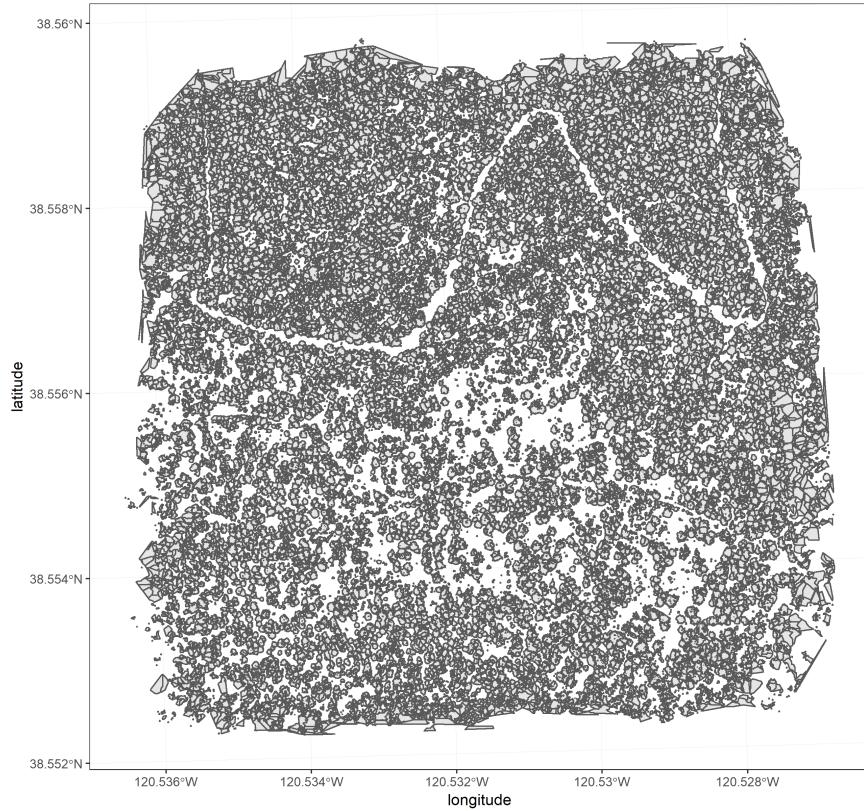


Figure 7: Individual crowns are delineated using a marker controlled watershed segmentation algorithm (Meyer and Beucher 1990, Plowright 2018) on the canopy height model (CHM) using the detected tree locations as a priority map. If the algorithm failed to delineate a crown for a tree that was identified in the tree detection step, a circular crown with a 0.5m buffer centered on point location of the detected tree was added as a crown.

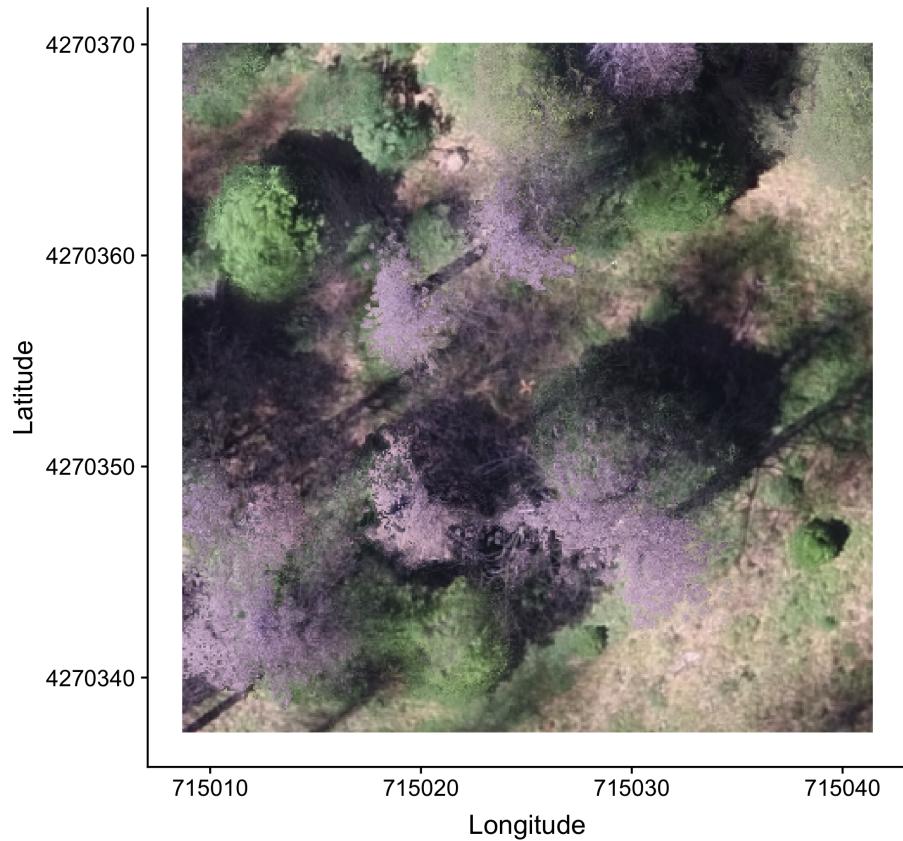


Figure 8: The orthomosaic for each of the 32 sites is generated with the Structure from Motion (SfM) processing, showing a top-down view of the whole survey area such that distances between objects in the scene are preserved and can be measured. Depicted is an example orthomosaic for one of the 32 sites cropped to the extent of a single ground plot (5 ground plots per site) showing the orange X placed at exactly the plot center prior to flight. The original orthomosaic for the whole site represents an area approximately 1000 times as large as the area depicted here.

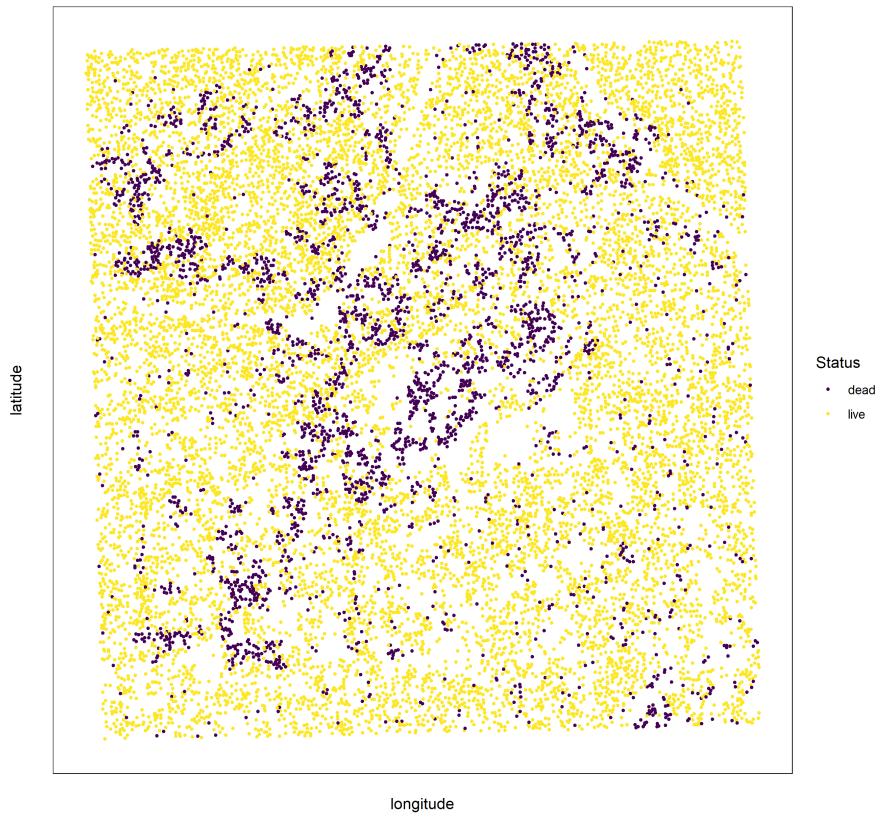


Figure 9: Each tree is classified as live or dead by extracting the pixel values from the 5 narrow bands of the Rededge3 camera (and 5 derived bands– see methods) in the orthomosaic within each segmented tree crown of the detected trees, taking their mean value, and using those means to predict live/dead status with a boosted logistic regression previously trained on a hand-classified set of segmented crowns from across the study area.

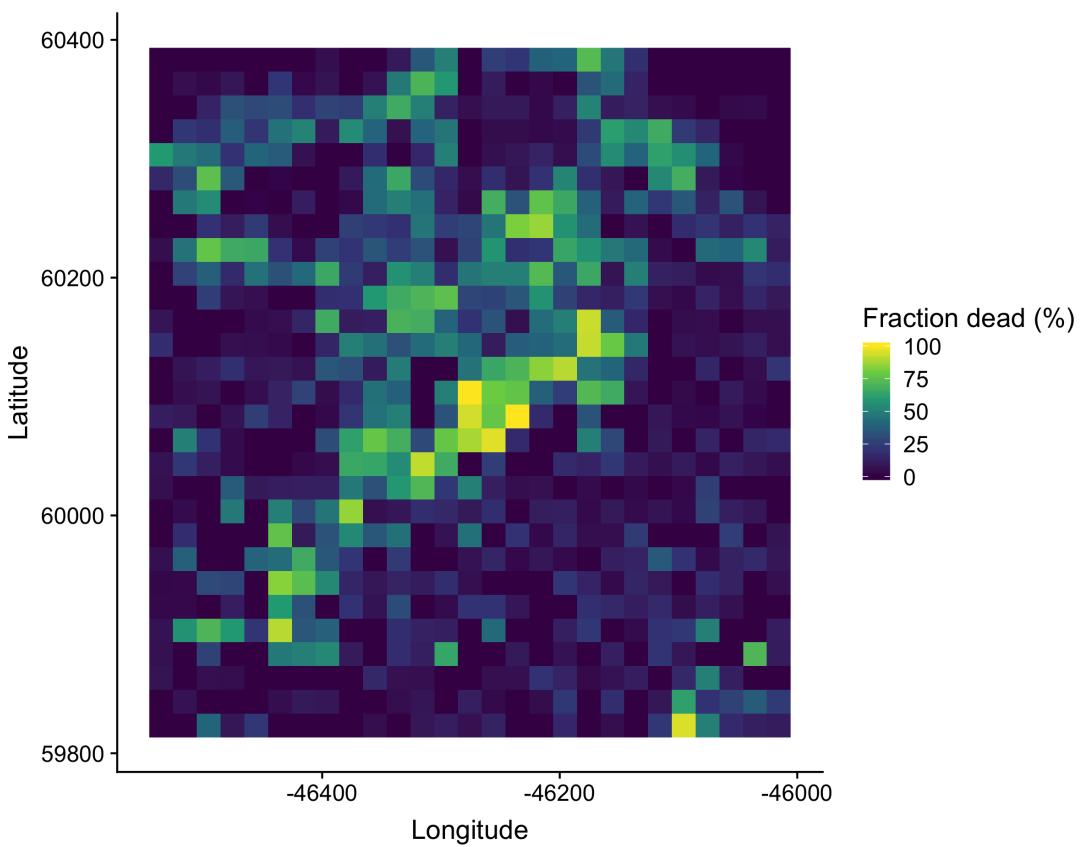


Figure 10: We rasterized the individual tree data by aggregating values to 20m x 20m cells. This example shows the proportion of dead trees per cell for the same example site as in the previous figures.

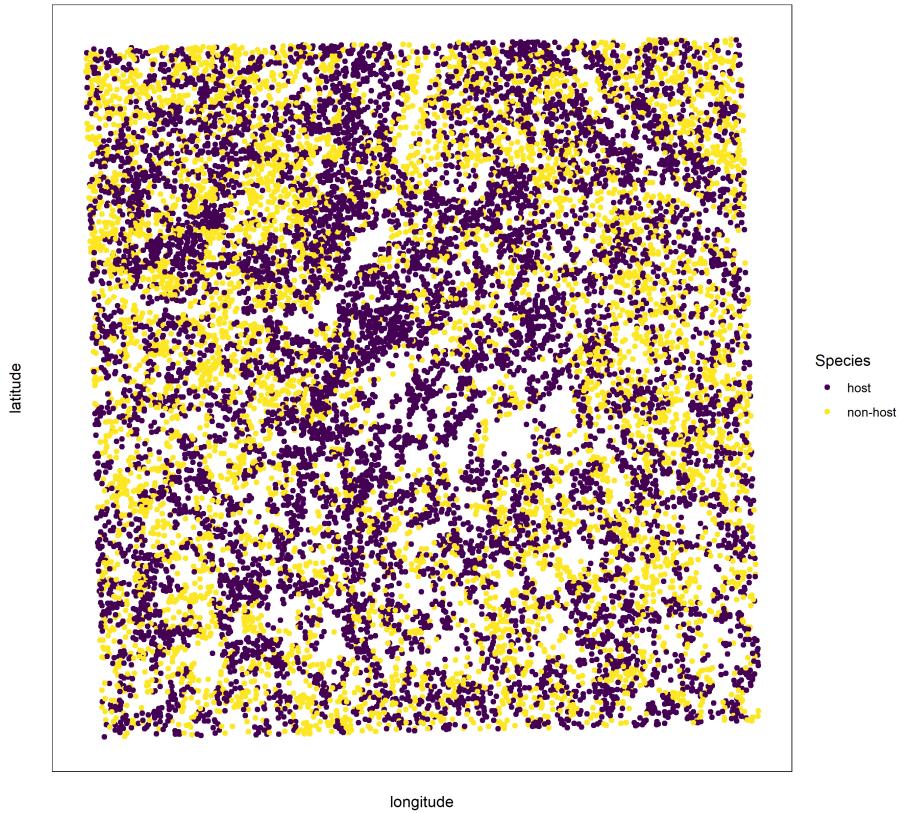


Figure 11: For each live tree, we classified its species using the same means of extracted pixel values across the 5 Rededge3 narrow bands (and 5 derived bands) as predictors in a regularized discriminant analysis previously trained on a hand-classified set of segmented crowns from across the study area. Host/non-host data were also rasterized as in the previous figure prior to analyses (not shown).

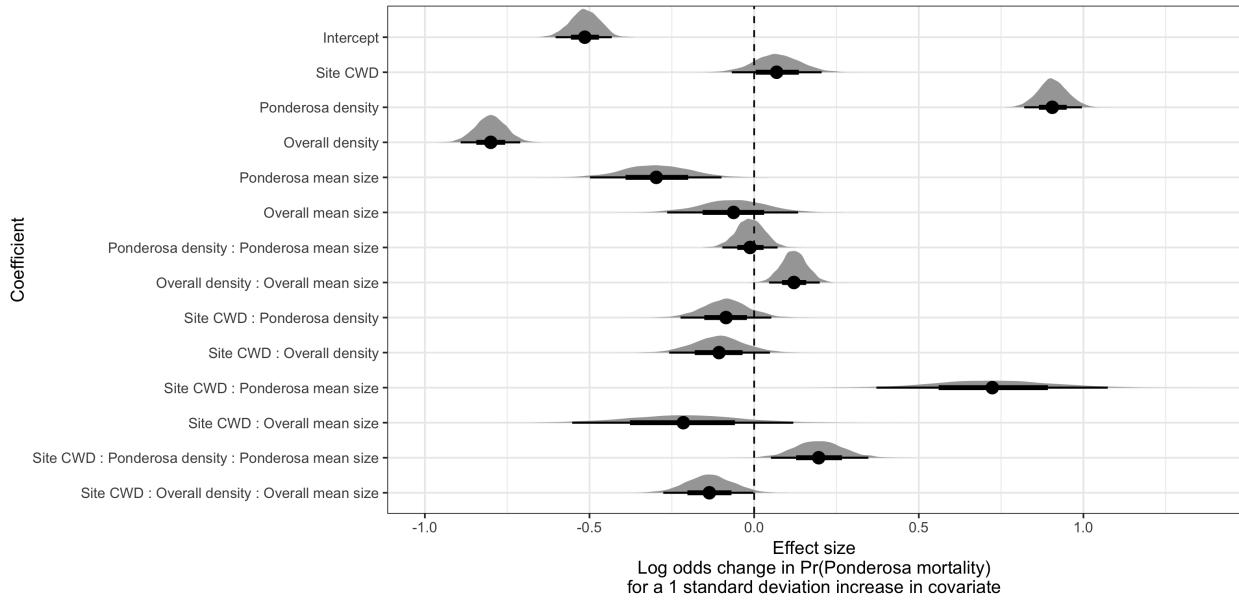


Figure 12: Posterior distributions of effect size from zero-inflated binomial model predicting the probability of ponderosa pine mortality in a 20m x 20m cell given forest structure characteristics of host trees and all trees within the cell, as well as a site-level climatic water deficit. The gray density distribution for each model covariate represents the density of the posterior distribution, the point underneath each density curve represents the median of the estimate, the bold interval surrounding the point estimate represents the 66% credible interval, and the thin interval surrounding the point estimate represents the 95% credible interval.

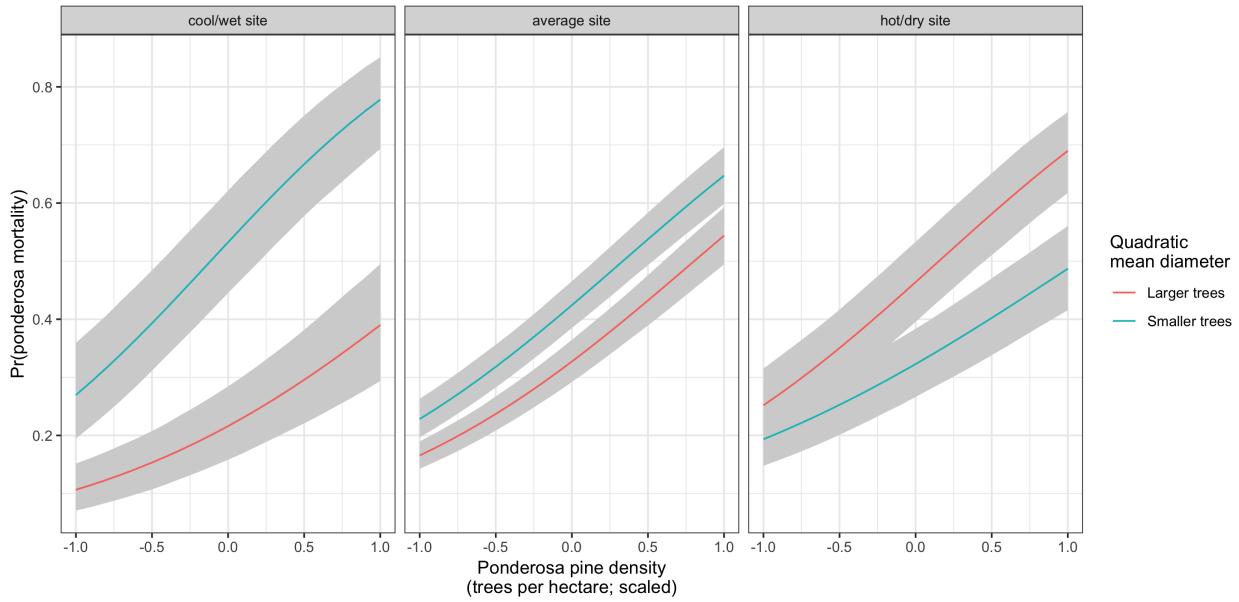


Figure 13: Line version of model results with 95% credible intervals showing primary influence of ponderosa pine structure on the probability of ponderosa pine mortality, and the interaction across climatic water deficit. The “larger trees” line represents the quadratic mean diameter of ponderosa pine 0.7 standard deviations above the mean, and the “smaller trees” line represents the quadratic mean diameter of ponderosa pine 0.7 standard deviations below the mean.

Table 4: Correlation and differences between the best performing tree detection algorithm (lmfx with dist2d = 1 and ws = 2.5) and the ground data. An asterisk next to the correlation or RMSE indicates that this value was within 5% of the value of the best-performing algorithm/parameter set. Ground mean represents the mean value of the forest metric across the 110 ground plots that were visible from the sUAS-derived imagery. The median error is calculated as the median of the differences between the air and ground values for the 110 visible plots. Thus, a positive number indicates an overestimate by the sUAS workflow and a negative number indicates an underestimate.

Forest structure metric	Ground mean	Correlation with ground	RMSE	Median error
total tree count	19	0.67*	8.68*	2
count of trees > 15m	9.9	0.43	7.38	0
dist to 1st nearest neighbor	2.8	0.55*	1.16*	0.26
(m)				
dist to 2nd nearest neighbor	4.3	0.61*	1.70*	0.12
(m)				
height (m); 25th percentile	12	0.16	8.46	-1.2
height (m); mean	18	0.29	7.81*	-2.3
height (m); 75th percentile	25	0.35	10.33*	-4

328 **Effect of local structure and regional climate on western pine beetle severity**

329 We detected no main effect of climatic water deficit on the probability of ponderosa pine mortality within  
 330 each 20m x 20m cell.

331 We found a strong main effect of ponderosa pine local density, accounting for quadratic mean diameter of  
 332 ponderosa pine, with greater density increasing the probability of ponderosa pine mortality.

333 Conversely, we found a generally negative effect of quadratic mean diameter of ponderosa pine on the  
 334 probability of ponderosa mortality, suggesting that the western pine beetle attacked smaller trees, on average.

335 There was a strong positive interaction between the climatic water deficit and ponderosa pine quadratic mean

336 diameter, such that larger trees were more likely to increase the probability of ponderosa mortality in hotter,  
337 drier sites.

338 We found negative main effects of overall tree density and overall quadratic mean diameter. There was a  
339 positive interaction between these variables, such that denser stands with larger trees did lead to greater  
340 ponderosa pine mortality.

341 **Spatial effects**

342 We were able to calculate the length scale of the spatial autocorrelation in the probability of ponderosa  
343 pine mortality at each site, accounting for forest structure and environmental factors. By fitting a separate  
344 approximate Gaussian process for each site on the interacting variables of the x- and y- position, we measured  
345 the spatial covariance inherent in the data, accounting for other factors.

346 **Discussion**

347 **Closer spacing between potential host trees facilitates dispersal**

348 If this drives mortality patterns, then we'd expect the local density of ponderosa pine trees, accounting for  
349 other variables, to have a strong positive effect.

350 **Host preference for large trees**

351 If this drives mortality patterns, then we'd expect the quadratic mean diameter of ponderosa pine trees,  
352 accounting for other variables, to have a strong positive effect.

353 **Denser forests augment pheromone communication**

354 If this drives mortality patterns, then we'd expect the local density of all trees, accounting for other variables,  
355 to have a strong positive effect.

356 **Tree crowding leads to greater average water stress per tree**

357 If this drives mortality patterns, then we'd expect the quadratic mean dimater of all trees, accounting for  
358 other factors, to have a strong positive effect.

359 **Interaction between host density and host size**

360 A positive coefficient would indicate a combined effect of WPB preference for large trees and nearby host  
361 availability.

362 **Interaction between all tree density and all tree size**

363 A positive coefficient would indicate a combined effect of tree crowding and pheromone communication  
364 enhancement.

365 **Implications of forest structure/regional climate interactions**

366 We found that the probability of ponderosa pine mortality generally increased with local host availability  
367 (host density), but also interacted with both host size and regional climate such that the role of tree size  
368 became increasingly important in more climatically extreme sites. A smaller average tree size led to a lower  
369 probability of ponderosa mortality in cool/wet sites and a larger average tree size led to a greater probability  
370 of ponderosa mortality in hot/dry sites. These mortality patterns highlight a possible distinction in behavior  
371 between the recent western bark beetle activity across the gradient of climatic water deficit. Even in the most  
372 highly impacted forest stands (because our study sites were selected conditional on there being high levels of  
373 western pine beetle activity), there is still a detectable effect of tree size such that the smaller (presumably  
374 weaker) trees are getting killed in cooler/wetter sites, and the larger (presumably more well-defended) trees  
375 are getting killed more in the hotter/drier sites. So while mortality is high everywhere, there does appear to  
376 be a difference in the beetle choosiness across the climatic water deficit gradient.

377 **Similarities and differences with Fettig et al. (2019)**

378 Fettig et al. (2019) found positive relationship between number of trees killed and: total number of trees,  
379 total basal area, stand density index.

380 Fettig et al. (2019) found negative relationship between the proportion of trees killed and: total number of  
381 trees, stand density index.

382 Host availability and suitability are usually considered the major factors affecting beetle population behavior  
383 (Reid 1963; Berryman 1973, 1976, 1978a, 1982a; Cole 1981; Amman 1984). (Raffa and Berryman 1987)

384 Hayes et al. (2009) and Fettig et al. (2019) found measures of host availability explained less variation in  
385 mortality than measures of stand density.

386 Negrón et al. (2009) reported positive association of probability of ponderosa pine mortality and tree density  
387 during a drought in Arizona.

388 Effect of competition may be masked because drought was so extreme Fettig et al. (2019); Floyd et al.  
389 (2009), which is perhaps why we saw a counter-intuitive signal of increasing total basal area leading to lower  
390 probability of ponderosa pine mortality.

391 **Broader context around field plots**

392 We surveyed 9 square kilometers of forest representing ~450,000 trees along a broad environmental gradient  
393 of climatic water deficit. Site selection and small plot size can influence inference. For instance, Fettig et  
394 al. (2019) reported statistically undetectable differences in overall mortality in their plot network across 4  
395 national forests. By expanding the hectarage surveyed by a factor of 200, we detected dramatic differences in  
396 overall mortality.

397 This is about more than sample size (though that helps). This is also about capturing the local disturbance  
398 phenomenon.

399 **Implications for future forest structure**

400 We have demonstrated that forest structure (local host density and size) affected the cumulative severity  
401 of the western pine beetle in the Sierra Nevada in the 2012 to 2015 drought and its aftermath. Clearly,  
402 this forest insect disturbance has reciprically impacted the forest structure, with uncertain consequences for  
403 long-term forest dynamics.

404 Small trees are getting killed in cooler/wetter sites, larger trees getting killed in hotter/drier sites. Perhaps  
405 the cooler/wetter sites are resisting even this massive disturbance event?

406 **Spatial effect**

407 The western pine beetle is known to exhibit strong aggregation and anti-aggregation behavior arising from  
408 its pheromone communication, and thus it is likely that the measured spatial covariance in this study is  
409 attributable in part to the magnitude of this effect at each site.

410 Some studies have suggested that “outbreak” conditions are distinguishable by clustered tree mortality, but  
411 this is perhaps challenging to tease apart (Raffa et al. 2008). Our modeling framework allows for a joint  
412 estimation of the effects of forest structure, environmental condition, and the spatial effect. This framework  
413 would be enhanced with confidence in individual tree level data, and a lot of it, along with a strong gradient  
414 of environmental conditions and forest structure.

415 We won’t interpret this measure of contagion, because the uncertainties in this particular study are too great  
416 (tree detection, species classification, dead trees all assumed to be WPB hosts, didn’t account for topographic  
417 effects which could also manifest as part of this spatial covariance process). We do suggest that this could be  
418 a meaningful and quantifiable means of assessing bark beetle “stage of outbreak”.

419 **Future spatial directions (will cut this; here for now so I can write it down elsewhere)**

420 Perhaps could also compare relative effect of individual tree spacing (Voronoi polygon area) with the length  
421 scale parameter at a certain site to get at a similar question. A big voronoi polygon area effect and a short  
422 covariance kernel tells us that it's a water stress effect— a crowded tree gets attacked regardless of whether  
423 nearby trees were attacked. A small voronoi polygon area effect and a long covariance kernel tells us that the  
424 mortality is patterned more based on there being spillover from nearby attacked neighbors instead of how  
425 crowded any given tree is. I expect we might see different relative magnitudes of voronoi polygon area and  
426 covariance kerel effects depending on CWD.

427 **Important considerations**

428 Cumulative effect of elevated insect activity, as mortality was spread out over 5 years and we surveyed at the  
429 end. All the detected dead trees were considered ponderosa pine— we know this is wrong. Only about 3 out  
430 of 4 dead trees in Fettig et al. (2019) were ponderosa.

431 **Room for improvement**

- 432 • Better geometry by using higher overlap, more spatially resolved images.
- 433 • Better image classification and scalability by using instrumentation having spectral overlap with more  
434 widely deployed instrumentation (e.g., Landsat).
- 435 • Better tree detection using machine learning approaches
- 436 • Our live/dead classifier works pretty well.
- 437 • Our species classifier could improve. Perhaps also using machine learning approaches.

438 (???) (Preisler et al. 2017)

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