PHYSICAL CHARACTERISTICS AND FINE ROOTS WITHIN DUFF MOUNDS OF OLD-GROWTH SUGAR AND JEFFREY PINE IN A FIRE-EXCLUDED SIERRAN MIXED-CONIFER FOREST

By

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ABSTRACT

PHYSICAL CHARACTERISTICS AND FINE ROOTS WITHIN DUFF MOUNDS OF OLD-GROWTH SUGAR AND JEFFREY PINE IN A FIRE-EXCLUDED SIERRAN MIXED-CONIFER FOREST

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Fire exclusion has profoundly impacted frequent fire forests in western North America, disrupting fundamental ecological processes while leaving large, old pine trees vulnerable to drought, insects and disease, and fire. Forest managers want to increase the pace and scale of prescribed burning, yet heavy accumulations of organic material (duff mounds) at the bases of large pines can smolder for prolonged periods, damaging the cambium or consuming fine roots occupying the O horizon and/or upper mineral soil horizons. Increased duff mound depth is associated with greater mortality risk during prescribed fire, yet the biotic and abiotic drivers of duff mound accumulation and fine root density in large old pines is poorly understood. To understand the relative importance of factors influencing duff mound physical characteristics and fine root density, I combined field-collected duff mound and tree data with lidar-derived tree crown and topographic metrics for 324 large, old sugar (*Pinus lambertiana*) and Jeffrey pine (*Pinus jeffreyii*) at Teakettle Experimental Forest, a mixed-conifer forest in the southern Sierra Nevada, CA, USA which last experienced wildfire in 1865. I specifically asked: 1) Do duff mound physical characteristics differ between tree species, and tree size (diameter at breast height)? 2) Does fine root density differ between tree species, tree size, and between the O horizon and upper mineral soil horizon? 3) Are topographic attributes and tree crown metrics important drivers of duff mound physical characteristics and fine root density for either tree species?

I found strong, positive relationships between tree size and total duff mound depth and volume for sugar and Jeffrey pine. Fine root density was greater in the upper mineral soil than the O horizon for both species. Fine root density increased with tree size in the O horizon, but was species dependent in the upper mineral soil: with a weak negative relationship for sugar pine and no relationship for Jeffrey pine. In terms of lidar-derived metrics, leaf area density, slope, and topographic position index (100 m) best explained total duff mound volume and maximum mound depth. Topographic wetness index (TWI) was the most important predictor of fine root density in the upper mineral soil horizon, whereas leaf area density, topographic position index (30 m) and TWI best explained O horizon fine root density. Overall low variance explained in models is likely due to uncertainty in tree age and time since the last fire consumed duff material for individual trees. These findings suggest efforts to mitigate large pine mortality in preparation for prescribed fire treatments should prioritize the largest individuals, while accounting for heightened risk associated with specific topographic features.

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INTRODUCTION

In western North America, lightning ignitions and intentional use of fire by Indigenous peoples shaped dry pine and mixed-conifer forests for millennia (Knight et al., 2023; Roos et al., 2022; Taylor et al., 2016). The fire regimes of these forests were characterized by frequent, low- to mixed-severity surface fires that sustained fundamental ecosystem processes while supporting the persistence of large, old pines as the dominant overstory species (Collins et al., 2011; Hessburg et al., 2005; Knapp et al., 2013). Fire exclusion has dramatically altered the composition and structure of frequent fire forests (Hagmann et al., 2021), leading to a decline in pine populations while encouraging the proliferation of shade-tolerant, fire-sensitive tree species (Knapp et al., 2013; North et al., 2007). Resulting forest densification, increased water stress, and climate-driven disturbances such as drought, insects, disease, and high-severity wildfire are having deleterious impacts on many western US forested ecosystems (Fettig et al., 2019; Restaino et al., 2019; Stephens et al., 2018). Of particular concern are mature conifer forests with populations of large, old pine trees that now face numerous threats due to a century-long legacy of fire exclusion.

Large, old trees serve critical ecological roles, yet are disproportionately rare on the landscape (Lindenmayer et al., 2012; Lindenmayer and Laurance, 2017; Lutz et al., 2018). Large old trees are “keystone structures” of forested ecosystems (Manning et al., 2006). They occupy a single space for centuries, modifying their local environment by creating distinct microclimates and influencing the surrounding stand structure and spatial arrangement of trees (Cholewińska et al., 2021). Large-diameter trees and old-forest ecosystems are critical habitat for many endangered and ecosystem indicator species across the globe. In the Sierra Nevada region, the Spotted Owl (*Strix occidentalis*), northern flying squirrel (*Glaucomys sabrinus*), and American pine marten (*Martes americana*) all prefer large-diameter trees and snags as nest and resting sites (Jones et al., 2018; Meyer et al., 2005; North et al., 2017; Spencer, 1987). Globally, old-growth trees and forests are important contributors to long-term carbon sequestration (Luyssaert et al., 2008). In Sierra Nevada mixed-conifer forests, frequent fire stabilizes forest carbon by reducing burn severity and area burned during extreme weather events, while protecting the carbon stored in large, old trees (Hurteau et al., 2019; Krofcheck et al., 2017).

The combination of drought, bark beetles, and wildfire have resulted in large declines of mature conifer forests in California over the past two decades (Steel et al., 2022). In central and southern California, the drought between 2012-2015 was the most severe in the instrumental record (Robeson, 2015), resulting in mass mortality of conifers (Stephens et al., 2018). Drought-weakened large-diameter pines were particularly affected by mass beetle attacks, leading to disproportionately high levels of mortality in pine species compared to other mixed-conifer tree species (Fettig et al., 2019; Stephenson et al., 2019). Widespread drought mortality caused a dramatic shift in aboveground biomass from living trees with higher moisture content, to dead trees and downed fuels with much lower moisture content, increasing potential heat release during wildfire (Goodwin et al., 2020, 2021). Consequently, extreme drought and a legacy of fire exclusion have resulted in vast expanses of Sierra Nevada mixed-conifer forests that are now more vulnerable to mortality and high-severity wildfire.

Following over a century of fire exclusion, management intervention is necessary to restore the ecological patterns, processes, and function of Sierra Nevada mixed-conifer forests. There is a strong desire to increase the pace and scale of forest treatments including prescribed fire, mechanical thinning, and managed wildfire (North et al., 2021; USDA Forest Service, 2022). Prescribed burning is widely applied in frequent fire forests to reduce fuels and restore fundamental ecosystem processes (Stephens et al., 2021), yet due to dramatic changes in forest structure, composition, and fuel loading, large pines are now more vulnerable to fire-induced mortality. While mechanical thinning treatments implemented prior to prescribed burning can restore some structural elements of frequent fire forests by removing ingrowth of fire sensitive tree species that serve as ladder fuels to large pine crowns, unprecedented surface fuels unaffected by thinning still pose substantial risks (Stephens et al., 2009). As a result, concern for causing unintended mortality in populations of large, old pines trees and a limited understanding of ways to mitigate mortality while still achieving restoration objectives is a significant impediment to the restoration and management of these forests.

One fundamental effect of fire exclusion on fuel loading in frequent fire forests is the substantial basal accumulations of litter and duff (duff mounds) around large old pines (Agee, 1993; Hood, 2010). Duff mounds can smolder for prolonged periods when burned, subjecting underlying fine roots, mineral soil, and tree stems to lethal heating, often resulting in acute physiological stress (Ryan & Frandsen, 1991; Swezy & Agee, 1991; Varner et al., 2009). Mineral soil heating associated with prolonged duff smoldering alters soil nutrient dynamics, reduces soil aggregation affecting overall structure, and increases soil hydrophobicity (Certini, 2005; Debano, 1990, 2000). Previous studies have documented lethal temperatures to a depth of 20 cm in mineral soil (Haase & Sackett, 1998; Kreye et al., 2020), which raises concern for the higher concentration of fine roots that may be present in the upper mineral soil horizon (Dumm et al., 2008). Varner et al. (2009) linked post-fire tree stress with reduced root carbohydrates resulting from long-duration mineral soil heating. Impaired allocation of nonstructural carbohydrates can contribute to long-term declines in radial growth and resin duct defenses that reduce vigor in large old pines (Slack et al., 2021). Combined with fire-induced fine root loss and impaired resource acquisition, these subtler effects of fire can lead to heightened susceptibility to bark beetle attacks, which often results in mortality for fire-weakened pines (O'Brien et al., 2010).

Previous studies have found that duff mound physical characteristics such as bulk density and depth influence ignition, smoldering combustion, and overall duff consumption in duff mounds (Frandsen, 1987, 1997). While the structure and composition of basal fuels can be highly variable at small spatial scales (Kreye et al., 2014), larger and older trees tend to have increased fuel depth and duff (Banwell & Varner, 2014; Dimario et al., 2018; van Wagtendonk et al., 1998). Bulk density is an important component of smoldering combustion in duff mounds, while overall duff consumption is constrained by thresholds in moisture and mineral content (Garlough and Keyes, 2011). Stephens et al. (2004) found that bulk density increased with depth in the

O horizon, and speculated that species-level differences in leaf morphology and factors affecting litter decomposition may be important drivers of bulk density. In addition to differences in leaf morphology, fuel deposition rates are highly variable for Sierra Nevada conifers (van Wagtendonk & Moore, 2010). While species' deposition rates vary by tree size class, interestingly, van Wagtendonk and Moore (2010) found that very large (> 120.1 cm in diameter) sugar and Jeffrey pine have nearly equivalent foliage deposition rates. This suggests that if litter deposition rates are held constant, crown characteristics including leaf morphology, crown size, crown area, and leaf density may be important factors contributing to duff mound physical characteristics such as volume, bulk density, and depth. Further, the effect of litter decomposition rates on duff mound physical characteristics likely depends on physical and chemical leaf properties, as well as environmental factors such as microsite, soil, and topographic features at small spatial scales (Fry et al., 2018; Stohlgren, 1988).

While fine root growth and distribution patterns are highly variable across space and time for many tree species, in temperate coniferous forests approximately half of root biomass is found in the upper 30 cm of the soil horizon (Jackson et al., 1996). Fine roots and their mycorrhizal symbionts are critical uptake organs for the acquisition of soil resources, and tend to grow opportunistically towards zones with higher soil moisture and nutrients (Persson, 2000; Vogt et al., 1993, 1995). Additional factors that influence root growth and density include microsite conditions, topographic factors, site productivity, tree age, stand density, and duff depth (Hood, 2010; Persson, 2000; Wang et al., 2018). Several studies have linked tree mortality to cambium tissue death resulting from long-duration duff smoldering (Bär et al., 2019; Hood, 2021; Ryan & Frandsen, 1991; Stephens & Finney, 2002; Varner et al., 2005, 2007), while fewer studies have focused on damage to fine roots present in the duff and upper soil horizon due to fire exclusion (Dumm et al., 2008; Swezy & Agee, 1991; Varner et al., 2009). Of these studies, there is very little information on fine roots within duff mounds of very large, old sugar and Jeffrey pine in the Sierra Nevada, USA (Hood, 2010). Addressing this knowledge gap is important in the context of post-fire tree mortality due to the potential fine root damage and loss following fire, and will provide valuable information to fire and fuel managers during the planning and implementation of prescribed fire.

Objectives

The primary objective of my research is to provide foundational information on the physical characteristics and fine root abundance within duff mounds of old-growth sugar and Jeffrey pine in a fire-excluded, mixed-conifer forest located in the Sierra Nevada, California, USA. Specifically, I addressed the following questions:

1. Do duff mound physical characteristics (i.e. bulk density, depth, and total volume) differ between tree species, and tree size (diameter at breast height)?
2. Does fine root density differ between tree species, tree size (diameter at breast height), and between the O horizon and upper mineral soil horizon?
3. Are topographic attributes and tree crown metrics important drivers of duff mound physical characteristics and fine root density for either tree species?

From these questions, there are three hypotheses:

H1. I expect that duff mound bulk density, depth, and total volume will be greater for sugar pine than Jeffrey pine due to species differences in crown leaf area and width that influence foliage deposition, and needle morphology and needle surface area to volume that may affect decomposition rates. I expect tree size for both species to have a positive relationship with duff bulk density, depth, and volume.

H2. Fine root density will be greater in the upper mineral soil horizon than the O horizon for both species. I expect this outcome due to evidence in related conifers that mineral soil contains higher concentrations of fine roots compared to duff (Dumm et al., 2008). I expect that tree size will have a positive relationship with fine root density, due to larger trees having greater duff mound depth.

H3. I expect larger duff mounds and higher fine root density on north and east aspects and in lower slope and valley topographic positions due to more water availability resulting in higher productivity. As the primary inputs, I expect tree crown metrics including crown area and leaf density to be strongly related to duff mound size.

2. MATERIALS AND METHODS

2.1 Study Area

I conducted the study at Teakettle Experimental Forest (Teakettle), a 1300-hectare USDA experimental area in the Sierra National Forest, CA. Specifically, my study area is an unmanaged, roughly 200-hectare old-growth mixed-conifer portion of Teakettle where Sierra National Forest is currently planning a large-scale prescribed burn (Figure 1). Elevation at Teakettle ranges from 1880 m to 2485 m. The climate is Mediterranean, consisting of hot, dry summers and cool, wet winters with a mean annual precipitation of 125 cm falling predominantly as snow between November-May (Adams et al., 2004). Soils are most commonly granite-derived frigid Dystric Xeropsamments (Cagwin series), characterized by loamy coarse sand texture, poor water-holding capacity, and low (< 5%) clay content (North et al., 2002). Frigid Typic Xerumbrepts (Gerle series) which are distinguished by a moist, deep A horizon are also present within a portion of the study area (North et al. 2002). The mixed-conifer forest at Teakettle is composed of white fir (*Abies concolor*), red fir (*Abies magnifica*), sugar pine (*Pinus lambertiana*), Jeffrey pine (*Pinus jeffreyi)*, and incense cedar (*Calocedrus decurrens*), with patches of California black oak (*Quercus kelloggii*) and bitter cherry (*Prunus emarginata*).

Fire scar analysis of trees at Teakettle indicate that prior to Euro-American settlement the site had a fire return interval of 12-17 years, and the last widespread wildfire occurred in 1865 (North et al., 2005). Indigenous use of fire at Teakettle is uncertain due to the inability to distinguish between lightning and anthropogenic ignitions in fire scar analyses, however, early presence of Nyyhmy (Western Mono/Monache) people is evidenced by multiple cultural sites (Personal communication, Megan Krietsch, former District Archaeologist, Sierra National Forest, High Sierra Ranger District). Twentieth century fire exclusion resulted in a dramatic shift in forest composition and structure at Teakettle, leading to a decline in large pines and dramatically increased densities of shade-tolerant white fir and incense-cedar (North et al., 2007).

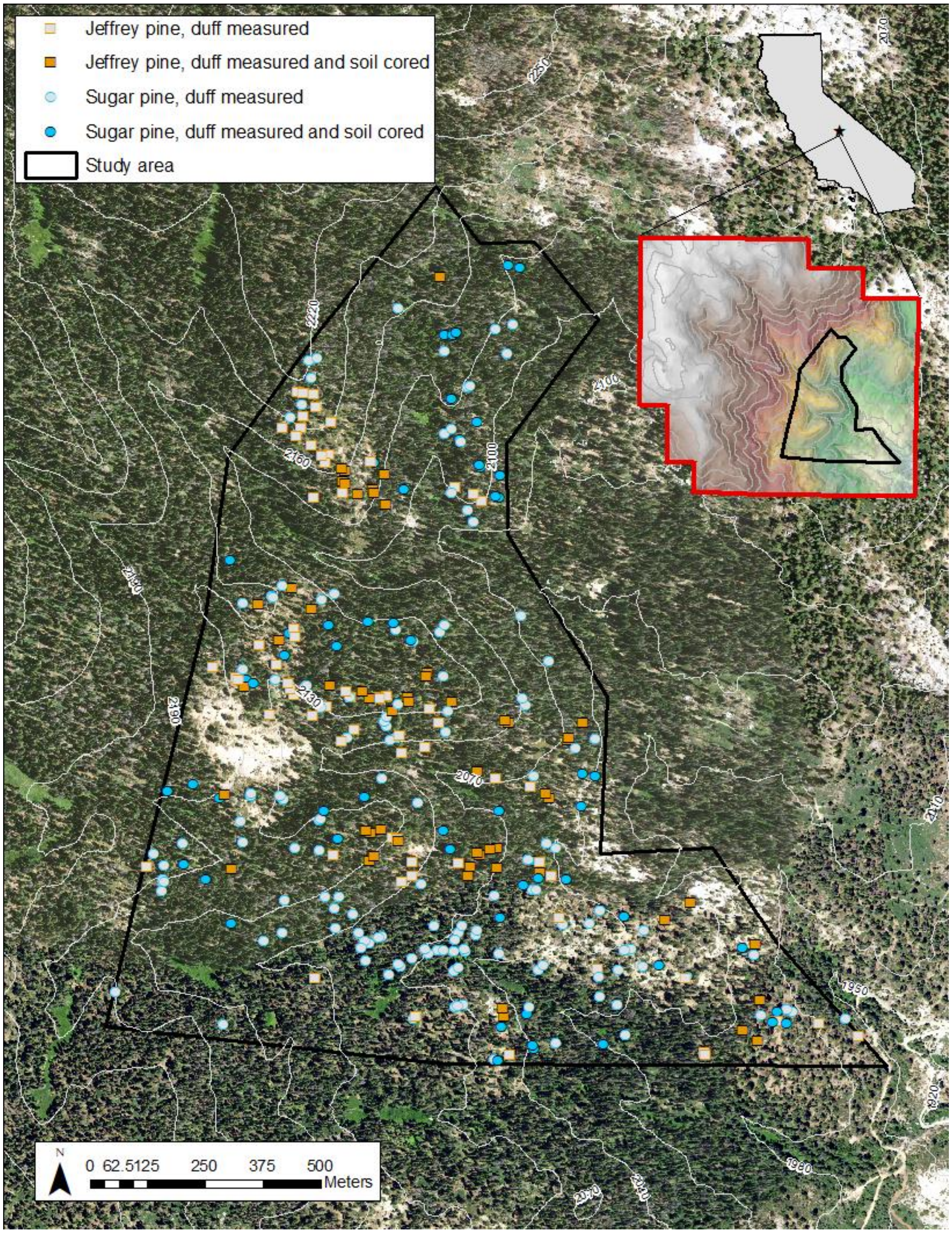

Figure 1. Study area boundary and locations of censused large sugar and Jeffrey pine in a 200-hectare unmanaged, old-growth mixed-conifer portion of Teakettle Experimental Forest, Sierra Nevada, USA. Inset map displays location of the study area within the overall administration boundary for Teakettle Experimental Forest.

2.2 Field Sampling

During the summers of 2019, 2021, and 2022, Marc Meyer (project collaborator and Southern Sierra Province Ecologist, U.S. Forest Service) conducted a census of 496 large pine trees within the unmanaged portion of mixed-conifer forests at Teakettle. He identified each tree to species, measured and recorded its diameter at breast height (DBH), visually assessed vigor following Salman and Bongberg (1942), assessed beetle activity following Meyer et al. (2016), and assessed sugar pines for blister rust infection status (presence or absence). He recorded terrain slope and aspect with a field compass and clinometer, and visually assessed topographic position (ridgetop, upper/mid/lower slope, and depression). He assigned each tree a fuel depth hazard rating of 1, 2, or 3, corresponding to low (<12 cm fuel depth), medium (12-24 cm fuel depth), and high (>24 cm fuel depth or coarse woody debris located at the base of basal fire scars), respectively. Additionally, he collected GPS coordinates for all trees. The population contained 338 sugar pine and 158 Jeffrey pine, all with a minimum DBH of 90 cm. Mean sugar pine DBH was 152.7 cm (SD = 25.58) and mean Jeffrey pine DBH was 124.7 cm (SD = 17.2).

In the summers of 2021 and 2022, I collected additional measurements on a subset of the censused large pines located within the 200-ha study area (see Figure 1). Within the subset, there were 197 sugar pine 92-214 cm DBH, and 127 Jeffrey pine 97-169 cm DBH. I tagged each tree with a numbered aluminum tag for long-term monumentation and collected high precision GPS coordinates using a Reach RS2 RTK GPS (Emlid Ltd., Budapest, Hungary). I verified tree attributes previously collected for accuracy including tree species, DBH, vigor, beetle activity assessment, blister rust infection status, terrain slope and aspect, and topographic position. Additionally, I reassessed the fuel depth hazard rating and measured tree height and height from base to live crown for each tree using a laser rangefinder.

I established four transects from the base of each tree (directly upslope, downslope, and perpendicular to the slope on either side) and collected transect azimuths with a compass (Appendix A). Special care was taken to avoid soil disturbance for trees located within long-term research plots. Along each transect, I recorded the length from the tree base to the edge of the duff mound, which I defined as where the incline of duff mound fuel accumulation became level with the general slope and surrounding fuels. Following Dimario et al. (2018), I measured litter and duff layer depths at four mound positions along each transect: adjacent to the tree bole (base), half the distance from the base to the mound edge (half), at the edge of the duff mound (edge), and 50 cm beyond the edge of the duff mound (beyond). Using a soil knife, I made an incision perpendicular to the duff mound at each location and measured litter and duff layer depths to the nearest 0.1 cm. I defined the litter layer (O_i) as the upper organic soil horizon containing recently deposited organic material (i.e. dead needles, bark, and cones). Beneath the litter layer, I defined the duff layer (O_e and O_a horizons combined) by the presence of partially decomposed vegetation particles, fungal hyphae, or dark colored humic material (Figure 2).

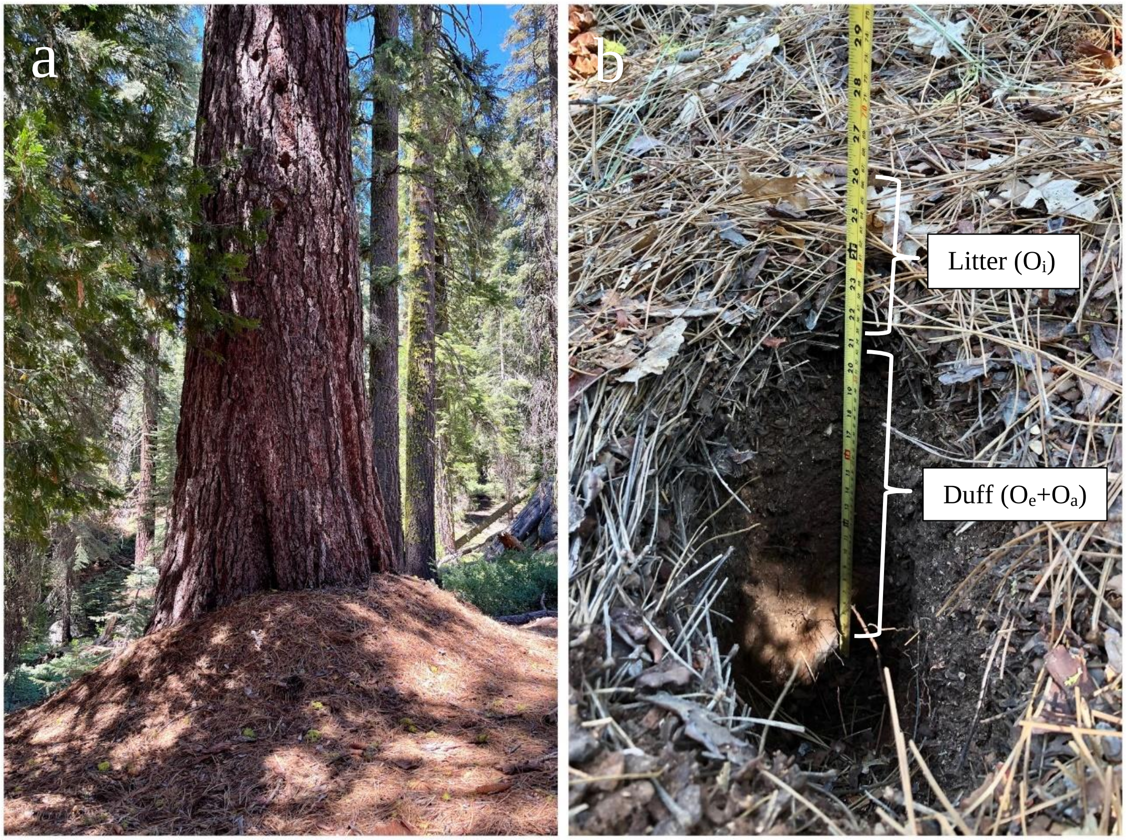

Figure 2. Duff mound of a large sugar pine in a fire-excluded mixed-conifer forest (a). Measurement of O horizon litter and duff depths following extraction of core sample for a large Jeffrey pine at Teakettle Experimental Forest, Sierra Nevada, USA (b).

I selected a random sample of 107 of the 324 large pines within the study area to estimate bulk density and fine root density within the O horizon and top 10 cm of mineral soil (n=55 sugar pine and 52 Jeffrey pine). At each tree, I collected O horizon and mineral soil cores at the midpoint (half the distance between the bole and edge of the mound) of each transect. To avoid contaminating samples with roots from other vegetation, I did not sample transects with a high abundance of shrubs or saplings. I excluded coring sites that occurred on rocky outcroppings and very rocky shallow soil due to lack of duff and mineral soil. I collected one core of the O horizon and one core of the top 10 cm of the mineral soil layer at each location using a 7 cm diameter hole saw attached to a cordless drill. I recorded the depth of the O horizon and placed all samples in labeled paper bags to air dry before processing them in the lab.

2.2 Lab Methods

Soil and Duff Cores

I employed a time (up to 25 minutes per sample) and effort-based system to process fine roots. I spread each O horizon sample over a white surface and used an illuminated magnifier and forceps to hand-separate roots from adhering organic matter, fungal hyphae, and mineral soil. Subsequently, I wet-sieved the samples using a 425-micron opening to remove any additional organic matter and mineral soil particles.

To separate fine roots from mineral soil samples, I first dry-sieved the entire sample using a 425-micron opening, which caused less dense organic matter to rise to the surface. I removed and set aside all organic matter and repeated the process once more to capture any additional fine roots. Next, I spread each sample over a white surface and used an illuminated magnifier and forceps to hand-separate fine roots from adhering mineral soil and organic matter. I then transferred the sample to a clean 425-micron sieve and rinsed it over a utility sink with faucet sprayer to remove additional mineral soil particles. Finally, I transferred each sample to a bucket with a spout and used a combination of water pressure and stirring to rinse and capture fine roots in a 425-micron sieve positioned below the bucket spout (Byrne, 2021).

I placed each clean root sample into a labeled aluminum tin and oven-dried all samples for 72 hours at 60 °C. I categorized roots from each sample into three diameter classes (0-2 mm, 2-4 mm, and >4 mm) using calipers and weighed them to the nearest 0.001 g to determine mass. Fine root mass included both living and dead fine roots due to the inability to refrigerate samples prior to processing.

I excluded roots greater than 2 mm from analysis due to their high variability at small spatial scales and defined fine roots as less than 2 mm in diameter. I report fine roots as dry mass per unit soil volume (mg cm^{-3}) due to the variation in depth among O horizon samples. Overall, I processed 363 O horizon samples collected from 107 individual trees, and 325 mineral soil core samples collected from 96 individual trees. Due to damage to a portion of the mineral soil samples, I was only able to process 232 of the samples for roots. Additionally, samples were removed from analysis if only one soil or duff core was obtained for an individual tree.

To quantify bulk density, I oven-dried mineral soil and O horizon samples for 72 hours at 60 °C and weighed them to the nearest 0.01 g. I calculated bulk density (g m^{-3}) following Maynard and Curran (2008), by dividing the oven dry mass of each sample by the volume of the soil sampled.

Duff Mound Variables

To quantify duff mound volume, I first calculated the volume of each mound position (base, half, and edge) by transect. I assumed that the length of each position was one-third the total duff mound length, and determined total mound volume from the sum of volumes by position and taking the average, as shown in the following formula:

$$\mathrm{V} = \left(\frac{\sum_{i\epsilon s} \pi \mathrm{h}(\mathrm{r}_2^2 - \mathrm{r}_1^2)}{n_b}\right)_{\mathrm{BASE}} + \left(\frac{\sum_{i\epsilon s} \pi \mathrm{h}(\mathrm{r}_3^2 - \mathrm{r}_2^2)}{n_h}\right)_{\mathrm{HALF}} + \left(\frac{\sum_{i\epsilon s} \pi \mathrm{h}(\mathrm{r}_4^2 - \mathrm{r}_3^2)}{n_e}\right)_{\mathrm{EDGE}}$$

where V is total mound volume, r_1 is the tree stem radius, r_2 is the tree stem radius plus one-third total mound length, r_3 is the tree stem radius plus two-thirds total mound length, r_4 is the tree stem radius plus total mound length, h is the combined litter and duff depth, n_b is the number of base observations, n_h is the number of half observations, and n_e is the number of edge observations (formula adapted from Dimario et al. 2018). This method allowed for missing observations on some transects due to the inability to collect measurements. I calculated mound area using the following formula:

$$A = \pi ab$$

where A is total mound area in square centimeters, a is the greater length between uphill and downhill transects, and b is the greater length between slope 1 and slope 2 transects.

Topographic Variables

I used a digital terrain model (DTM) derived from airborne discrete return light detection and ranging (lidar) data collected at Teakettle to generate gridded slope, aspect, potential solar radiation, and topographic wetness index (TWI). Lidar data were collected in October 2010 by Watershed Sciences Inc. (Portland, Oregon, USA) using a Leica ALS50 Phase II sensor mounted on a Cessna Caravan 208B flown at 1100-1500 m above ground level. Lidar data averaged 8.8 points/m^2 and 0.89 points/m^2 for total pulse and ground pulse densities, respectively. From the DTM, I calculated elevation, slope, cosine transformed aspect, and topographic position index (TPI) at 5 m resolution using the raster package in R (Hijmans, 2023). TPI is an index representing position on the landscape compared to surrounding features, and is calculated by comparing the elevation of a cell to its neighboring cells. To detect effects of topography on ecological processes at multiple spatial scales, I calculated TPI at three neighborhood sizes: 10 m, 30 m, and 100 m. Potential solar radiation, calculated using the Area Solar Radiation Model in ArcMap 10.7.1 (Fu & Rich, 1999), is an insolation model that employs topographic inputs to interpolate soil temperature across complex and spatially heterogenous terrain. I estimated soil moisture using TWI, a physically-based, variable contributing model of basin hydrology (Beven & Kirkby, 1979) using the following formula:

$$\text{Topographic Wetness Index } = \ln \frac{\alpha}{\tan\ \beta + \mathrm{c}}$$

where b is the upslope contributing basin area, β is the slope at that cell (Moore et al., 1991), and c is a small constant (= 0.01) to avoid division by zero in flat terrain cells (Fricker et al., 2019). I cropped all topographic variables to the study area and extracted average slope, aspect, elevation, TPI, PSR, and TWI values for each large pine using high precision GPS coordinates gathered in the field.

Crown Variables

I generated crown metrics by using a lidar-derived canopy height model (CHM) to detect and segment individual tree crowns. To reflect recent drought mortality and temporally align the lidar with field-collected data, I used a lidar acquisition collected in 2019 by the National Ecological Observatory Network (NEON). I obtained lidar point cloud data (DP1.30003.001) as an .las file through the NEON data portal (National Ecological Observatory Network, 2023). The NEON Airborne Observation Platform data was collected using an Optech Gemini sensor mounted on a DeHavilland DHC-6 Twin Otter aircraft flown at 1000-2000 m above ground level. Average point density was approximately 3.82 points/m^2. Using the lidR package in R (Roussel et al., 2020; Roussel & Auty, 2023), I clipped the point cloud to the study area, removed outlier points, and normalized the point cloud to remove terrain influence on aboveground vegetation measurements. I generated the CHM at 0.5 m resolution using the triangulation method and a "pit-free" algorithm to improve accuracy of individual tree detection (Khosravipour et al., 2014). From the CHM, I followed individual tree detection (ITD) and individual tree segmentation (ITS) methods from Dalponte and Coomes (2016) and the watershed segmentation method from Chen et al. (2006). Individual tree detection (ITD) is the process of spatially locating individual trees, while ITS delineates the tree in the point cloud to extract specific values for the crown and other structural characteristics. For each ITS method, I visually compared the crown polygons to the CHM around each tree, and found the watershed segmentation method to be most effective at correctly delineating crowns while balancing errors of over and under segmentation. Crown metrics extracted for each study tree included 95th percentile of height, mean height, percent cover of first returns above 2 m, crown area, and leaf area density. Leaf area density is the total leaf area per unit of volume and for each study tree I extracted its sum, mean, and coefficient of variation (Bouvier et al., 2015).

2.3 Statistical Analysis

I conducted all statistical analyses in the R statistical package (R Core Team, 2023). I used two different data sets for the analysis. One set contained the census of large pines within the study area (n = 324), and is associated with response variables total duff mound volume and maximum depth. The other contained a sample of trees from the census from which I collected additional duff and soil core samples for (n = 107), and is associated with upper mineral soil and O horizon bulk density and fine root density. Due to non-normal residuals in QQ plots, I natural log transformed the following variables: duff mound total volume, maximum depth, O horizon bulk density, O horizon fine root density, and upper mineral soil fine root density in all models to meet normality assumptions.

To assess whether there were species-level differences in response variables, I performed Mann-Whitney-Wilcoxon tests for response variables with non-normal distributions, and a two-sample t-test for soil bulk density which had a normal distribution. To evaluate the effect of tree species and tree size (hereafter, DBH) on duff mound physical characteristics (bulk density, depth, and total volume) and fine root density within the O horizon and upper mineral soil horizon, I fit linear models where explanatory variables included species and DBH. Additionally, I examined the relationship between duff mound depth and bulk density using a linear model with species as the explanatory variable. I ran each model as additive and with an interaction between species and the explanatory variable to check for significance. When I found the interaction term to not be significant, I removed it from the final model. For each final model, I conducted post-hoc pairwise analyses using the emmeans package to assess overall differences in response between sugar and Jeffrey pine (Length, 2023).

To determine differences in fine root density between the upper mineral soil and O horizons, I performed a non-parametric Kruskal-Wallis test with combined upper mineral and O horizon root data as the response variable, and horizon (upper mineral or O) as the independent factor. I fit linear models to determine if fine root density in either the O horizon or upper mineral horizon were associated with duff mound depth, volume, or bulk density, following the same approach as above by checking for species interactions in the models, and running final models with only additive terms if interactions terms were not significant in preliminary models.

To understand the relative importance of topographic variables and tree crown metrics in explaining duff mound physical characteristics and fine root density, I fit multiple linear regression models. Topographic variables considered included slope, aspect, elevation, TPI at three neighborhood sizes (10 m, 30 m, and 100 m), potential solar radiation, and TWI. Crown variables considered included sum of leaf area density (LAD) and crown area. I verified linearity and constant variance by examining residuals vs. fitted values plots. Additionally, I used variance inflation factors to check for collinearity between explanatory variables with a tolerance level of less than 2. I used Akaike Information Criteria (AIC) to choose the best explanatory and least complex model for each response variable. I chose the most informative model for each response variable based on having the lowest AIC score. When $\Delta AIC \leq 2$ between competing models, I chose the model with fewer predictor variables and greater ecological interpretability.

3. RESULTS

3.1 Duff Mound Physical Characteristics

Over 50% of the censused large pines within the study area had a fuel depth hazard rating of moderate, indicating fuel depths between 12-24 cm (Figure 3). Less than 10% of trees in the census had a fuel depth hazard rating of high (> 24 cm or coarse woody debris at the base of basal fire scars), and over one-third of trees fell into the low category (0-12 cm). Relative distribution by hazard rating class was similar for the two species. Additionally, all three hazard ratings were represented across the range of DBH values for both species (Figure 3).

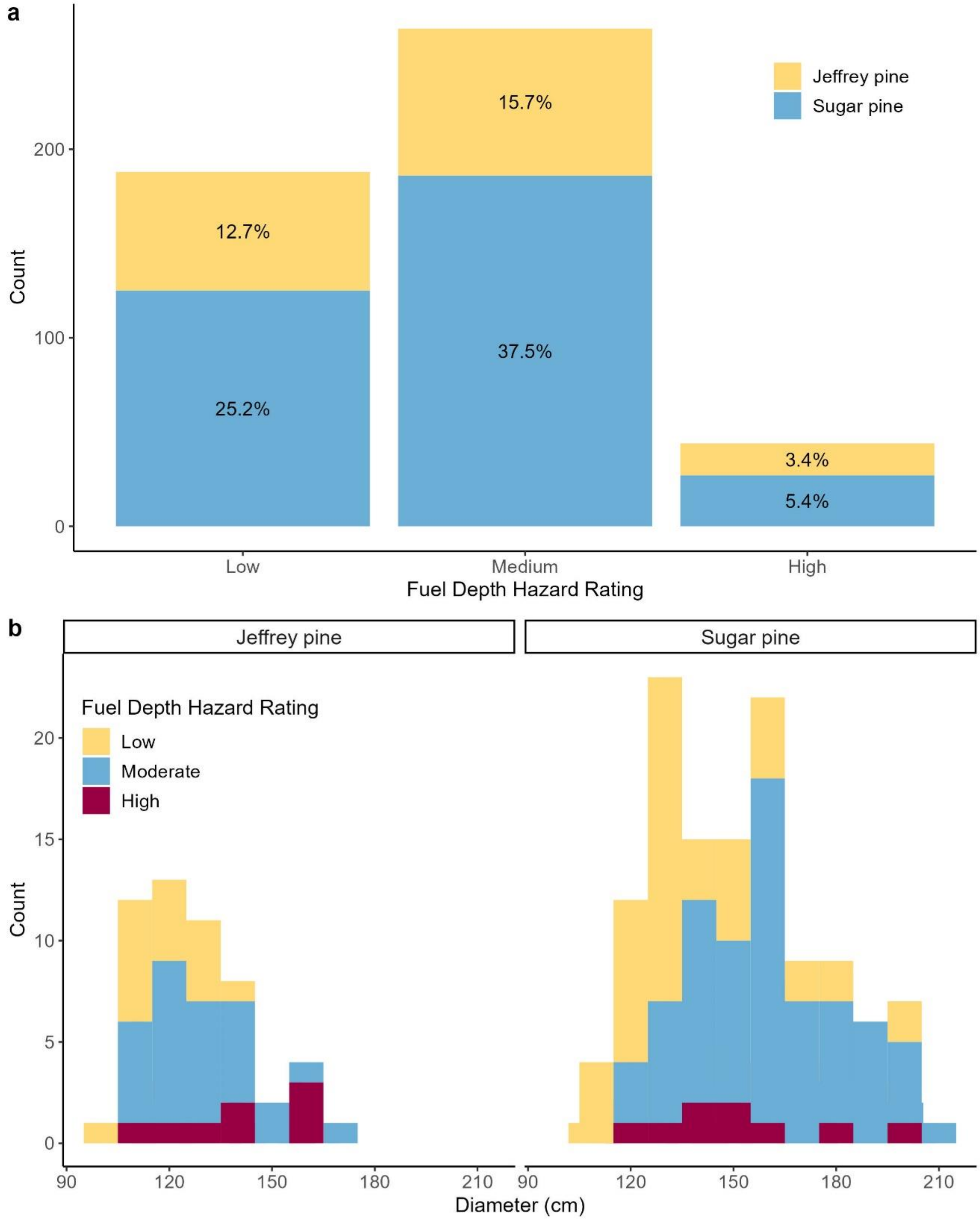

Figure 3. Total counts of large pines by fuel depth hazard rating category (a) and fuel depth hazard rating distributions by tree diameter for sugar and Jeffrey pine (b).

Duff mound volume was marginally greater for sugar pine (2.55 ± 0.14 m^3) than Jeffrey pine (2.27 ± 0.16 m^3; p = 0.0839). In contrast, average duff mound depth was marginally greater for Jeffrey pine (31.35 ± 1.86 cm) than sugar pine (29.70 ± 1.44 cm; p = 0.0867). There were no species differences for duff mound bulk density, mineral soil bulk density, O horizon root density, or mineral soil root density (Table 1).

Table 1. Mean bulk density (g cm^{-3}) and fine root density (mg cm^{-3}) and 95% confidence intervals (95% C.I.) for O horizon and upper mineral soil horizon between sugar and Jeffrey pine.

		Bulk Density g cm^{-3}	(95% C.I.)	Fine root mass mg cm^{-3}	(95% C.I.)
	n	Organic horizon	Mineral soil	Organic horizon	Mineral soil
Sugar pine	55	0.133 (0.126, 0.140)	0.680 (0.647, 0.712)	0.302 (0.241, 0.362)	1.153 (0.951, 1.355)
Jeffrey pine	52	0.128 (0.123, 0.135)	0.689 (0.661, 0.717)	0.288 (0.214, 0.363)	1.239 (1.015, 1.463)

Duff mound depth and volume both had strong, positive relationships with DBH , and there were no interaction effects between DBH and species in either model (Figure 4). Duff mound depth increased with DBH ($t = 8.070$, $p < 0.0001$), and average depth was greater for Jeffrey pine than sugar pine ($t = 5.145$, $p < 0.0001$). Duff mound volume also increased with DBH ($t = 14.660$, $p < 0.0001$), and was greater for Jeffrey pine ($t = 4.791$, $p < 0.0001$). Overall, more variance was explained for duff mound volume ($r^2 = 0.40$) compared to depth ($r^2 = 0.17$).

Duff mound bulk density had a negative relationship with DBH ($t = -2.103$, $p = 0.04$), and was higher for sugar pine than Jeffrey pine ($t = 1.999$, $p = 0.05$), although there were no interactions between DBH and species. The overall model was only marginally significant with very little variance explained ($p = 0.08$, $r^2 = 0.03$). Duff mound bulk density decreased with depth ($t = -3.281$, $p = 0.002$), but there were no differences in duff mound bulk density between species ($t = 0.218$, $p = 0.83$), nor interactions between species and depth. Overall, variance explained by the model was low ($p = 0.005$, $r^2 = 0.1$; Figure 5).

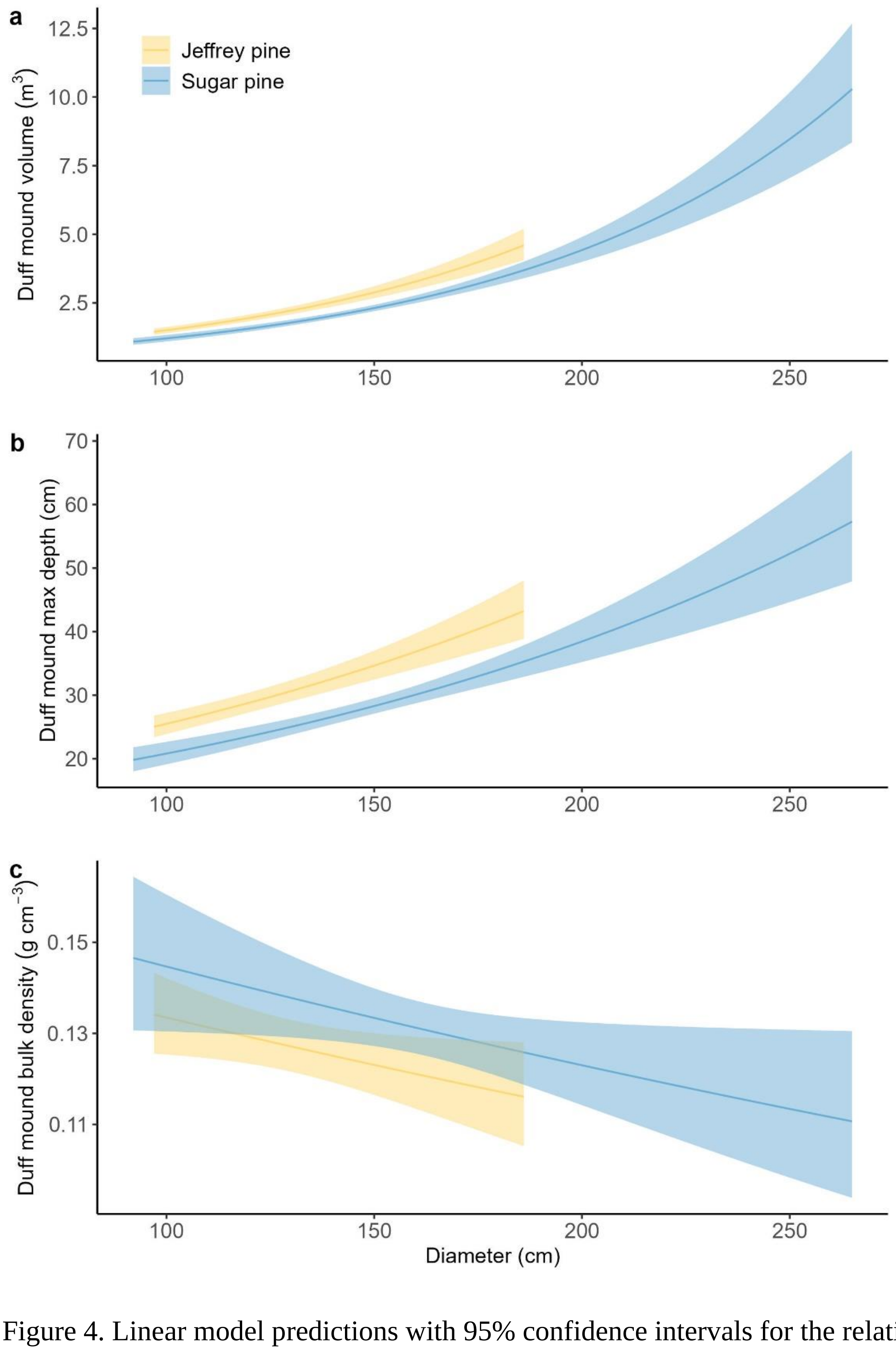

Figure 4. Linear model predictions with 95% confidence intervals for the relationship between diameter and duff mound volume (a), duff mound maximum depth (b), and duff mound bulk density (c) for sugar and Jeffrey pine.

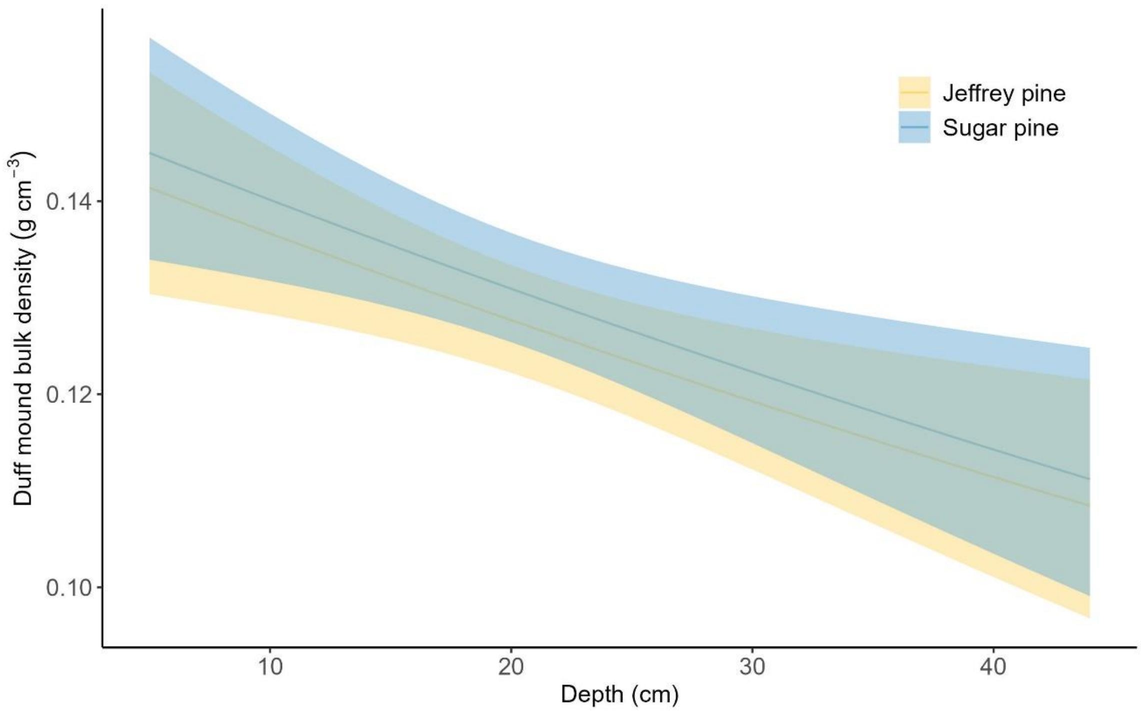

Figure 5. Linear model predictions with 95% confidence intervals for the relationship between duff mound bulk density and depth for sugar and Jeffrey pine.

3.2 Relationships between Species, DBH, and Fine Root Density

Fine root density was lower in the O horizon (Mean 0.386, 0.322 – 0.449 mg cm^{-3} 95% CI) than the upper mineral soil horizon (Mean 1.560, 1.367 – 1.753 mg cm^{-3} 95% CI; Kruskal-Wallis test statistic value, $p < 0.0001$), but there were no differences between species (Kruskal-Wallis test statistic value, $p = 0.6977$; Figure 6).

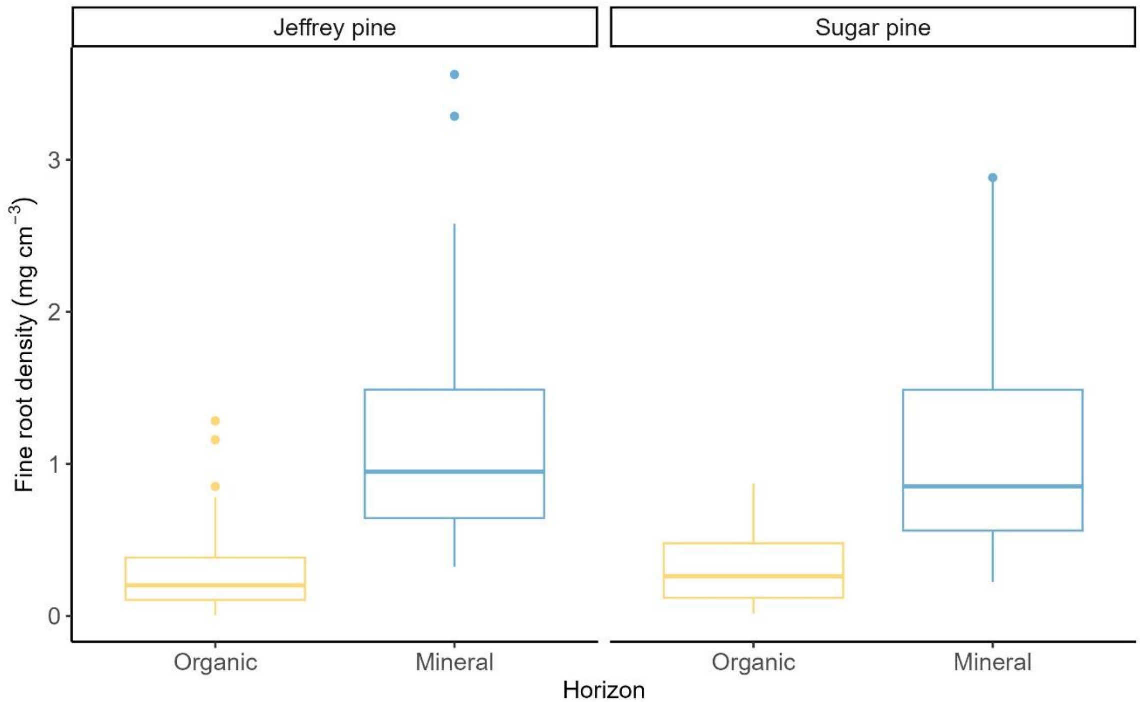

Figure 6. Mean fine root density in the O horizon and upper mineral soil horizon for sugar and Jeffrey pine.

There was a marginal weak positive relationship between O horizon fine root density and DBH ($r^2 = 0.038$, $p = 0.071$), but no differences between species (Figure 7). Mineral soil fine root density declined with increasing DBH for sugar pine ($t = 2\text{-}2.080$, $p = 0.0414$), but did not vary with tree size for Jeffrey pine ($t = 1.110$, $p = 0.2709$).

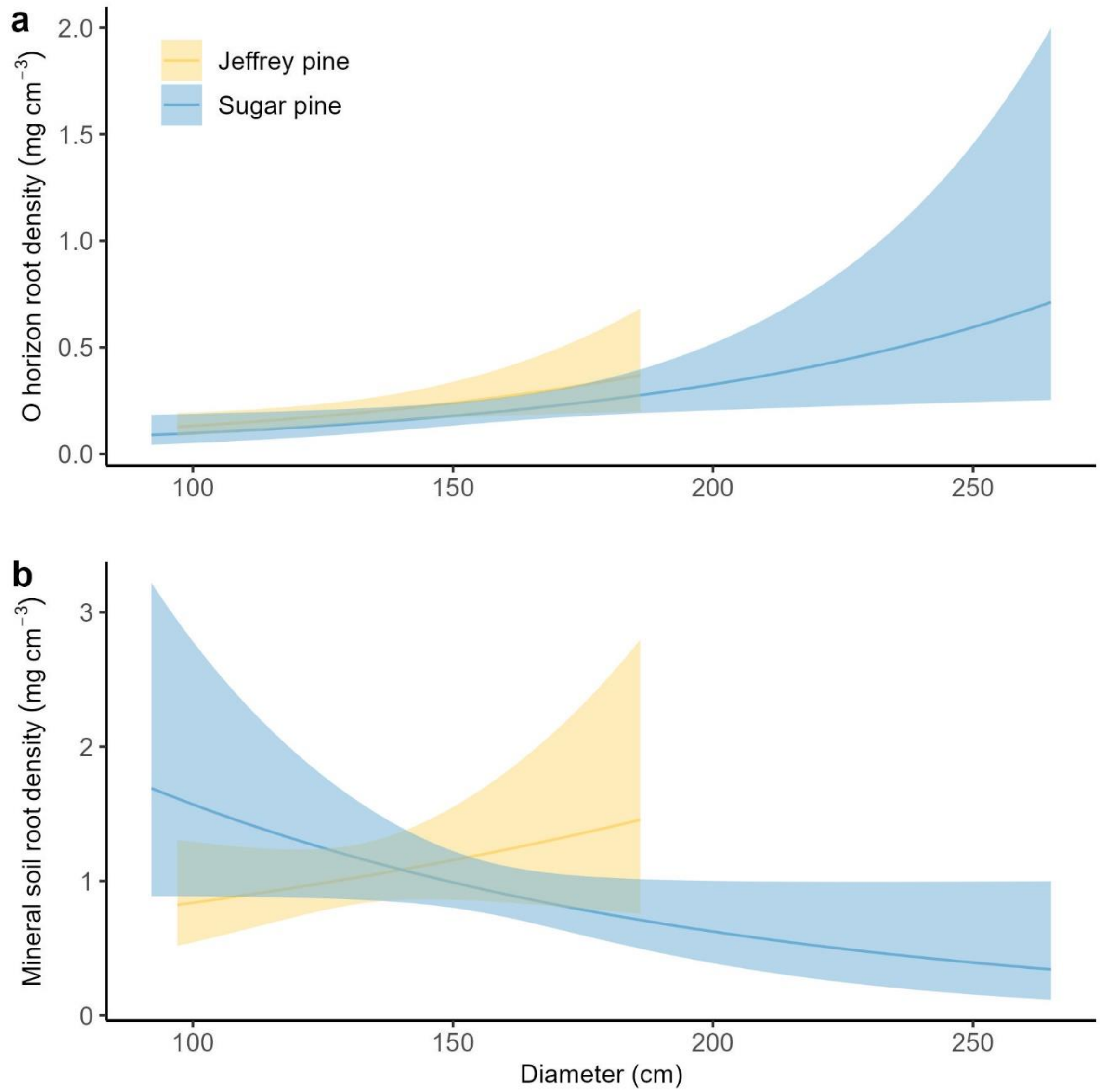

Figure 7. Linear model predictions with 95% confidence intervals for the relationship between O horizon root density (a) and upper mineral soil root density and diameter for sugar and Jeffrey pine (b).

O horizon fine root density increased with greater duff mound volume ($r^2 = 0.153$, $p < 0.0001$) and maximum duff mound depth ($r^2 = 0.247$, $p < 0.0001$), while O horizon fine root density did not vary by species, nor interactions of species with duff mound volume or maximum depth. (Figure 8).

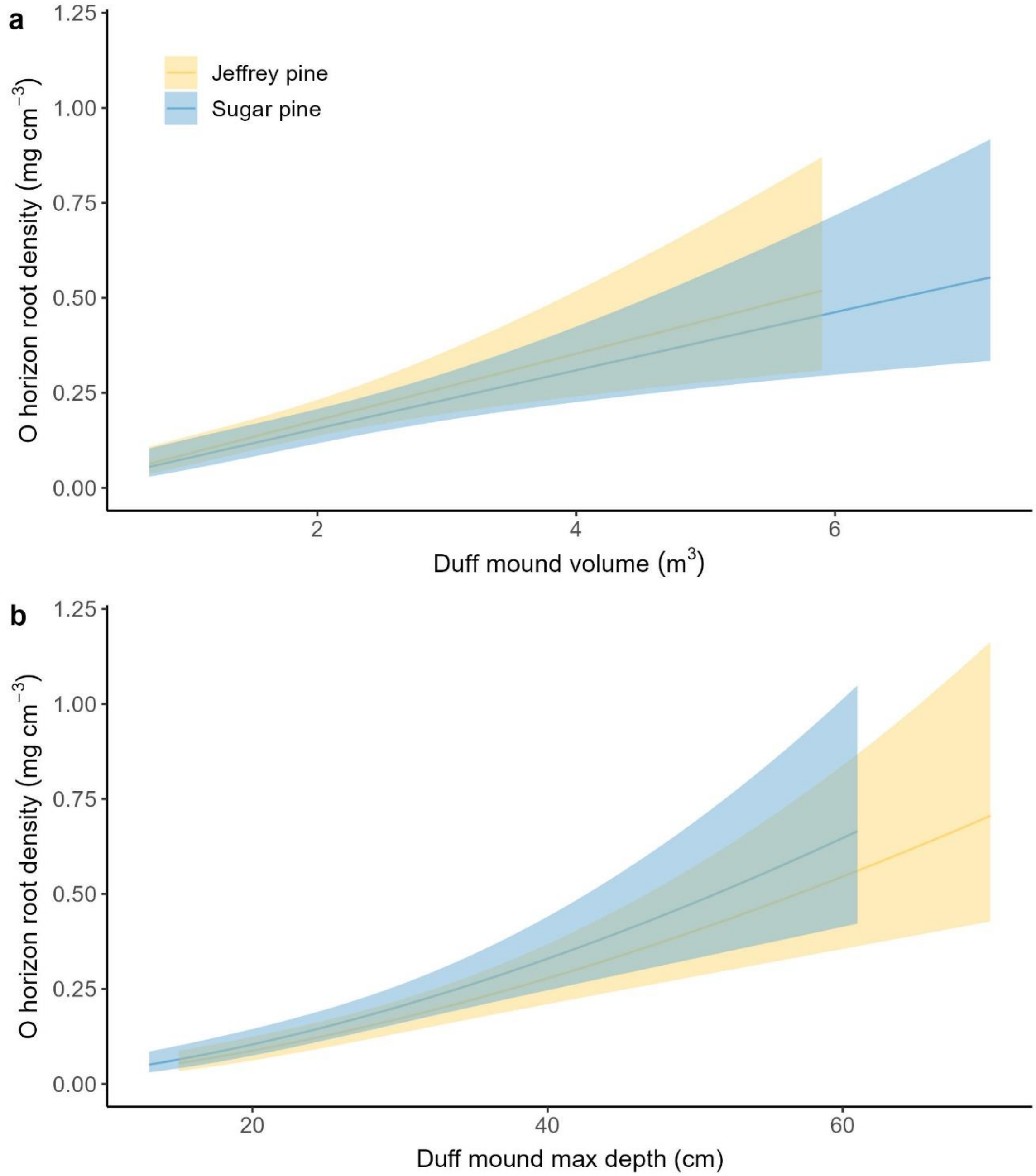

Figure 8. Linear model predictions with 95% confidence intervals for the relationship between duff mound volume (a) and duff mound maximum depth (b) and O horizon fine root density for sugar and Jeffrey pine.

3.3 Topographic and Crown Drivers of Duff Mound Size and Fine Root Density

The best explanatory topographic and tree crown predictor variables for total duff mound volume were LAD, crown area, slope, and topographic position index at a neighborhood size of 100 m (TPI 100; Figure 9). Crown area was the strongest predictor and there was a positive relationship between crown area and duff mound volume ($t = 4.307$, $p < 0.0001$). Sum of leaf area density represents the amount of leaf material in the canopy, and tree crowns with higher LAD had higher duff mound volume ($t = 3.086$, $p = 0.002$). There was a strong negative relationship between slope and duff mound volume ($t = -3.697$, $p < 0.0001$). Moreover, trees in lower topographic positions such as valleys and depressions were associated with higher duff mound volume versus trees on upper slopes and ridgetops ($t = -2.120$, $p < 0.0348$). The overall r^2 was 0.146 for the top model explaining duff mound volume.

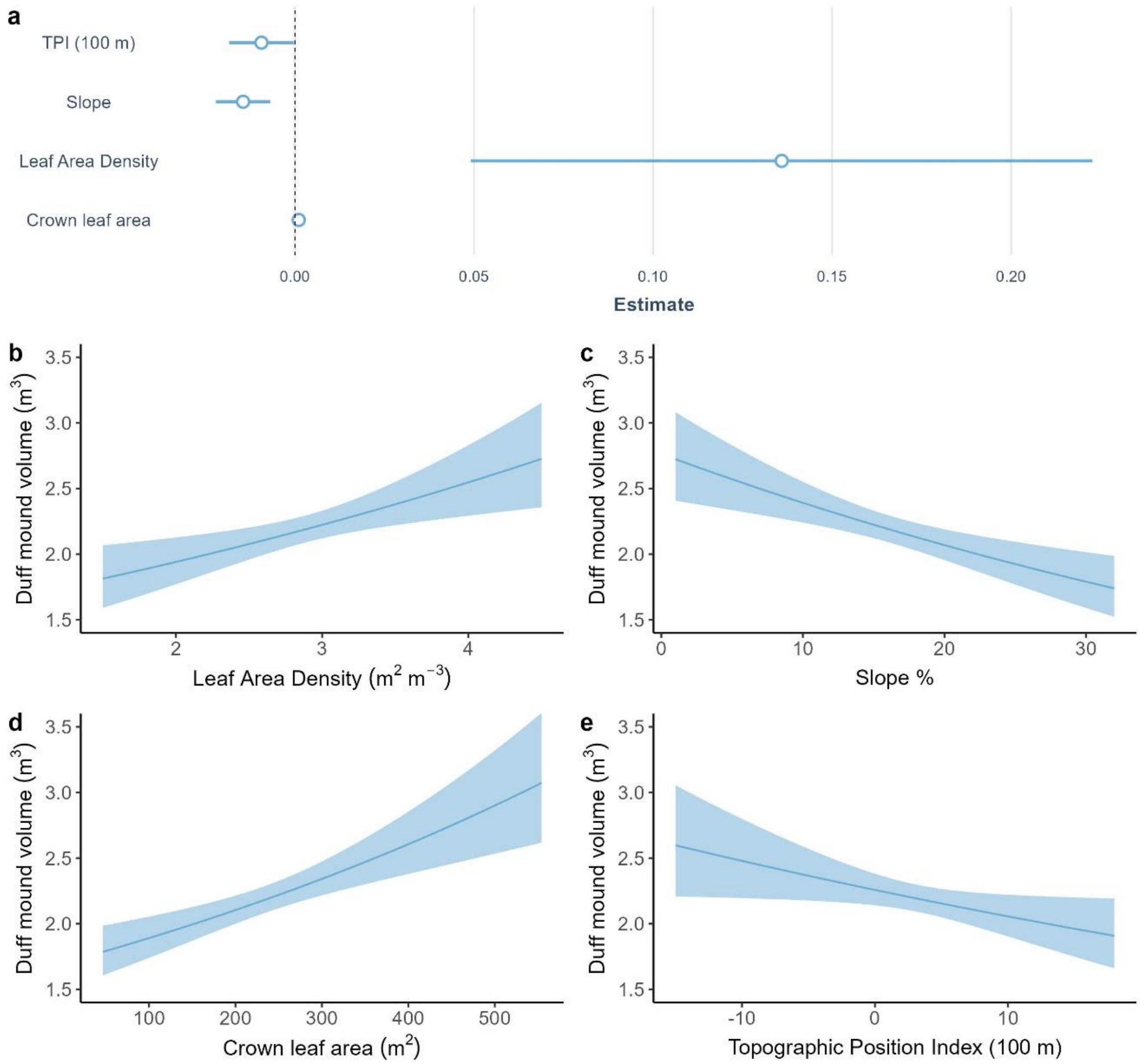

Figure 9. Scaled coefficients for the top linear model explaining duff mound volume (a). Linear model predictions with 95% confidence intervals for duff mound volume response by leaf area density (b), slope (c), crown leaf area (d), and topographic position index (e).

The most important predictors for maximum duff mound depth were slope, TPI 100, and LAD in descending order of importance (Figure 10). Duff mound depth was lower for trees on steep slopes ($t = -3.991$, $p < 0.0001$) and lower topographic positions ($t = -2.700$, $p = 0.0073$). LAD had a positive relationship with depth, yet confidence intervals were wide ($t = 2.393$, $p = 0.0173$). Furthermore, overall variance explained by the model was very low ($r^2 = 0.068$).

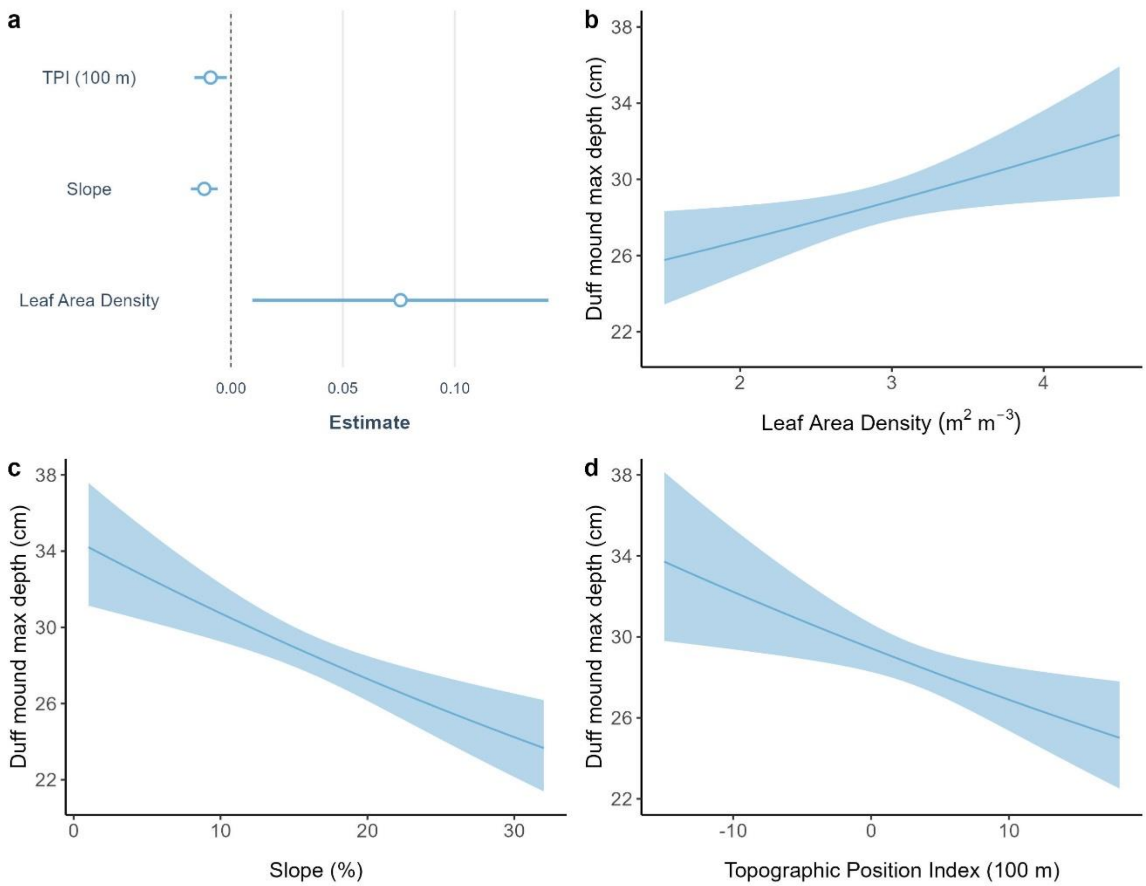

Figure 10. Scaled coefficients for top linear model explaining duff mound maximum depth (a). Linear model predictions with 95% confidence intervals for duff mound maximum depth response by leaf area density (b), slope (c), and topographic position index (d).

The strongest predictors of fine root density were LAD in the O horizon and TWI in the upper mineral horizon (Figure 11). Fine root density in the O horizon increased moderately with increasing LAD ($t = 2.766$, $p = 0.00673$). Mineral soil fine root density was greater in areas with higher soil moisture ($t = -2.237$, $p = 0.0285$), although the overall r^2 value of the model was only 0.054. Higher O horizon fine root density was also associated with higher soil moisture ($t = -2.875$, $p = 0.0049$) as well as lower topographic positions and depressions ($t = -2.914$, $p = 0.00439$). TPI at the 30 m neighborhood size indicates that topographic variability is important at relatively small spatial scales. The overall r^2 value was 0.127 for the model explaining O horizon fine root density.

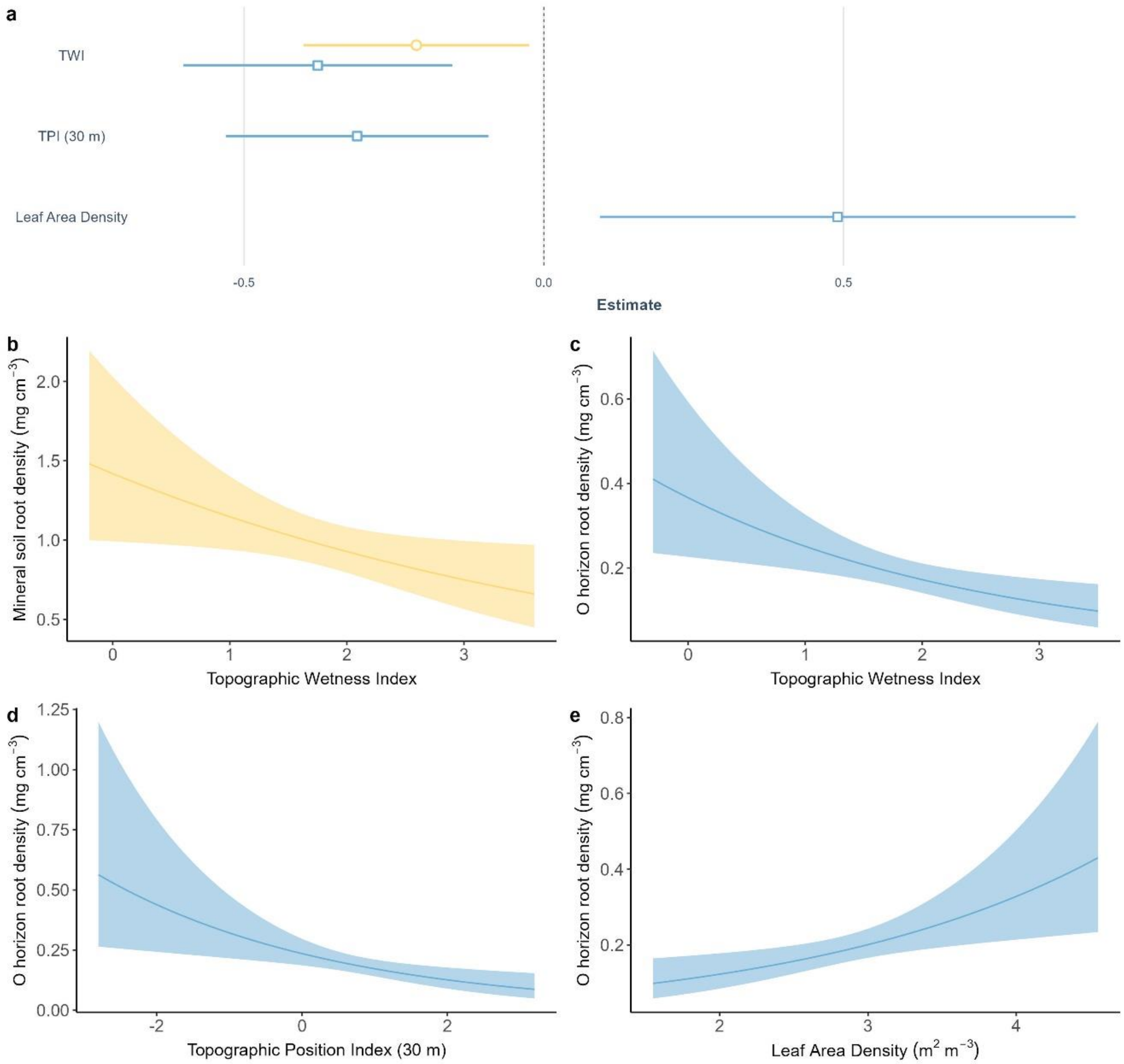

Figure 11. Scaled coefficients for the top linear model explaining O horizon and upper mineral soil fine root density (a). Linear model predictions with 95% confidence intervals of fine root responses by topographic wetness index (b), and O horizon fine root responses by topographic position index (c), and leaf area density (d).

The only important topographic predictor of mineral soil bulk density was TPI 10, although the negative relationship was only marginally significant ($t = -1.733$, $p =$

0.0866) and variance explained was extremely low ($r^2 = 0.022$). This indicates that topographic features at very small spatial scales are weakly explanatory of mineral soil bulk density. Overall, there were no significant topographic or crown predictor variables for O horizon bulk density.

4. DISCUSSION

Over a century of fire exclusion in old-growth mixed-conifer forests has resulted in deep duff mounds around large, old pines, which pose significant risks when fire is reintroduced to these ecosystems. Overall, I found that greater than 60% of the large pines had a fuel depth hazard rating of moderate or higher. Duff mound depth and volume increased with greater tree DBH, but there were not interaction effects between species and DBH, indicating relationships between duff mound size and tree size did not differ between sugar and Jeffrey pine. Lidar-derived topographic and crown metrics were strong predictors of duff mound depth and volume, highlighting their potential use in locating large pines with substantial duff mounds across large landscapes. I found higher concentrations of fine roots in the top 10 cm of mineral soil compared to the O horizon, demonstrating possible differences in moisture and nutrient availability between these horizons. Overall, my results illustrate the roles of tree size, topography, microclimate, and tree crown attributes in driving duff mound physical characteristics and fine root density for large old pines in fire excluded mixed-conifer forests in the Sierra Nevada.

4.1 Relationship between DBH and Duff Mound Physical Characteristics

I found that duff mound depth and volume inconsistently increased with greater DBH (Figure 4). This finding is supported by similar studies that explored the relationship between duff mound depth and DBH in sugar and Jeffrey pine (Banwell & Varner, 2014; Dimario et al., 2018). Contrary to my first hypothesis, I found that bulk density decreased with increasing DBH. This was somewhat unexpected because the proportion of duff to total combined duff and litter in duff mounds of large pines in my study increases with DBH. Previous studies found that the fermentation and humus layers, collectively duff, have dramatically higher bulk densities than the litter layer (Banwell & Varner, 2014; Dimario et al., 2018; Stephens et al., 2004), which I inferred would cause overall bulk density to increase with DBH. However, the mean DBH for Jeffrey pine sampled by Banwell and Varner (2014) was nearly half the size in my study (68.8 cm compared to 124.7 cm). Likewise, Dimario et al. (2018) sampled much smaller sugar pine than my study (50 – 150 cm DBH compared to a mean of 152.7 cm). This suggests an unclear relationship between duff mound fuel composition, decomposition, and associated bulk densities as pines get older and larger.

Interestingly, while Stephens et al. (2004) found that bulk density increased with strata depth, they also found that total depth had a strong negative relationship with bulk density for old-growth ponderosa pine in the southern Sierra. This substantiates my results that also found bulk density to decrease with total duff mound depth. Furthermore, van Wagdondonk (1998) found that bulk density decreased in duff mounds of sugar pines in the lowest stratum of duff. Thus, I speculate that as DBH increases for large old pines, overall duff mound bulk density decreases due to a higher proportion of less dense “lower duff” in the humus layer that is in the final stages of decomposition.

Mean bulk density of combined litter and duff found in this study (Mean 0.131 ± 0.002 g cm^{-3} SE; Table 1) was similar to values for sugar and Jeffrey pine found in van Wagtendonk et al. (1998), but higher than those found in other studies (e.g. Banwell &

Varner, 2014; Dimario et al., 2018). Some possible explanations for the discrepancy among studies include differences in stand age and composition, tree size, site differences affecting deposition and decomposition rates, and different sampling collection techniques. Furthermore, it may not be appropriate to compare bulk density values between species of different size and age classes. Duff mounds of old trees in fire-excluded forests are compositionally different than those of younger trees due to higher proportions of duff and potentially larger quantities of bark and cone fragments that may affect density.

My study found average duff mound volume to be marginally higher for sugar pine compared to Jeffrey pine, while duff mound depth was marginally higher for Jeffrey pine. One possible explanation is differences in crown area, LAD, and needle morphology between these two species. In my study, mean crown area was lower in Jeffrey pine than sugar pine (187.26 ± 5.67 SE m^2 compared to 281.22 ± 5.86 SE m^2), and LAD was also lower in Jeffrey pine (2.63 ± 0.04 m^2m^{-3} compared to 3.06 ± 0.03 m^2m^{-3}). The smaller crown of Jeffrey pine may have contributed to greater mean depths by concentrating litter deposition in a smaller area. Moreover, although Jeffrey pine had lower overall LAD, its longer needles may create more porous litter resulting in relatively comparable duff mound volume to sugar pine. Additionally, it is worth noting that these two species have similar litter deposition rates (van Wagtendonk & Moore, 2010), which may also be a contributing factor.

There were no significant differences between sugar and Jeffrey pine duff mound bulk density. Fuel bed bulk density values reported by van Wagtendonk et al. (1998)

were similar between sugar and Jeffrey pine. Banwell and Varner (2014) also did not find differences in bulk density between Jeffrey pine and white fir in their study, but attributed the lack of species differences to mixed stand composition in their study. For example, they observed substantial contributions from nearby Jeffrey pine in the white fir litter (Banwell & Varner 2014). Thus, contrasts between species, if any, would likely be clearer by sampling pure stands where inputs from other tree species are unlikely, as demonstrated by previous studies (Stephens et al., 2004; van Wagtendonk et al., 1998).

4.2 Relationships between DBH and Fine Root Density within the O Horizon and Upper Mineral Soil Horizon

O horizon fine root density was weakly associated with DBH, however had a strong positive relationship with duff mound depth. In general, thicker O horizons have higher root densities, and across forested ecosystems, overall rooting depths decrease as O horizon depths increase (Schenk & Jackson, 2002). Interestingly, thicker duff is known to burn under higher moisture levels once smoldering combustion is achieved by trapping heat and thus limiting convective heat loss at the surface (Miyanishi & Johnson, 2002). For deep duff mounds, the combination of higher fine root density with a greater capacity to smolder under higher moisture conditions suggests these roots are more vulnerable to consumption by fire.

There were no differences in fine root density between sugar and Jeffrey pine, despite potential differences between these species in overall rooting architecture. The lack of species differences warrants more investigation, yet there are no studies I am aware of that have examined fine root dynamics for sugar and Jeffrey pine, and only a few for western dry forests in general. One related study that examined fine root dynamics in different-aged ponderosa pine stands found that peak root production was tightly coupled with bud expansion in all ages (Andersen et al., 2008), indicating that seasonal patterns in fine roots are associated with climate and edaphic characteristics of a given location, as well as endogenous factors driving plant phenology (Fukuzawa et al., 2007; Joslin et al., 2001; Wang et al., 2023). They also found that mean annual production and mortality were higher for the young stand (15-20 years old) compared to the older stand (≥ 250 years old), indicating age-related species differences (Andersen et al., 2008).

I found higher fine root density in the upper 10 cm of mineral soil compared to the O horizon, which was also found by Dumm et al. (2008) in a ponderosa pine/Douglas-fir stand. In Sierra Nevada mixed-conifer forests, moisture is the primary factor limiting belowground respiration (Concilio et al., 2009), and may also drive seasonal patterns and distributions of fine roots. As a result, the dry, hot summers typical of Mediterranean climates may deplete available moisture in the O horizon during prolonged dry periods, making it inhospitable as a rooting medium. In addition, root sampling for this study occurred during an extreme drought in the Sierra Nevada region of California (Sheffield & Kalansky, 2021). One study conducted in pine forests of the Sierra Norte region in Mexico measured a 60% reduction in fine roots during a drought year versus non-drought year (Valdés et al., 2006). This highlights an important gap in knowledge to better understand how temporal variability in moisture and nutrient availability affects rooting depths in fire-excluded dry pine and mixed conifer forests of western North America.

4.3 Effects of Topographic Attributes and Tree Crown Metrics on Duff Mound Physical Characteristics and Fine Root Density

I found that duff mound depth and volume increased for large pines with more foliage, and decreased on steep slopes, and in upper topographic positions and ridgetops. LAD and crown leaf area were both strong predictors of duff mound volume, which as lidar-derived metrics represent powerful tools for capturing the three-dimensional structure of the canopy. In particular, the sum of LAD can be used to estimate the amount of foliage in a tree crown, which directly affects the quantity of litterfall deposition and resulting surface fuel accumulation. Keane (2008) studied deposition and decomposition rates across several forest types in the Rocky Mountains, USA and found leaf area index to be the strongest predictor of foliage deposition ($r = 0.722$). Leaf area index is equivalent to the sum of LAD used in this study. Thus, LAD in conjunction with lidar-derived crown metrics that serve as decent proxies for tree size (e.g. crown area and height), have potential to locate large pines with substantial duff mounds across broad extents.

The amount of variance explained by models of duff mound depth and volume was low, and may reflect variables not measured such as microclimate and litter chemistry that may influence the decomposition processes. Regardless, lidar is an informative tool for quantifying crown fuels over large landscapes, and is thus a promising tool for determining where pines with large duff mounds are found across the landscape. This is highly advantageous from a management perspective because it could greatly increase the efficiency of locating vulnerable pines in landscapes slated for fuel reduction and restoration prescribed burning treatments..

Large pine duff mounds located on lower slopes, depressions, and areas associated with higher soil moisture also tended to have higher fine root density in the O horizon. This is likely due to microsite conditions in these areas that contribute to higher moisture and nutrient availability in the duff layer, increasing resource availability for fine roots. There may also be a relationship between soil texture and topographic attributes, where lower slopes and depressions have finer soils with higher water-holding capacity. At Teakettle, moist, cool microsites have thicker soil and higher aboveground productivity, while ridgetops and areas with exposed granite are more likely to have shallow (< 50 cm), coarse soils underlain with granitic bedrock (Meyer et al., 2007). My findings suggest that these areas have lower fine root density in the upper mineral soil horizon.

Finally, the weak positive relationship between leaf area density and fine root density in the O horizon may not point to a direct mechanism, but could be associated with high vigor trees on deep, moist microsites. Large pines with highly dense crowns may have more photosynthate available to allocate towards fine root production, resulting in increased acquisition of water and nutrients by fine roots, ultimately supporting the vigor of the tree.

4.4 Limitations

This study was subject to a few limitations. Unexplained variance in models of duff mound depth and volume indicates that there are additional factors at play. While DBH, crown area, and LAD were all strong predictors, they may fail to capture the effect of time on duff mound growth and decay for large pines in this system. Conceptually, duff mounds are a mass balance of inputs (deposition) and outputs (decomposition) that vary over time. While DBH is highly correlated with age for large pines at Teakettle, the relationship is imperfect ($\rho = 0.65$ for sugar pine and $\rho = 0.78$ for Jeffrey pine; Zald et al., 2022). As a result, large pines in my study could be anywhere between 150 to greater than 400 years old, representing a substantial temporal window not captured by my models.

This relationship is further complicated by uncertainty in fire history at the tree level, and high spatial variability in fire effects at the landscape level. It is highly likely that most of the large pines in this study were established prior to the last widespread wildfire in 1865, and before that experienced a mean fire interval of approximately 11-17 years (North et al., 2005). However, for very old pines that have experienced many fire events, the patchy spatial structure indicative of southern Sierra mixed-conifer forests likely limited fire spread while producing highly localized effects. This is evident in the Sierra de San Pedro Mártir range of northwestern Mexico, where old-growth Jeffrey pine mixed-conifer forests have not been as severely impacted by contemporary fire suppression, and thus provide reference conditions for similar frequent fire mixed-conifer forests (Stephens, 2004). Within this region, Fry et al. (2018) found significant variability in deposition and decomposition at the stand level that was not explained by structural characteristics, illustrating the inherent complexity in systems shaped by frequent fire regimes.

Second, fine root data includes combined biomass and necromass, which assumes that the ratio is constant across the population of large pines in this study. However, if the ratio between live and recently dead roots is not constant, this research may not fully capture the effect of DBH, species, and topographic metrics on fine root density. To address this, future studies should separate fine root biomass and necromass. Additionally, future work could explore the horizonal and vertical distributions of fine roots around large old pines in more detail by quantifying fine root biomass at varying distances from the tree bole, as well as up to a depth of 20 cm in the mineral soil horizon.

Finally, duff mound bulk density includes combined litter, fermentation, and humus layers, which is limited in its interpretation. To better understand vulnerability of large pines to heat impacts from duff consumption, it may be more informative to focus on the density of the fermentation and humus layers, where smoldering combustion is more likely to occur. More detailed information could inform spatial variability and patterns of fuel consumption, as well as heat impacts to the stem and underlying mineral soil. In addition, temperature and moisture sensors could be used to collect temporal data on microclimate in and around large pine duff mounds to inform decomposition.

4.5 Management Implications and Future Directions

As prescribed fire treatments attempt to address long-term fire deficits across frequent fire landscapes, land managers need to understand how to mitigate potential large pine mortality due to unprecedented basal fuel accumulations. Duff mound raking is a widely applied management tool intended to reduce tree stem and root damage during prescribed burning (Hood et al., 2007). However, the efficacy of raking treatments in mitigating mortality have been mixed. Some studies demonstrated success raking in the fall (Fowler et al., 2010; Noonan-Wright et al., 2010), versus spring when more fine roots were observed in duff mounds of large ponderosa pine (Kolb et al., 2007; Swezy & Agee, 1991). The most relevant study to Teakettle raked 457 sugar pine prior to burning at Sequoia and Kings Canyon National Park and found that raking only had a significant effect when basal fuels exceeded 15 cm (Nesmith et al., 2010). At the same time, any benefits of raking were negated when fire intensity resulted in high crown scorch. This demonstrates that raking can be highly effective, but in some cases should be applied in conjunction with ladder and surface fuel removal beyond the duff mounds of large old pines to limit scorch and associated crown injuries. Otherwise, prescribed fire in old growth may need to be constrained to fuel moisture and fire weather conditions that reduce fire intensity. Yet, this would place additional constraints on prescribed burn periods already operationally limited by air quality and wildfire considerations (Miller et al., 2020; Quinn-Davidson & Varner, 2012).

Regardless, my findings suggest that duff mound raking at Teakettle should place greater focus in areas associated with higher risk. My models indicate that large pines with higher LAD located in lower topographic positions are more likely to have deep duff mounds with more fine roots. I also found higher fine root density in the upper 10 cm of mineral soil compared to the O horizon. With respect to duff mound raking, this suggests that fine root damage and associated physiological stress from raking the O horizon may be less likely for many of the large pines in this study. In addition, raking basal duff will directly benefit higher fine root density in the upper mineral soil that may otherwise be severely damaged from long-duration duff smoldering.

My findings suggest that large pines on steep slopes and ridgetops with shallow soils may warrant less overall attention due to having smaller duff mounds. Large pines on steep slopes are likely more threatened by heightened fire intensity during upslope travel, in which case ladder fuels, canopy base height, surrounding surface fuels, and species composition should be evaluated as risk factors for crown scorch. Lastly, my study did not find substantial differences between duff mounds of sugar and Jeffrey pine. This could be beneficial in terms of time and cost efficiency by simplifying prescriptions for duff mound raking and other management interventions between these two species. However, potential differences in tolerance to basal and root heating between sugar and Jeffrey pine should also be considered.

In conclusion, this study contains foundational duff mound data for a censused population of large, old sugar and Jeffrey pine located in the Sierra Nevada, USA. My study was originally designed with a prescribed burn to measure post-burn effects, but the

COVID-19 pandemic and Creek Fire in 2020 impacted the ability of the Sierra National Forest to plan and implement prescribed burns. Nonetheless, the unmanaged 200-ha study area is within a larger project area where a prescribed burn is being planned for implementation in 2024-2025. This represents a unique opportunity to study the long-term effects of reintroduced fire on large old pines in an old-growth mixed-conifer forest. In particular, the relationship between duff depth and heat impacts to the tree stem, fine roots, and underlying mineral soil is poorly understood. Future research is needed to investigate whether there is a critical threshold for duff depth to better inform mortality mitigation measures. At present, data and results from my study have informed a randomized duff mound raking experiment on the censused trees, while long-term post-burn monitoring will improve our understanding of duff consumption and post-burn mortality in large old pines.

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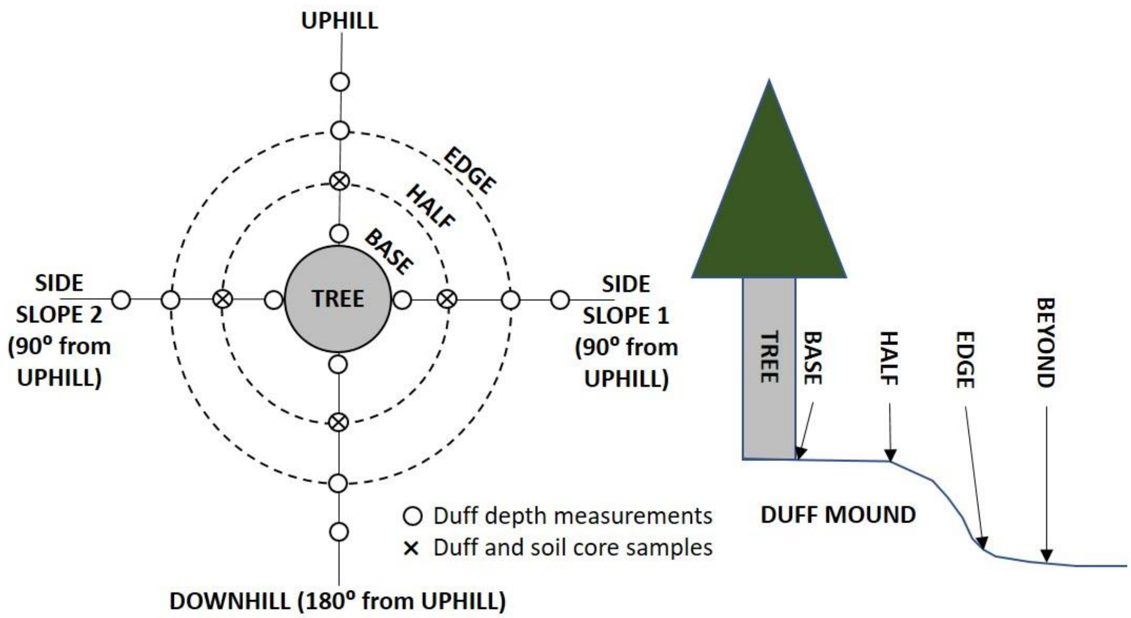
APPENDICES

Appendix A. Diagram of sampling layout for duff mound litter and duff measurements, locations of duff and soil core samples, and description of transect positions.



Duff Mound Transect Positions

- Base: adjacent to the root collar
- Half: half the distance from the base to the mound edge
- Edge: visually assessed as where the descending incline of local fuel accumulation meets the general slope of the hillside.
- Beyond: 30 cm beyond the edge of the duff mound

Appendix B. Summary of multivariate linear regression model results for top models explaining duff mound physical characteristics (volume, maximum depth, O horizon roots, mineral soil roots, and mineral soil bulk density) with topographic and crown metrics. Coefficients of the model reflect a natural log-transformed response and are not back-transformed. There were no significant topographic or crown variables for O horizon bulk density.

	Estimate	2.5%	97.5%	*t value*	*P value*	Adjusted R^2
Duff mound volume					4.64E-11	0.146
Slope	-0.014	-0.022	-0.007	-3.697	2.57E-03	
Topographic Position Index (100 m)	-0.009	-0.018	-0.001	-2.12	0.035	
Crown Area	0.001	0.001	0.002	4.307	2.20E-05	
Leaf Area Density (sum)	0.136	0.049	0.223	3.086	0.002	
Duff mound maximum depth					1.32E-05	0.068
Slope	-0.009	-0.016	-0.002	-2.7	0.007	
Topographic Position Index (100 m)	-0.012	-0.018	-0.006	-3.991	8.18E-05	
Leaf Area Density (sum)	0.076	0.013	0.138	2.393	0.017	
Organic horizon roots					1.00E-03	0.127
Topographic Wetness Index	-0.377	-0.637	-0.117	-2.875	0.005	
TPI 30	-0.311	-0.523	-0.099	-2.914	0.004	
Leaf Area Density (sum)	0.49	0.139	0.842	2.766	0.007	
Mineral soil roots					0.029	0.054
Topographic Wetness Index	-0.213	-0.402	-0.023	-2.237	0.029	
Mineral soil bulk density					0.087	0.022
Topographic Position Index (10 m)	-0.076	-0.164	0.011	-1.733	0.087	