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NATIVE PONDEROSA PINE AT JOINT BASE LEWIS-MCCHORD, WASHINGTON

Running footer: Ponderosa Pine in Western Washington

3 tables, 6 figures

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Abstract

Joint Base Lewis-McChord, WA, has the largest population of ponderosa pine (*Pinus ponderosa*) west of the Cascade Range in the Pacific Northwest. Field mapping showed a modern geographic range of ≈ 13,270 ha. The ages and locations of the largest, oldest pines indicated that at the time of EuroAmerican settlement in the mid-1800's, most pines grew in a single area of ≈ 1,730 ha within a landscape of woodland, savanna, and grassland maintained by Native American fire. After settlement ended burning, conifer forest replaced much of the original vegetation and the range of pine expanded. I repeatedly measured permanent plots over an 11-yr period (2007–2018) within the two forest types with pine: Closed Forest (canopy cover ≥ 60%), dominated by Douglas-fir (*Pseudotsuga menziesii*), and Woodland/Savanna (cover 5–59%), often mixed with Douglas-fir and Oregon white oak (*Quercus garryana*). Pine basal area and density were similar between types. Overstory pines in Woodland/Savanna had larger diameter growth and crown ratio, lower height and height:diameter ratio, and averaged 40 yr younger, than those in Closed Forest. Pine regeneration was scarce in both forest types. The only notable temporal trends were increasing Douglas-fir regeneration density in Closed Forest and log accumulation in Woodland/Savanna. Pine diameter and age distributions showed an increasing deficit of young pines over time. Major impediments to pine regeneration are fires that burn hotter than historically and competition from a non-native shrub, Scotch broom (*Cytisus scoparius*). Active management will be necessary to perpetuate this pine population, at least in Woodland/Savanna.

Keypoints

- Joint Base Lewis-McChord, WA, has the largest population of ponderosa pine west of the Cascade Range in the Pacific Northwest.

- Pine is much more abundant, grows faster, and has proportionally bigger crowns in woodlands and savannas than in dense conifer forests.
- Pine reproduction is declining over time, so active management will be necessary to maintain pine on the landscape, at least in woodland/savanna.

Keywords: fire ecology, forest stand structure, Joint Base Lewis-McChord, ponderosa pine

Introduction

Ponderosa pine (*Pinus ponderosa*) has a wide distribution in western North America (Burns and Honkala 1990). The entire geographic range has a semiarid continental climate, except for populations in the lowlands west of the Cascade Range in the Pacific Northwest, where the climate is moist maritime. These "Westside" populations are widely scattered in the Willamette Valley of Oregon, the southern Puget Lowland of Washington, and the upper Skagit River valley in Washington and British Columbia (Agee et al. 1990, Foster 1997, Hibbs et al. 2002, Lepofsky et al. 2003, Fletcher 2005, BC Parks 2023, Oregon Biodiversity Information Center 2023).

Westside pine's ecological niche differs from that of "Eastside" pine (i.e., east of the Cascade Range) because it grows in a much wetter climate, and, in the Willamette Valley, sometimes on wetland soils (Kirschner 2008). Gene flow between Westside and Eastside pine is largely prevented by the Cascade Range, although some may occur via long-distance pollen dispersal through the Columbia River gorge (Williams 2010). Not surprisingly, Westside and Eastside pine are genetically distinct, as indicated by common-garden studies of height growth (Squillace and Silen 1962, St. Clair 1999, Rehfeldt et al. 2014) and genetic analyses (Potter et al. 2013, Willyard et al. 2017).

Most historic Westside pine stands have disappeared or been ecologically degraded due to logging, development, and invasion by other conifers and non-native shrubs, forbs, and grasses in the absence of fire. Interest is growing in ecological restoration of remnant stands (Foster 1997) and in using Westside pine seed to establish new pine stands (Oregon State University Extension Service 2003; Jeff DeBell, Washington State Department of Natural Resources, Olympia, WA, personal communication).

There are few descriptions of the structure and species composition of native Westside pine stands (Foster 1997, Agee et al. 1990, Hibbs et al. 2002) and none of the temporal dynamics of such stands, perhaps because most existing stands are small and isolated from other stands. The ponderosa pine population on Joint Base Lewis-McChord (JBLM), an Army/Air Force military installation near Tacoma, WA, is by far the largest occurrence of Westside pine, yet it has had only a preliminary description of its structure and species composition, using a small number of sample plots across a portion of its local geographic range (Foster 1997).

The JBLM landscape has changed dramatically since EuroAmerican settlement in the mid-19th century, as indicated by comparison of General Land Office survey quarter-section notes to modern forest inventories (Public Forestry Foundation 1995). Approximately 31% of the JBLM landscape is hilly terrain consisting of glacial till and moraine, with soils that developed under forest vegetation. This area was covered by conifer forest, dominated by Douglas-fir (*Pseudotsuga menziesii*), both historically and today. A more profound change occurred on the flat or gently undulating terrain, underlain by glacial outwash, that occupies 58% of the JBLM landscape, with excessively well-drained soils that developed under grassland vegetation. Here, the presettlement vegetation was a complex mosaic of grassland, savanna (5–24% canopy cover), woodland (25–59% cover), and closed forest (≥ 60% cover). Most of the closed forest was in areas where Douglas-fir had invaded former grassland that escaped fire long enough for trees to establish (15% of JBLM) (Foster 2001);

these "prairie colonization" forests were probably, at most, a few hundred years old. Douglas-fir was the dominant species, but ponderosa pine and Oregon white oak (*Quercus garryanna*) were often present. Also occurring on outwash soils were woodlands (6% of JBLM) and savannas (7% of JBLM), consisting of various mixtures of Douglas-fir, pine, and oak. The remainder of the outwash soils was grassland (36% of JBLM) (Public Forestry Foundation 1995).

The relatively open outwash landscape was maintained by frequent, Native American-set fires (Perdue 1997, Storm and Shebitz 2006) which prevented dense accumulations of surface and understory fuels. In woodlands and savannas, these fires typically burned on the ground with low intensity, killing Douglas-fir saplings with thin bark. By contrast, pine saplings often survived the fires because at basal diameters as small as 2 cm, thick insulating bark protects the cambium from heat damage (Graham and Jain 2005). Understory Douglas-fir, but not pine, were often killed, too. Overstory stems of both species had thick enough bark that they usually survived. The ground fires also created bare soil patches where the litter layer and understory vegetation were consumed and mineral ash deposited. These were good microsites for conifer regeneration because pre-fire litter layers can prevent pine seeds from germinating (Haase 1986, Bonnet et al. 2005) and Douglas-fir seedlings from emerging above the litter (Caccia and Ballaré 1998). In contrast, post-fire litter accumulation as mature trees drop scorched needles benefits pine regeneration by reducing temperature and slowing moisture loss in surface soil (Bonnet et al. 2005). Thus, fire was an important ecological process maintaining pine on the landscape.

Indigenous burning ended following settlement, and wildfires were actively suppressed starting circa 1900. As a consequence, Douglas-fir invaded much of the woodlands, savannas, and prairies from which it had formerly been excluded by fire, converting thousands of hectares to new prairie colonization forest (Foster 2001), as shown by stand chronosequences (Foster and Shaff 2003), stand history reconstructions (Peter and Harrington 2014), and anecdotal accounts (Olson 1947).

Today, prairie colonization forest occupies 37% of JBLM (U.S. Army 2017), a more than two-fold increase since settlement, while grasslands have decreased by two-thirds, to 12% of JBLM. Woodlands and savannas have decreased to 5% and 1%, respectively.

The purpose of this paper is to answer three questions associated with the shift from the historically fire-maintained to the modern fire-excluded landscape on JBLM's outwash soils: (1) How did the local geographic range of ponderosa pine change? (2) What are the structure and temporal dynamics of modern pine-containing stands? (3) What is the current status of the pine population and the prospects for maintaining pine on the landscape?

Study Site

Located in the southern Puget Lowland near Tacoma, WA, JBLM has a maritime climate with mean annual temperature of 11.1ºC and mean annual precipitation of 986 mm. On average, daily maximum temperatures in summer are 26–27ºC, freezing temperatures occur 62 days per year, and winter snow is uncommon (annual average 99 mm). Droughts of 1–3 month duration occur every summer; on average, only 36-40 mm of rain falls in July and August (US Army, 1st Weather Squadron, Gray Army Airfield, JBLM, personal communication; period of record 1960–2023).

With few exceptions, all ponderosa pines at JBLM grow on excessively well-drained, often very rocky, Spanaway and Nisqually soils that developed on glacial outwash (Lindsay and Briggs 2014). These have a deep, organic matter-rich A horizon typical of soil development under grassland vegetation (Ugolini and Schlichte 1973), an attribute that persists for at least 130 yr in prairie colonization forest (Foster and Shaff 2003).

Pine grows mostly within two vegetation types (US Army 2017): (1) Closed Forest. Here, pine occurs mostly as individual overstory trees or small clusters of trees scattered within a matrix of Douglas-fir. (2) Woodland/Savanna. Oregon white oak is often present, and sometimes Pacific madrone (*Arbutus menziesii*) or lodgepole pine (*Pinus contorta*). Woodland/Savanna is very patchy, with, at a local scale (0.05–0.1 ha), total canopy cover varying from 0% to 85% and the relative cover of pine varying from 0% to 100%. The boundaries between Closed Forest and Woodland/Savanna are often abrupt due to current (e.g., military firing ranges) and past (e.g., agriculture) land uses.

Closed Forest understories range from moss and scattered forbs to well-developed shrub layers of hazelnut (*Corylus cornuta*), Indian plum (*Oemleria cerasiformis*), and serviceberry (*Amelanchier alnifolia*), with swordfern (*Polystichum munitum*) often present. Scotch broom (*Cytisus scoparius*), a non-native shrub with rapid growth, photosynthetic stems, and abundant seed that can remain dormant in the soil for many years (Bossard and Rejmanek 1994, Sheppard et al. 2002), is frequently found in, and often dominates, larger (≥ 0.1 ha) canopy gaps and stands with mean canopy cover < 50%. Woodland/Savanna understories range from grass/forb to dense shrub layers of snowberry (*Symphoricarpos alba*) or Scotch broom; tall Oregongrape (*Mahonia aquifolium*) is often present.

Methods

Geographic Range

Range Mapping–I used an existing Geographic Information System (GIS) layer, derived from Crawford et al. (1995), as the starting point for detailed mapping of ponderosa pine occurrences on JBLM. This layer indicates that ponderosa pine grows across 1,734 ha of undeveloped military training lands on the Fort Lewis portion of JBLM. In 2009, I conducted a roadside search within the geographic scope of this layer. I soon realized that the layer excluded much of the actual area occupied by pine and included some areas where pine did not grow. Therefore, in 2010–2011, I conducted a systematic search for pine, by vehicle and on foot, across all JBLM training lands occupied by colonization forests, woodlands, and savannas, using a geographic positioning system (GPS; GeoXH, Trimble Navigation, Sunnyvale, CA). Occurrences ≥ 0.05 ha were mapped as polygons in ArcMap 9.3 (ESRI, Inc., Redmond, CA). Otherwise, pine stems and clusters of stems, regardless of stem size (i.e., saplings to old-growth trees), were mapped as points.

Scattered native ponderosa pine also occurs within developed areas on and adjacent to JBLM. Native pine is usually distinguished from planted pine by being larger and having more defects (e.g., forked stems). I searched for such pines in the JBLM cantonment, McChord Field, and those portions of the towns of Spanaway and Roy, WA, within one mile of the JBLM boundary.

Fourteen forest plantations (total area 124 ha), established prior to 2000 and containing ponderosa pine, were excluded from the range mapping because the pine was of Eastside provenance, the only seed source available for this species in Washington State until 2010, when the JBLM Forestry Branch contracted with a local tree nursery to grow seedlings from native ponderosa pine seed collected on JBLM. Two other plantations (total 27.4 ha), established more recently, were included because the seed source was native pine on JBLM.

All polygons and points were buffered by 30 m. Then, viewing at a 1:12,000 scale, I drew new polygons around clusters of multiple polygons and points. The cumulative area of the new set of polygons represented the "extent of occupancy" (*sensu* Gaston and Fuller 2009) for ponderosa pine. Outside of the new polygons, there were some individual pines or small clumps of pines that were mapped as outlying points. I drew a final polygon that included both these points and the extent of occupancy polygons; this polygon represented the geographic range.

Historic Range/Big Pine Characteristics–To elucidate changes in the geographic range of ponderosa pine between the mid-19th century and today, and to describe the characteristics of "legacy" pines that occur here and there within the modern range, I sampled 125 pine stems across the current geographic range in 2012–2013. They were subjectively chosen as the largest (≥ 76 cm diameter at breast height [DBH], 1.47 m above the ground), and thus likely the oldest, trees within the JBLM pine population, and are referred to here as "Big Pines." In areas near the currrent range boundary that lacked Big Pines, the largest pines < 76 cm DBH that could be found (n = 5) were sampled for age only. I assumed that mapping the locations of the oldest (≥ 150 yr old) of these trees would represent the range of pine at the time of settlement.

Measured on each Big Pine were: (1) DBH (n = 125). (2) Total height for all stems except one missing the upper half of its crown due to stem breakage (n = 124). (3) Crown ratio (live crown depth/total height x 100) of the trees with measured heights, excepting 46 whose crown depth data were lost (n = 78). The base of the live crown was at the lowest live branch whorl, but if this whorl had less than three branches, the base of the live crown was half the distance between the lowest live whorl and the next-highest whorl with three branches. (4) Height:diameter (H:D) ratio for all trees except the one with a partially missing crown (n = 124). DBHs were measured using a logger's tape (Spencer Products Co., Seattle, WA), and heights and crown depths were measured with a laser rangefinder (TruPulse 200, Laser Technology, Inc., Centennial, CO).

For all but one of the Big Pines, an increment borer (Haglöf Sweden, Långsele, Sweden) was used to extract a breast-height wood core reaching to or near the pith of each tree. Except for six trees with rotten centers, annual growth rings were counted at 10-power under a dissecting microscope (n = 118 trees). When the rings on a fresh core were too narrow to reliably count, the core was dried, glued to a wooden mount, and sanded to a 220-grit surface before the rings were counted. If a core missed the center, transparencies of concentric rings of different ring widths were used to estimate the number of rings to the pith (Applequist 1958). Five years was added to each age to account for growth from seedling to breast height. All ages were standardized to the end of the 2019 growing season (e.g., a 182-yr-old tree in 2012 was 189 yr old in 2019) to provide a standard baseline for comparing Big Pine ages between Forest Types.

The remaining Big Pine had a rotten center and was the largest pine on JBLM, first found in 1997. Its DBH and height were measured in November 2006. During a windstorm in early 2008, the bole snapped off ≈ 4 m above ground, revealing basal heart rot. Later that year, its crown ratio was measured and a stem cross-section was removed from just above the heart rot, at a point 7.2 m up the stem from the ground while the tree was still standing. This section was allowed to air-dry, then one surface sanded to 220-grit. Rings were counted along three radii. The largest of the three ring counts was the age at 7.2 m height. Assuming height growth rate from breast height to 7.2 m was the same as from germination to breast height (1.37 m over 5 yr = 0.274 m yr^{-1}), 7.2/0.274 = 26 years was added to the ring count to estimate total age.

Structure and Change in Forests Containing Pine

Sampling Considerations–The patchiness of JBLM's Closed Forest and Woodland/Savanna is primarily a natural phenomenon resulting from the spatially variable process of tree colonization of grasslands (Foster and Shaff 2003). Human activities have caused further patchiness. For example, timber sales (mostly light thinnings) have occurred across much of the Closed Forest, with some stands receiving as many as three entries. Also, since the mid-1990s, much of the Woodland/ Savanna has received ecological restoration treatments that included one or more of the following: commercial logging, precommercial thinning, Scotch broom control, prescribed fire, and planting pine seedlings. In addition, wildfires from military ignitions have affected multiple pine stands, the largest occurring across 20.6 ha of Woodland/Savanna in 2014. Finally, military training and construction have destroyed young pines in several small areas.

The timber sales and restoration treatments were not carried out as part of an overall experimental design to separate the effects of natural succession from those of human activities, and the wildfires confound the effects of both natural and human disturbance. Retrospective analysis of the responses of forest structure and dynamics is difficult because, at the stand level, replication for particular combinations of forest type and disturbance type is, at best, just three stands, and often only one. A further complication is that the boundaries of most of the older (pre-1996) fires and timber sales were not mapped with GPS. Thus, my sampling regime was limited to comparing Closed Forest to Woodland/Savanna. And rather than stands, my unit of replication was individual plots. This was statistically appropriate because in subsequent data analysis, each plot was considered to be an independent observation from either the Closed Forest or Woodland/Savanna pine populations.

Plot Establishment and Measurement–In 2007–2008 (the first sampling), 116 permanent pine monitoring plots were established within those portions of the then-known (Crawford et al. 1995) geographic range of pine on the Fort Lewis portion of JBLM, plus additional plots in Closed Forest known to contain pine within the Central Impact Area (an area usually closed to access because of multiple small-arms firing ranges around its perimeter) and a few outlying areas. These plots were systematically laid out, using a 183 x 183-m grid generated in GIS across 1,196 ha of Woodland/ Savanna (one plot every 12.6 ha; n = 95 plots) and a 366 x 366-m grid across 538 ha of Closed Forest (one plot every 25.6 ha; n = 21 plots). I sampled less intensively in Closed Forest because plots there took much longer to locate and measure than in Woodland/Savanna. Plots were located on the ground by reference to aerial photographs and without assistance of GPS, so any given plot could be up to 30 m distant from the GIS grid point, as shown by later GPS measurement. Each plot center was marked with a 30.5-cm-long iron rebar, topped by an aluminum cap and pounded into the ground until the cap was level with the surface.

I recorded the species and DBH of all overstory (≥ 20 cm DBH) stems within a variable-radius plot centered on each plot center, using a Spiegel Relaskop (Silvanus, Kirchdorf, Austria). This type of point sampling selects trees based on size, not frequency, such that sampling probability is proportional to tree diameter (Iles 2003). Each plot had a separate basal area factor (BAF, the amount of basal area per ha represented by each tree in a plot), based on the local density of overstory stems, so that there were, on average, 4–6 stems in each plot (for some Woodland/ Savanna plots at BAF = 5.0, fewer than four stems were measured).

In each plot, the stems were measured in a clockwise direction, starting with the first stem at or east of true north from the plot center. A numbered aluminum tag was affixed to each stem with an aluminum nail. If a tree was forked at or below breast height, each stem ≥ 20 cm DBH was separately measured and tagged.

I used concentric, fixed-radius subplots, centered on the plot center, to sample smaller stems. Pole-size stems were tallied by species and diameter class (0.1–9.9, 10.0–19.9 cm DBH) on a 0.02-ha (8.0-m-radius) subplot. Regeneration stems were tallied by species: saplings (0.46–1.37 m tall) on the 0.02-ha subplot and seedlings (< 0.45 m tall) on a 0.008-ha (5.1-m radius) subplot. Overstory cover was visually estimated, and the DBH, height, and decay class (Harmon et al. 2006) of snags measured, on a 0.08-ha (16.1-m-radius) subplot. To minimize observer bias, the author did all cover measurements in this study. The midpoint diameter, length, and decay class (Sollins 1982) of logs ≥ 25.4 cm mid-point diameter and ≥ 3.05 m length were measured on the 0.02-ha subplot. The criterion for inclusion was that the midpoint was located within the subplot.

Tree basal area and density for each plot were calculated following standard equations for variable-radius plot sampling: basal area = number of trees in plot x BAF and tree density = Σ expansion factor for each tree in the plot, where expansion factor = BAF/basal area of tree (Iles 2003). Density of pole-size and regeneration stems, snag density, and cumulative log lengths were calculated from their respective fixed-plot areas.

Average Pines–To describe the characteristics of typical overstory pines, termed "Average Pines" in this paper, I sampled the nearest live overstory pine stem to each plot center (but not more than 16.1 m distant) for DBH, total height, crown ratio, H:D ratio, recent diameter growth, and age. A breast-height wood core was taken to measure age and radial growth. The combined width of the outermost five growth rings was measured, excluding the outermost ring because trees sampled earlier than mid-summer had not completed current-year radial growth. This value was doubled to estimate 5-year diameter growth. The total ring count from the center of the tree through the year preceding the start of the sampling period, plus five years for growth from seedlings to breast height, represented age; thus, ages were for the end of the 2006 growing season. Total sample size was 97 (87 Woodland/Savanna, 10 Closed Forest) because not all plots, especially in Closed Forest, had a pine stem near the plot center that could serve as an Average Pine.

Plot Remeasurement–All but one of the original plots were remeasured in 2012–2013 (second sampling) because one Woodland/Savanna plot had been destroyed by military construction. In addition, using the same plot spacings as in the first sampling, 28 additional plots (n = 7 for Woodland/Savanna, n = 21 for Closed Forest) were established to complete sampling of the enlarged geographic range that I had mapped in 2010–2011, and a new Woodland/Savanna plot was established at McChord Field, which had by then become part of JBLM. Thus, total sample size was 144 (102 Woodland/Savanna, 42 Closed Forest). Average Pine sample size changed to 106 (87 Woodland/Savanna, 19 Closed Forest) as the net result of the addition of new plots and mortality of some Average Pines measured in the first sampling. I remeasured all variables measured during the first sampling except for the ages of Average Pines on pre-existing plots.

All plots measured in the second sampling were remeasured in 2018–2019 (third sampling) except for an additional Woodland/Savanna plot destroyed by military construction. Thus, total sample size was 143 (101 Woodland/Savanna, 42 Closed Forest). Continued mortality of pines first measured in the first two samplings reduced Average Pine sample size to 94 (83 Woodland/Savanna, 11 Closed Forest). I measured the same variables as in the second sampling except for the ages of Average Pines on pre-existing plots. In addition, log sampling was changed to the approach of Gove and Van Deusen (2011), using the "sausage method" for defining the whole-log area of inclusion. Briefly, the probability of a log being selected was proportional to its length and was influenced by the ratio between plot radius and log length.

An important limitation on these samplings is that they took place on an active military training base. At certain times and/or in certain areas of JBLM, access to training areas and impact areas is restricted. As a result, my sampling regimes were often not optimal. For example, during each sampling, it took up to 18 months to measure all plots because of access difficulties, especially in impact areas where live fire occurs (e.g., 36% of all plots in the third sampling). In the first sampling, I collected data between June 2007 and March 2008; in the second, between April 2012 and November 2013; and in the third, between June and October 2018. Therefore, 4–6 growing seasons (for trees, typically May to mid-August in the Puget Sound lowlands) elapsed between successive samplings of each plot.

Statistical Analysis

The objectives of my analysis were exploratory: characterize and try to explain the differences, if any, for each variable between Years within each Forest Type and between Forest Types within each Year, and possible interactions between Year and Forest Type, while accounting for the random effect of Plot. I used linear mixed models (LMMs) or generalized linear mixed models (GLMMs) to accommodate random effects and the unbalanced design of my study. For these analyses, each plot was treated as a replicate within its associated Year x Forest Type category. In the case of Species-level variables, analyses were run separately for all species combined (All Species) and just ponderosa pine (Pine Only).

If the raw-data distribution for a variable approximated the normal distribution, I constructed LMMs using the "lmer" function in package "lme4" (Bates et al. 2015) in R software (version 4.1.2; R Core Team 2021). To determine a valid linear model for each Plot-level and Species-level variable, I started with a "full" model in which the fixed effects were Year, Forest Type, and the Year x Forest Type interaction, and the random effect was Plot nested within Type, with both random-intercept and random-slope terms. To test the significance ($\alpha = 0.05$) of these effects, I used sequential maximum likelihood ratio tests (function "anova" in lmer) that compared a model which included the effect of interest to a nested model that lacked the effect (Luke 2016). If the ratio test was significant, then the missing term in the nested model improved model fit; otherwise, it was excluded from further analysis. A final model that included only the intercept and the fixed and random effects that improved model fit was then run, using restricted maximum likelihood to provide unbiased estimates of model parameters.

If a variable's raw data appeared to fit the Poisson distribution, and less than 20% of the data values were zeroes, I used GLMM (package "glmmTMB" in R) with the log-link function for the conditional model and Laplace approximation for the random effect (Brooks et al. 2017). If $\leq$ 5 % of the data were negative values, which have no logarithms, I excluded these from the analysis; if > 5%, I concluded that a valid linear model was not possible because I no longer had a representative sample.

If a variable's data were decimal, then prior to analysis I approximated count data by multiplying each value by a power of 10 to convert the data to integers. The coefficients of the final model were then divided by the same power of 10 to provide estimates in the original units of measurement.

If a dataset had an apparent excess of zeroes (20% or more of the values) (snag density, log length, Pine Only basal area and density, All Species and Pine Only pole-size and regeneration density), I used a zero-inflated GLMM that added a simple zero submodel (i.e. "z=1" in glmmTMB) to the conditional submodel. This model assumes that the zero data are attributable both to the same process(es) as the conditional model, plus additional process(es) that apply only to the zero data (Welsh et al. 1996). This made sense because there were multiple reasons why pine could be absent from a plot: too distant from seed sources, killed by wildfire or prescribed burns, other causes of mortality. This model also provides better estimates of the variances and Type I errors associated with zero-inflated data than does standard GLMM (Martin et al. 2005). All model runs used the Poisson distribution for the conditional submodel. Determination of a final model then proceeded in the same fashion as for LMMs.

I used normal probability plots and plots of residuals vs. model-fitted values for each final model to determine if the residuals approximately met the assumptions of normality and equal variances. If the residuals of an LMM model clearly violated one or both assumptions, I reran the analysis, using a Poisson GLMM. If the assumptions were still not satisfied, I concluded that no valid linear model could be fit to the data.

For each Year x Forest Type category in each valid model, I used R package "emmeans" to calculate estimated marginal means, i.e., the category means conditional on the other fixed factors in each model and corrected for unbalanced data (Searle et al. 1980), and associated 95% confidence intervals (CIs), and to do all possible pairwise comparisons with associated *P* values, using Tukey's correction for multiple contrasts and the Kenward-Roger estimate of degrees of freedom (Lenth et al. 2023).

I prepared frequency distributions of pine diameter (DBH) in each Year x Forest Type category. Since each variable-radius plot had a separate BAF, and the smallest DBH classes (0.1-9.9, 10.0-19.9 cm) were pole-size stems on fixed-area plots, I calculated frequency data as the stem density represented by individual stems, summed for each DBH class within each category. I also prepared age frequency distributions for Average Pines in each Year.

Results

Geographic Range

Range Mapping–The modern geographic range of the JBLM ponderosa pine population encompasses 13,270 ha and lies entirely on JBLM, excepting 112 ha in the adjacent towns of Spanaway and Roy (Figure 1). The extent of occupancy is 1,939 ha, or ≈ 15% of the geographic range, and consists of one large area of occupancy (1,285 ha) and 66 smaller areas of occupancy (0.03–96.8 ha). Four of the latter are outliers ≥ 2.3 km from the main area of occupancy; the most distant (13.6 km) near the southern boundary of JBLM.

Historic Range–With one exception, all the oldest (≥ 150 yr of age in 2019) pines were located in the southeastern portion of the Central Impact Area, the adjoining right-of-way of the Burlington Northern-Santa Fe Railroad (BNSF) , and adjacent training land to the east and northeast, an area encompassing 1,730 ha (≈ 13% of the modern geographic range; Figure 2, inset). This represents the putative historic range of pine at the time of settlement.

Big Pine Characteristics–Big Pines varied widely in their characteristics, as shown by the large ranges in Table 1. Pearson's correlations showed that neither DBH and height ($r = 0.06$, $P > 0.05$) nor DBH and 2019 age ($r = 0.10$, $P > 0.05$) were significantly related. The smallest-DBH (79 cm) pine was 163 yr old. The largest-DBH pine, growing in a grazed pasture on private property just outside the eastern boundary of JBLM, had a broad, deep crown and a highly tapered stem, a height of 44 m, crown ratio of 90, and H:D ratio of 27. Despite its size, it was only 105 yr old. The tallest pine, 64 m to an intact top, was growing in Closed Forest in the Central Impact Area, surrounded by Douglas-fir trees of somewhat shorter height. It had a DBH of 123 cm, a crown ratio of 35% with a very narrow crown, an H:D ratio of 52, and an age of 154 yr.

The largest pine on JBLM, in terms of bole volume, was the tree in the Central Impact Area that was toppled by a windstorm in 2008 (Figure 2 inset). When still standing, it had a DBH of 153 cm, a diameter of 94 cm at the base of the live canopy, and a height of 55 m to an intact top. It was also the oldest pine on JBLM, with an estimated 2019 age of 334 yr.

Stand Structure and Short-Term Temporal Change

Valid (i.e., met the assumptions of normality and equal variances) linear models were fit to 10 out of 21 of the stand-structure variables measured in this study. Eight variables had valid LMMs, one variable had a valid GLMM, and one variable had a valid zero-inflated GLMM (Tables 2 and 3). Significant effects were Year in one model, Forest Type in two models, both Year and Forest Type in three models, and Year, Forest Type, and the Year x Forest Type interaction in four models.

The reasons that valid models could not be fit to 11 of the variables were unbalanced designs, large and heterogeneous variances, and/or too many zero or negative values (e.g., for Pine Only regeneration, 85% of Woodland/Savanna and 98% of Closed Forest plots had zero values). All valid models included a random-intercept term, but none included a random-slope term.

For the variables with valid models, estimated marginal means were available for statistical comparisons between Year x Forest Type categories. For the remaining variables, only qualitative assessments could be made, based on comparisons of observed means and confidence intervals.

Plot-Level Variables–For overstory cover, Forest Type and the intercept were significant fixed effects ($P \leq 0.016$) (Table 2). Depending on the Year, mean cover was 100–125% greater in Closed Forest compared to Woodland/Savanna (LMM, $P \leq 0.001$), but did not differ between Years in either Forest Type ($P > 0.05$) (Table 2, Figure 3).

Valid LMMs could not be fit to either snag density or log length data. Qualitatively, due to overlapping confidence intervals, there were no clear patterns in mean snag density, either between Forest Types or between Years. Mean cumulative log length was similar between Forest Types in all three Years, and for both Types, length was similar between 2007 and 2012, then increased substantially in 2018 (Figure 3).

Species-Level Variables–For All Species basal area, Year, Forest Type, and the Year x Forest Type interaction were significant fixed effects (LMM, $P \leq 0.003$) (Table 2). Depending on the Year, mean basal area was 63–68% higher in Closed Forest than in Woodland/Savanna ($P \leq 0.001$) (Table 2, Figure 4). It did not change over time in Woodland/Savanna ($P > 0.05$), but in Closed Forest, it increased 17% between 2007 and 2018 ($P \leq 0.001$) (Table 2, Figure 4). A valid LMM could not be fit to the data for Pine Only basal area. Qualitatively, it appeared not to differ between Forest Types in 2007, but to be a little higher in Woodland/Savanna than in Closed Forest in 2012 and 2018 (Figure 4).

For All Species tree density, Year, Forest Type, and the Year x Forest Type interaction were significant fixed effects (LMM, $P \leq 0.021$) (Table 2). Mean density was much greater in Closed

Forest than in Woodland/Savanna in all Years ($P \leq 0.003$), the difference increasing from 94% in 2007 to 167% in 2018 (Table 2, Figure 4). In Woodland/Savanna, mean density decreased 27% between 2007 and 2018 ($P \leq 0.001$), while there was no change over time in Closed Forest ($P > 0.05$) (Table 2, Figure 4). A valid LMM could not be fit to the data for Pine Only tree density. Qualitatively, it appeared to be similar between Forest Types and across all Years (Figure 4).

Valid LMMs could not be fit to the pole-size and regeneration stem density data for either All Species or Pine Only. Qualitatively, mean All Species density of pole-size stems appeared to be similar in Closed Forest and Woodland/Savanna in 2007 and 2012, but less in 2012, whereas mean regeneration density was lower in Woodland/Savanna than in Closed Forest in all Years. The only temporal change appeared to be an increase over time in All Species regeneration density in Closed Forest (Figure 4). Mean density of Pine Only pole-size stems was similar in Closed Forest and Woodland/Savanna in 2007, but in 2012 and 2018, pine was absent in Closed Forest. Mean pine regeneration density was absent in Closed Forest and very low in Woodland/Savanna in 2007 and 2012; a little bit of pine regeneration was present in both Forest Types in 2018 (Figure 4).

Average Pine Variables–For DBH, Year, Forest Type, the Year x Forest Type interaction, and the intercept were significant fixed effects (LMM, $P \leq 0.016$). Mean DBH was higher in Closed Forest than in Woodland/Savanna in all Years, the difference decreasing from 20% in 2007 to 6% in 2018 ($P < 0.016$). In Closed Forest, it was the same for all Years ($P > 0.05$), but in Woodland/Savanna, it increased by 14% between 2007 and 2018 ($P < 0.001$) (Table 2, Figure 5).

For height, Year, Forest Type, and the intercept were significant fixed effects (LMM, $P < 0.007$) (Table 2). Mean height was 55–61% greater in Closed Forest than in Woodland/Savanna in all Years ($P < 0.001$) (Table 2, Figure 5). In both Forest Types, mean height was the same in 2007 and

2012 (*P* > 0.05), then increased by 7% in Closed Forest and 11% in Woodland/Savanna in 2018 (*P* < 0.001) (Table 2, Figure 5).

For diameter growth, Year, Forest Type, and the intercept were significant fixed effects in the conditional model (zero-inflated GLMM, *P* < 0.001), and the intercept of the zero model was also significant (*P* < 0.001) (Table 3). Mean diameter growth was 300% higher in Woodland/Savanna than in Closed Forest in all Years (*P* ≤ 0.01) (Table 3, Figure 5). It did not differ between 2007 and 2012 in either Forest Type (*P* > 0.05), then decreased 15–16% in by 2018 in both Forest Types (*P* < 0.001) (Table 3, Figure 5).

For mean crown ratio, Year, Forest Type, the Year x Forest Type interaction, and the intercept were significant fixed effects (LMM, *P* ≤ 0.012) (Table 2). The Woodland/Savanna mean ratio was 140% greater than that of Closed Forest in 2007 and 71% greater in 2012 (*P* ≤ 0.001), but did not differ in 2018 (*P* > 0.05) (Table 2, Figure 5). Mean crown ratio was similar in all Years in Closed Forest (*P* > 0.05), but in Woodland/Savanna was the same in 2007 and 2012 (*P* > 0.05), then decreased 20% in 2018 (*P* < 0.001) (Table 2, Figure 5).

For mean H:D ratio, Forest Type and the intercept were significant fixed effects. (LMM, *P* < 0.001) (Table 2). Mean H:D ratio was 33–35% greater in Closed Forest than in Woodland/Savanna in all three Years (*P* < 0.001) but did not differ between Years in either Forest Type (*P* > 0.05) (Table 2, Figure 5).

For tree age, Year and Forest Type were significant fixed effects (LMM, *P* < 0.001) (Table 2). Closed Forest mean age was 44, 35, and 37 yr higher than that of Woodland/Savanna in 2007, 2012, and 2018, respectively (*P* < 0.001) (Table 2, Figure 5). Woodland/Savanna mean tree age increased by 15 yr between 2007 and 2012, and by 5 yr between 2012 and 2018, compared to 6 yr and 7 yr, respectively, for Closed Forest (*P* < 0.001) (Table 2, Figure 5).

Diameter and Age Distributions–The diameter distribution of pines in both Forest Types was right-skewed, i.e, a long "tail" towards larger DBH classes, in all Years (Figure 6). In 2007 and 2018, the shapes of the distributions were similar in Closed Forest and Woodland/Savanna, although the Woodland/Savanna stem densities were almost always larger than those of Closed Forest, regardless of DBH class. In 2012, Closed Forest stem density was much less than that of Woodland Savanna in DBH classes 15 through 45, but only somewhat less, or even more, in the larger DBH classes. There were no pine stems in Closed Forest in DBH class 5 in 2012 and 2018, nor in DBH class 15 in 2018; in Woodland/Savanna, there were no stems in DBH class 5 in 2018 (Figure 6).

The age distribution of Average Pines in Woodland/Savanna was right-skewed in all Years, with a mode in age class 30 in 2007 and age class 50 in 2012 and 2018 (Figure 6). The age distribution was more even in Closed Forest, with a broad mode in age classes 90 and 110 in all Years; no stems were present in age class 30 in any Year, or in some of the other age classes, depending on Year (Figure 6).

Discussion

Geographic Range

Prior to the mid-19th century, ponderosa pine on JBLM had a much smaller geographic range than today, as indicated by the clustering of Big Pines ≥ 150 yr old within a relatively small "core area" and their absence from the rest of the modern range. The earliest known map of the JBLM area shows "Red Pines" at the location of the core area (Tilton 1855), and Huggins (1902) confirmed that these pines were *Pinus ponderosa*.

Was I correct in assuming that, historically, few pines grew outside the core area? Ponderosa pine decays relatively quickly for a conifer, so after ≈ 50 yr, there were likely no large cut stumps to show where pine on JBLM once grew before it was cut. However, historical records indicate that there were at least some pines outside the core area before settlement. Witness trees from the 1853 survey of the JBLM area, in the portion north of the Nisqually River (i.e., Pierce County, WA), included eight ponderosa pines at several locations outside of the core but within the modern areas of occupancy (Public Forestry Foundation 1995: Appendix D-1). These trees' average DBH was 78.7 cm, so they had been on the landscape for at least several decades. The surveyor's notes also indicated that the vegetation types along their traverse lines included 2.0 km of "prairie/pine/oak" and 4.0 km of "prairie/oak/pine," or 10% of the total traverse line distance. Cutting of pine undoubtedly occurred post-settlement, but to what extent is unclear. The only evidence is Huggins (1898), who stated that local ponderosa pine was the source for the redecking of the Hudson Bay Company's SS *Beaver*, the first paddlewheel steamship on the West Coast, in 1841. By 1910, nearly all JBLM's forests north of the Nisqually River had been logged (US Army 2017). With the establishment of Fort Lewis in 1917, pine removal would likely have ceased. The Army did very little forest management prior to 1953, when the modern Forestry program began (US Army 2017), but this program never cut ponderosa pine. Thus, the pre-settlement range of pine was larger than my study found, but by how much is unknown.

The fact that Big Pines in the 100–149 yr age class occurred at multiple locations near the current range boundary suggests that, following the cessation of indigenous fire and concurrent with Douglas-fir invasion of the open landscape, the geographic range of ponderosa pine rapidly expanded outwards in all directions from the core population (and perhaps from some mature pines outside of the core). Since wind dispersal of ponderosa pine seed is usually less than 50 m from parent trees (Fryer 2018), pine expansion was probably facilitated by animal seed dispersal.

Douglas-fir invasion and pine expansion accelerated after World War II, as revealed by time series of aerial photographs (Foster and Shaff 2003) and by the fact that most colonization forests are ≤ 80 yr old.

The four largest ponderosa pine occupancy polygons on JBLM (maximum 3,729 ha) are much larger than any of the pine occurrences in the Willamette Valley (≤ 115 ha; Oregon Biodiversity Information Center 2023) or the upper Skagit River valley (≤ 61 ha; Agee et al. 1990, BC Parks 2023). Thus, the JBLM population is the largest existing example of Westside ponderosa pine.

Today, the extent of occupancy of pine on JBLM is evenly split (41% each) between prairie colonization forest and woodland/savanna, plus 18% in grassland and Scotch broom shrubland.

Big Pines

The oldest Big Pines (≥ 200 yr age in 2019, n = 11) fit the definition of individual old-growth ponderosa pine, possessing large orange bark plates, no signs of old branch attachments on the lower boles, and complex crowns (Van Pelt 2008). However, three of the four largest (≥ 137 cm DBH) Big Pines were too young (age < 150 yr) to be old-growth.

Big Pines grew in varying stand conditions (55 in Closed Forest, 44 in Woodland/Savanna, 14 at edges between Closed Forest and large openings, two emergent above young pine stands, one isolated in a cow pasture) and many had forked stems, so it is not surprising that DBH and height, and DBH and age, were not correlated.

Big Pines with 2019 ages > 187 yr (n = 12) started growth prior to EuroAmerican settlement at JBLM, which began when the Hudson's Bay Company established Fort Nisqually in Dupont, WA, in 1833. The oldest (age = 334 yr) Big Pine germinated in 1685, so in 1833 it was already a large tree. However, just how long ponderosa pine has been in the JBLM vicinity is unknown. Local palynological evidence (one pollen core from Nisqually Lake on JBLM; Hibbert 1979), showing the appearance of diplopoxylon pine pollen ca. 9,600 years BP, is inconclusive because the pollen of lodgepole pine and ponderosa pine can't be distinguished (Cathy Whitlock, Montana State University, personal communication).

The generally large crown ratios and small H:D ratios of Big Pines, characteristic of open-grown trees, indicate that most became established in Woodland/Savanna or grassland. Later, as colonization forests expanded, most of these pines ended up inside Closed Forests. Those that survived to the present day are almost all dominant trees that have, so far, avoided overtopping by Douglas-fir.

Stand Structure and Short-Term Change

Direct comparisons of the results in this paper with those of the initial survey of ponderosa pine on JBLM (Foster 1997) are not possible because the latter sampled only 8% of the geographic range, differed in plot design and, most importantly, used different cutoff values of DBH and height between the overstory, pole-size, and regeneration size classes.

Statistical Issues–Working on a military installation with its restricted access to training and impact areas, plus the risk of permanent plots being compromised by military training, meant that balanced sampling was not achieved. In addition, unknown temporal error (seasonal and year-to-year variability) was included in each model by the fact that it took up to 18 months to finish measuring all plots during each sampling.

All valid models included Plot as a random-intercept term, but none included a random-slope term, probably because there were too few data to parameterize models of this complexity (Bates et al. 2015). Sample size was always too small or the data too unbalanced among categories for the lmer, LMM and 201 and or GLMM models to converge when random slope was included.

There was possible bias in comparisons between the first and second samplings, due to geographic expansion of the population of plots that was sampled. The proportion of all sampled plots that was Closed Forest increased from 18% to 29% between 2007 and 2012. Thus, my sampling was more representative of Woodland/Savanna than of Closed Forest in 2007, but less so in 2012 and 2018.

Plot-Level Variables–Overstory cover did not change over time in Closed Forest, despite increases in both All Species basal area and tree density. This is surprising, given that mean cover was only 50–60%, implying unoccupied space in the canopy available for lateral crown extension by Douglas-fir, which can produce substantial epicormic branches (Punches and Puettmann 2018) (ponderosa pine lacks this characteristic). Offsetting this gain, however, might have been foliage loss due to an ice storm in December 2012, which caused major branch loss and top breakage in the upper crowns of intermediate and suppressed trees in Closed Forest. In Woodland/Savanna, despite much faster Average Pine diameter growth than in Closed Forest, there was no change over time of canopy cover, or of All Species basal area and tree density, implying that tree mortality was offsetting increases in tree size.

In Closed Forest, snag creation was likely dominated by suppression mortality, while in Woodland/Savanna, wildfires and prescribed burns were the major sources of tree mortality. Both suppression mortality and fire mortality primarily affect small-diameter trees, which decay more rapidly and convert more quickly to logs than do larger trees. Additionally, fire burns out the bases of some large-diameter pines, which fall down immediately or shortly thereafter.

Most log creation in Closed Forest was likely due to falling over of decayed suppression-mortality snags, plus occasional windthrown trees. In Woodland/Savanna, falling of fire-killed snags and live trees with burned-out bases was the major process creating logs, especially those found in 2018, and a minor contribution was made by thinning during ecological restoration.

The actual numbers of logs measured during each sampling were quite small, 12 in 2007 and 2012, 46 in 2018 (in all Years, only two in Closed Forest), so the mean and variance of the cumulative lengths could be substantially increased by the addition of just one long log. Hence, there was low statistical power to detect even large changes in mean log length.

The accumulation of dead wood (snags, logs) increased fuel loadings, and thus fire risk, in both Forest Types.

Species-Level Variables–Not surprisingly, mean All Species basal area and tree density were much higher, and mean Pine Only basal area and tree density much lower, in Closed Forest than in Woodland/Savanna in all Years, primarily due to the absence of fire in Closed Forest. Also contributing to these differences were the overtopping of pine by Douglas-fir in Closed Forest and girdling of Douglas-fir during restoration treatments in Woodland/Savanna.

Natural regeneration on JBLM was very patchy spatially, temporally, and in terms of stem density. Both pole-size and regeneration stems were often clumped. In Closed Forest, these clumps occurred mostly within canopy gaps in Closed Forest, where increased light levels permit establishment and growth of shade-intolerant pine and Douglas-fir. In Woodland/Savanna, the clumping appears related to the proximity of mature tree seed sources, especially for pine. Two other factors possibly contributing to the patchiness were: (1) Variable frequency of masting years, especially of pine (Krannitz and Duralia 2004, Mooney et al. 2011, Fryer 2018). Between 1996 and 2020, there were only two years with high pine cone production at JBLM. (2) The spatially patchy presence of suitable seedbeds – bare soil for Douglas-fir, ash-covered forest floors following fire for pine – especially in Closed Forest.

Average Pine Variables–Average Pines in Woodland/Savanna were substantially younger than in Closed Forest because most of the pine occurrences classified as Woodland/Savanna represented tree colonization of grassland since World War II (Foster and Shaff 2003). Despite this age difference, mean DBH did not differ between the two Forest Types, although Closed Forest pines were consistently taller than Woodland/Savanna pines. As a result, mean H:D ratios were lower (i.e., pine stems had more taper) in Woodland/Savanna than in Closed Forest.

Crown ratios and H:D ratios of conifers are negatively and positively related, respectively, to stand density, and thus are indicators of the aboveground competitive environment (Oliver and Larson 1996). Large crown ratios and small H:D ratios are associated with greater growth responses to thinning (Mustard and Harper 1988, Wonn and O'Hara 2001, Qui et al. 2021). Therefore, one would expect lower mean crown ratios and higher mean H:D ratios of ponderosa pine in Closed Forests compared to Woodland/Savannas, as was the case for Average Pines in this study. Because of these differences, I expected faster mean diameter growth of Average Pines in Woodland/ Savanna compared to Closed Forest, and indeed, in all Years they increased in diameter 3–4 times as quickly as those in Closed Forest.

The reduced mean Average Pine diameter growth in Closed Forest in 2018 could be the result of increasing All Species basal area and density, which intensified Douglas-fir competition with pine. The decreased crown ratio of Average Pines in Woodland/Savanna in 2018 may be due to the 2014 wildfire and prescribed burns killing the lowermost live branches. These fires also scorched foliage in the entire crown of pole-size stems and in the lower to middle crown of overstory trees. The resultant loss of green foliage would have decreased whole-tree photosynthetic capacity, thus reducing radial growth. However, height growth actually increased.

Pine Diameter and Age Class Distributions–The pine diameter distributions show that in Closed Forest, pole-size pines were absent in 2018, as were stems in DBH class 5 in Woodland/Savanna. In addition, there is near or complete absence of pine regeneration in all Years and both Forest types. These results suggest that current understory conditions in JBLM's pine occurrences are not conducive to pine reproduction, so there are insufficient young pines to eventually replace existing overstory pines as they die. This is a particularly acute problem in Closed Forest because in pines and other shade-intolerant tree genera, the density of young trees in forest understories needs to be much higher than that of mature trees if sufficient young trees are to survive long enough to replace mortality of overstory trees. This is not as much an issue in more open forests (woodlands and savannas), which have less suppression-related mortality, but with no regeneration in either Forest Type, overstory pine can't be maintained much longer as part of the overstory.

Loss of young pines is probably the result of both reduced seed production and/or germination and increased mortality. These trends can't be attributed to increasing shade as Closed Forests mature, since canopy cover is constant over time. However, mean tree basal area is increasing over time in this forest type, which suggests greater belowground (root) competition between overstory trees and young pines. Today, wildfires and prescribed fires burn hotter than historical fires, almost certainly increasing fire-related tree mortality, particularly of young pine, and primarily in Woodland/Savanna. In addition, infrequent mast years in mature pines lower the probability of adequate seed dispersing to suitable germination sites in any given year,

Implications for the JBLM Pine Population

Two objectives of the JBLM Forest Management Plan (U.S. Army 2017) are: (1) Maintain the presence of ponderosa pine across its local geographic range. (2) Conduct ecological restoration of degraded stands containing pine. The results of this paper have implications for successful accomplishment of these objectives.

Except for occasional wildfires due to military training, fire is absent from Closed Forest. Most of the wildfires burn only surface and understory fuels, but occasionally, during summer drought, stand-replacement fires can occur. In Woodland/Savanna, military training (e.g., tracer bullets on firing ranges during summer drought) causes multiple wildfires every year. In addition, prescribed fire has been used since the late 1980s, and today is occurring every 3–4 yr in the majority of Woodland/Savanna. However, the new fire regime is dissimilar to the historical regime because the fires burn hotter in the presence of increased fuels, especially logs and highly flammable Scotch broom, thus killing much of the pine regeneration and scorching the foliage of, or even killing, some overstory pines.

Invasion of Woodland/Savanna, and of larger canopy gaps in Closed Forest, by Scotch broom may be as important as fire in limiting regeneration density. Broom seeds are spread widely across JBLM, the most-likely vector being soil picked up by the boot soles of soldiers and the tires of military vehicles and logging equipment. These seeds can remain dormant in the soil for many years, yet readily germinate following fire or mechanical ground disturbance. Rapid growth (up to 4.5 m height, 6 yr following seed germination; Carter et al. 2021) means that broom can quickly overtop tree seedlings and saplings. Early maturity (2–3 yr of age) and large seed production (up to 26,000 seeds yr^{-1}; Bossard and Rejmanek 1994) produce a quick build-up of broom soil seed banks (as large as 28,000 viable seeds m^{-2} ground area; Downey 1988). In addition, mature plants often resprout from the base following cutting (as much as 90% of plants, less during drought periods; Bossard and Rejmanek 1994). Over time, ever-denser broom thickets occupy infested sites, suppressing the growth of tree seedlings and saplings.

Oregon white oak woodlands are a Priority Habitat in Washington State (Washington Department of Fish and Wildlife 2008). On JBLM, there are approximately 3,700 acres of Woodland/Savanna containing oak, and three stands are co-dominated by oak and pine (US Army 2017). Oak was present every Year on one Closed Forest plot and 4–6 Woodland/Savanna plots; 3–5 of the latter also had pine. Like pine, oak is shade-intolerant and has thick, fire-resistant bark on mature trees, which suffer low mortality from fires except those that are exceptionally hot (Anonymous 2007). Seedlings and saplings have thinner bark and are more likely to be killed by fire. However, fires also stimulate stump sprouting, which is the primary means of oak regeneration following fire (Anonymous 2007). Therefore, treatments designed to maintain pine on the JBLM landscape will also help maintain the oak component of JBLM's woodlands and savannas, provided that prescribed burns are low intensity, with protection from flames afforded to regenerating oak.

In Closed Forest, existing overstory pines, except for dominant Big Trees, will eventually be overtopped by Douglas-fir and die unless adjacent Douglas-fir stems are removed. This is now standard practice for JBLM timber sales, but with most Closed Forest overstory pines being in impact areas, it will be necessary to make special entries into these areas to girdle Douglas-fir competing with pine. Except in larger canopy gaps that may have pine regeneration, there will be no replacement of overstory pine, so pine will, over time, become a progressively smaller fraction of the overstory.

In Woodland/Savanna, many of the existing pole-size stems will eventually enter the overstory, but afterwards there will be a hiatus in overstory recruitment until more regeneration becomes established. To facilitate this, understory fuels (brush, woody fuels) must be progressively reduced by frequent (at least every 3-4 yr) prescribed burning, preceded by mechanical treatments (e.g., mowing/cutting of Scotch broom and other brush, precommercial thinning, slash chipping). These activities should be applied to most of the existing Woodland/Savanna, i.e., a substantially greater area than is currently treated. As a result, subsequent wildfires and prescribed fires will burn with lower intensity, allowing much of the pine regeneration to survive. In addition, natural regeneration of pine in Woodland/Savanna should be supplemented by planting seedlings grown from JBLM seed sources, timed to occur shortly after prescribed burns that create the mineral ash substrate that favors successful pine establishment. Because climate change may, in the future, reduce how well local ponderosa pine is adapted to its environment, JBLM's forest managers could also look into the possibility of using additional, currently available Westside seed from the Willamette Valley (e.g., Oregon Department of Forestry 2024), where summer temperatures are higher than at JBLM, for pine reforestation. In the long run, these actions should maintain substantial pine presence in Woodland/Savanna.

Pine still establishes as individual trees in JBLM's grasslands, and if these trees reach reproductive age, new pines may become established near them to form gradually expanding tree islands. Fire, however, can prevent this phenomenon. Therefore, protection of individual pines and pine clumps should be a priority during wildfires and prescribed burns in grasslands. With protection, deliberate establishment of pines on grasslands by planting pines becomes possible. These actions could increase the extent of pine occupancy, helping offset losses of pine occupancy in Closed Forest.

To summarize, maintenance of the JBLM pine population will require a substantial increase in the amount of ecological restoration, including actions to increase the frequency and decrease the intensity of fires compared to the present situation. It may take extra effort, but there is no inherent reason why this can't be accomplished within the limitations of JBLM's primary mission of military training.

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Conflict of Interest

The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Animal Care and Use

No permits or Animal Care Committee compliance were necessary.

Data Availability Statement

The datasets used in this study can be found in the Figshare repository (**link**)

Author Contributions

J.F. was responsible for all aspects of this research: conceptualization, methodology, resources, investigation, validation, formal analysis, curation, writing - original draft, visualization, project administration, and funding acquisition.

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Literature Cited

Agee, J. K., M. Finney, and R. de Gouvenain. 1990. Forest fire history of Desolation Peak, Washington. Canadian Journal of Forest Research 20:35-356. doi:10.1139/x90-05

Anonymous. 2007. *Quercus garryana*. Fire Effects Information System, US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory, MT. Available online at https://www.fs.usda.gov/database/feis/plants/tree/quegar/all.html#FIRE%20EFFECTS (accessed July 22, 2024).

Applequist**,** M. B. 1958. A simple pith locator for use with off-center increment cores. Journal of Forestry 52:141.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1-4/8. doi:10.18637/jss.v067.i01

BC Parks. 2023. Ross Lake Ecological Reserve. Ministry of Environment, Province of British Columbia, Victoria, Canada. Available online at https://nrs.objectstore.gov.bc.ca/kuwyyf/ross_lake_detailed_description_fda2869ae7.pdf (accessed 25 June 2023).

Bonnet, V. H., A. W. Schoettle, and W. D. Shepperd. 2005. Postfire environmental conditions influence the spatial pattern of regeneration for Pinus ponderosa. Canadian Journal of Forest Research 35:37–47. doi:10.1139/x04-157

Bossard, C. C., and M. Rejmanek. 1994. Herbivory, growth, seed production, and resprouting of an exotic invasive shrub, *Cytisus scoparius*. Biological Conservation 67:193-200. doi:10.1016/0006-3207(94)90609-2

Brooks, M. E., K. Kristensen, K. J. van Benthem, and A. Magnusson. 2017. Modeling zero-inflated count data with glmmTMB. The R Journal 9:378-400. doi:10.1101/132753

Burns, R. M., and B. H. Honkala (technical coordinators). 1990. Silvics of North America, Volume 1: Conifers. USDA Forest Service, Agriculture Handbook 654, Washington, DC.

Caccia, F. D., and C. L. Ballaré. 1998. Effects of tree cover, understory vegetation, and litter on regeneration of Douglas-fir (*Pseudotsuga menziesii*) in southwestern Argentina. Canadian Journal of Forest Research 28:683–692.

Carter, D. R., R.A. Slesak, T. B. Harrington, and A. W. D'Amato. 2021. Soil texture and other site-level factors differentially affect growth of Scotch broom (*Cytisus scoparius*) and Douglas-fir (*Pseudotsuga menziesii*) seedlings in the western Pacific Northwest. Canadian Journal of Forest Research 52:1-13. doi:10.1139/cjfr-2021-0011

Crawford, R. C., C. Chappell, B. Stephens, C. Soper, and D. Rolph. 1995. Inventory and mapping of endangered native ecosystems on Fort Lewis. The Nature Conservancy, Seattle, WA, and Washington Natural Heritage Program, Olympia.

Downey, P. O. 1988. Broom (*Cytisus scoparius* (L.) Link) and fire: management implications. *In* A. W. Sheppard and J. R. Hosking (editors), Broom Management. Cooperative Research Centre for Weed Management Systems, University of Adelaide, Australia. Pp. 178-183.

Fletcher, R. 2005. Willamette Valley ponderosa pine making a comeback. Northwest Woodlands 21(2):20-21.

Foster, J. R. 1997. Westside story: restoration of a ponderosa pine forest at Fort Lewis Military Reservation. *In* P. Dunn and K. Ewing (editors), Ecology and Conservation of the South Puget Sound Prairie Landscape. The Nature Conservancy, Seattle, WA. Pp. 217-229.

Foster, J.R. 2001. Statistical power in forest monitoring. Forest Ecology and Management 151:211-222. doi:10.1016/s0378-1127(01)00591-6

Foster, J. R., and S. E. Shaff. 2003. Forest colonization of Puget Lowland grasslands at Fort Lewis, Washington. Northwest Science 77:283–296.

Fryer, J. L. 2018. *Pinus ponderosa* var. *benthamiana*, *P. p.* var. *ponderosa*: ponderosa pine. *In* Fire Effects Information System, USDA Forest Service, Rocky Mountain Research Station, Missoula Fire Sciences Laboratory. Available online at https://www.fs.usda.gov/database/feis/plants/tree/pinponp/all.html (accessed 12 June 2023).

Gaston, K. J., and R. A. Fuller. 2009. The sizes of species' geographic ranges. Journal of Applied Ecology 46:1-9. doi:10.1111/j.1365-2664.2008.01596.x

Gove, J. H., and P. C. Van Deusen. 2011. On fixed-area plot sampling for downed coarse woody debris. Forestry 84:109-117. doi:10.1093/forestry/cpq049

Graham, T. G., and T. B. Jain. 2005. Ponderosa pine ecosystems. *In* Ritchie, M. W., D.A. Maguire, and A. Youngblood (Technical Coordinators), Proceedings of the Symposium on Ponderosa Pine: Issues, Trends, and Management, October 2004, Klamath Falls, OR. USDA Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-198, Albany, CA. Pp. 1–32.

Haase, S. M., 1986. Effect of prescribed burning on soil moisture and germination of southwestern ponderosa pine seed on basaltic soils. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Note RM-462, Fort Collins, CO. DOI:10.2737/rm-rn-462

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr, and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133-302. doi:10.2307/1311697

Hibbert, D. M. 1979. Pollen analysis of late-Quaternary sediments from two lakes in the southern Puget Lowland, Washington. M.S. Thesis, University of Washington, Seattle.

Hibbs, D. E., M. V. Wilson, and A. L. Bower. 2002. Ponderosa pine of the Willamette Valley, western Oregon. Northwest Science 76:80-84.

Huggins, E. 1898. Letter to Frank B. Cole, September 26, 1898. NBAG11, Edward Huggins Papers, Special Collections, University of Washington Library, Seattle.

Huggins, E. 1902. Letter to Frank B. Cole, February 15, 1902. NBAG11, Edward Huggins Papers, Special Collections, University of Washington Library, Seattle.

Iles, K. 2003. A Sampler of Inventory Topics: A Practical Discussion for Resource Samplers, Concentrating On Forest Inventory Techniques. Kim Iles & Associates, Ltd., Nanaimo, British Columbia, Canada.

Kirschner, K. 2008. Willamette Valley pine soil correlation study. Annual report of the Willamette Valley Ponderosa Pine Conservation Association, Portland, OR. Available online at https://www.westernforestry.org/wvppca/pre2008/soilcorrelationstudy.htm (accessed 2 June 2023).

Korb, J. E., P. J. Fornwalt, and C. S. Stevens-Ruman. 2019. What drives ponderosa pine regeneration following wildfire in the western United States? Forest Ecology and Management 454:117663. doi:10.1016/j.foreco.2019.117663

Krannitz, P. G., and T. E. Duralia. 2004. Cone and seed production in *Pinus ponderosa*: a review. Western North American Naturalist. 64:208-218.

Lenth, R.V., B. Bolker, P. Buerkner, I. Giné-Vázquez, M. Hervé, M. Jung, J. Love, F. Miguez, H. Riebl, and H. Singmann. 2023. Package emmeans: estimated marginal means, aka least-squares means. Available online at https://rdrr.io/cran/emmeans (accessed 15 March 2023).

Lepofsky, D., E. K. Hyerdahl, K. Lertzman, D. Schaepe, and B. Mierendorf. 2003. Historical meadow dynamics in southwest British Columbia: a multidisciplinary analysis. Conservation Ecology 73:5-22. doi:10.5751/es-00559-07035 doi:10.575/es-00559-07035

Lindsay, B., and C. Briggs. 2014. Soil survey of Joint Base Lewis-McChord Area, Washington, and parts of Pierce and Thurston Counties. USDA Natural Resources Conservation Service, Washington, DC.

Luke, S.G. 2016. Evaluating significance in linear mixed-effects models in R. Behavioral Research Methods 49:1494-1502. doi:10.3758/s13428-016-0809-y

Martin, T. G., B. A. Wintle, J. R. Rhodes, P. M. Kuhnert, S. A. Field, S. J. Low-Choy, A. J. Tyre, and H. P. Possingham. 2005. Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecology Letters 8:1235-1246. doi:10.1111/j.1461-0248.2005.00826.x

Mooney, K. A., Y. B. Linhart, and M. A. Snyder. 2011. Masting in ponderosa pine: comparisons of pollen and seed over space and time. Oecologia 165:651-661. doi:10.1107/s00942-010-1742-x

Mustard, J., and Harper, G., 1998. A summary of the available information on the height to diameter ratio. Unpublished report on file at Research, Innovation and Knowledge Management Branch, British Columbia Ministry of Forests and Range/Environment, Victoria, BC.

Oliver, C. D., and B. C. Larson. 1996. Forest Stand Dynamics, update edition. McGraw-Hill Book Company, New York.

Olson, H. 1947. The prairie that vanished. Seattle Daily Times, May 18, 1947.

Oregon Biodiversity Information Center. 2023. Geographic distribution of ponderosa pine in the Willamette Valley, Oregon. ArcMap GIS layer available from the Institute for Natural Resources, Portland State University, Portland, OR.

Oregon Department of Forestry. 2024. Oregon seed bank. J. E. Schroeder Seed Orchard, St. Paul, OR. Available online at https://www.oregon.gov/odf/Documents/workingforests/seed-bank-brochure.pdf (accessed 23 July 2024).

Oregon State University Extension Service. 2003. Establishing and Managing Ponderosa Pine in the Willamette Valley. EM8805, Corvallis.

Perdue, V. 1997. Land use and Fort Lewis. *In* P. Dunn and K. Ewing (editors), Ecology and Conservation of the South Puget Sound Prairie Landscape. The Nature Conservancy, Seattle, WA. Pp. 17-30.

Peter, D. H., and T. B. Harrington. 2014. Historical colonization of South Puget Sound prairies by Douglas-fir at Joint Base Lewis-McChord, Washington. Northwest Science 88:186–205. doi:10.3955/046.088.0303

Potter, K. M., V. D. Hipkins, M. F. Mahalovich, and R. E. Means. 2013. Mitochondrial DNA haplotype distribution patterns in *Pinus ponderosa* (Pinaceae): range-wide evolutionary history and implications for conservation. American Journal of Botany 100:1562-1579. doi:10.3732/ajb.1300039

Public Forestry Foundation. 1995. A Forest Management Strategy for the Fort Lewis Military Reservation, Washington. Public Forestry Foundation, Eugene, OR. On file at the Forestry Branch, Public Works, Joint Base Lewis-McChord, WA.

Punches, J. W., and K. J. Puettmann. 2018. Distribution of epicormic branches and foliage on Douglas-fir as influenced by adjacent canopy gaps. Canadian Journal of Forest Research doi:48:1320-1330.10.1139/cjfr-2018-071

Qiu, H., S. Liu, Y. Zhang , and L. Jianjun. 2021. Variation in height-diameter allometry of ponderosa pine along competition, climate, and species diversity gradients in the western

United States. Forest Ecology and Management doi:497:119477. 10.1016/ j.foreco.2021.119477

R Core Team (2021). R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org (accessed May 16, 2022).

Rehfeldt G. E., L. P. Leites, J. B. St Clair, B. C. Jaquish, C. Sáenz-Romero, J. López-Upton, and D. G. Joyce. 2014. Comparative genetic responses to climate in the varieties of *Pinus ponderosa* and *Pseudotsuga menziesii*: clines in growth potential. Forest Ecology and Management 324:138-146. doi:10.1016/j.foreco.204.02.041

St. Clair, B. 1999. Genetic variation in height growth of Willamette Valley ponderosa pine: results from four-year-old trees in the ODF Schroeder Seed Orchard. Willamette Valley Ponderosa Pine Conservation Association, Portland, OR. Available online at https://westernforestry.org/ wvppca/pre2008/geneticvariation.htm (accessed June 15, 2021).

Searle, S. R., F. M. Speed, and G. A. Milliken. 1980. Population marginal means in the linear model: an alternative to least squares means. The American Statistician 34:216-221. doi:10.2307/2684063

Sheppard, A. W., P. Hodge, Q. Paynter, and M. Rees M. 2002. Factors affecting invasion and persistence of broom *Cytisus scoparius* in Australia. Journal of Applied Ecology 39:721–734. doi:10.1046/j.1365-2664.2002.00750.x

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Canadian Journal of Forest Research 12:18-28. doi:10.1139/x82-003

Squillace, A. E., and R. R. Silen. 1962. Racial variation in ponderosa pine. Forest Science Monograph 2.

Storm, L., and D. Shebitz. 2006. Evaluating the purpose, extent, and ecological applications of indigenous burning practices in southwestern Washington. Ecological Restoration 24:256-268. doi:10.3368/er.24.4.256

Tilton, J. 1855. Plan of the Pugets Sound Agricultural Company's land claim at Nisqually Washington Territory. AR270B-3459, Washington State Archives, Olympia.

Ugolini, F. C., and A. I. Schlichte. 1973. The effect of Holocene environmental changes on selected Western Washington soils. Soil Science 116: 218–227. doi:10.1097/00010694-197.309000-00010

U.S. Army. 2017. Forest Management Plan, US Army, Joint Base Lewis-McChord, Washington. On file at Forestry Branch, Public Works, Joint Base Lewis-McChord, WA.

Van Pelt, R. 2008. Identifying Old Trees and Forests in Eastern Washington. Washington State Department of Natural Resources, Olympia, WA. Available online at https://www.dnr.wa.gov/publications/lm_hcp_eastside_oldgrowth_guide.pdf (accessed 18 May 2023).

Washington Department of Fish and Wildlife. 2023. Priority habitats and species list. Olympia, WA. Available online at https://wdfw.wa.gov/sites/default/files/publications/00165/wdfw00165.pdf (accessed July 23, 2024).

Welsh, A.H., R. B. Cunningham, C. F. Donnelly, and D. B. Lindenmayer. 1996. Modelling the abundance of rare species: statistical models for counts with extra zeros. Ecological Modelling 88:297–308. doi:10.1016/0304-3800(95)00113-1

Williams, C.G. 2010. Long-distance pine pollen still germinates after meso-scale dispersal. American Journal of Botany 97:846–855. doi:10.3732/ajb.0900255

Willyard, A., D. S. Gerhardt, K. Potter, V. Hipkins, P. Marquardt., M. F. Mahalovich, S. K. Langer, F. W. Telewski, B. Cooper, C. Douglas, K. Finch, H. H. Karamera, J. Lefler, P. Lea, and A.

Wofford. 2017. *Pinus ponderosa*: a checkered past obscured four species. American Journal of Botany 104:161–181. doi:10.3732/ajb.1600336

Wonn, H.T., and K. L. O'Hara. 2001. Height:diameter ratios and stability relationships for four Northern Rocky Mountain tree species. Western Journal of Applied Forestry 16:87-94. doi:10.1093/wjaf/162.85

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Figures

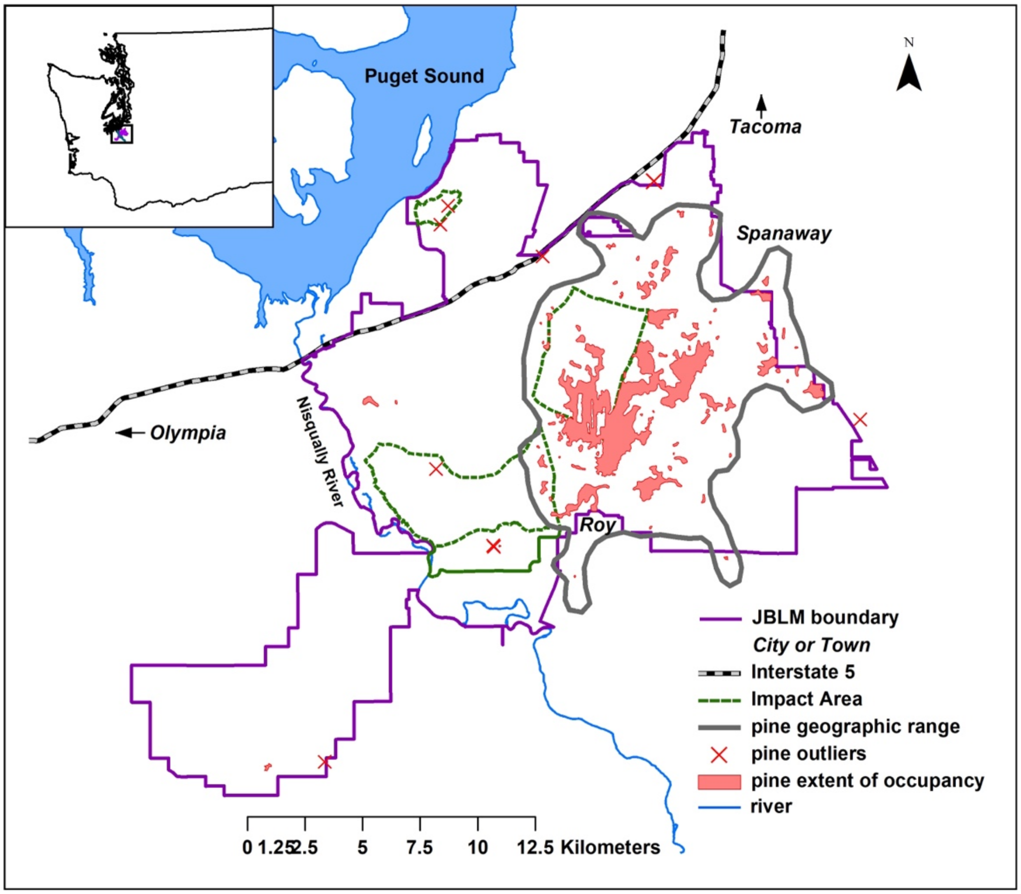

Figure 1. Map of Joint Base Lewis-McChord, WA, showing the geographic range and area of occupancy of native ponderosa pine. Pine occurrences are shown with polygons and Xs.

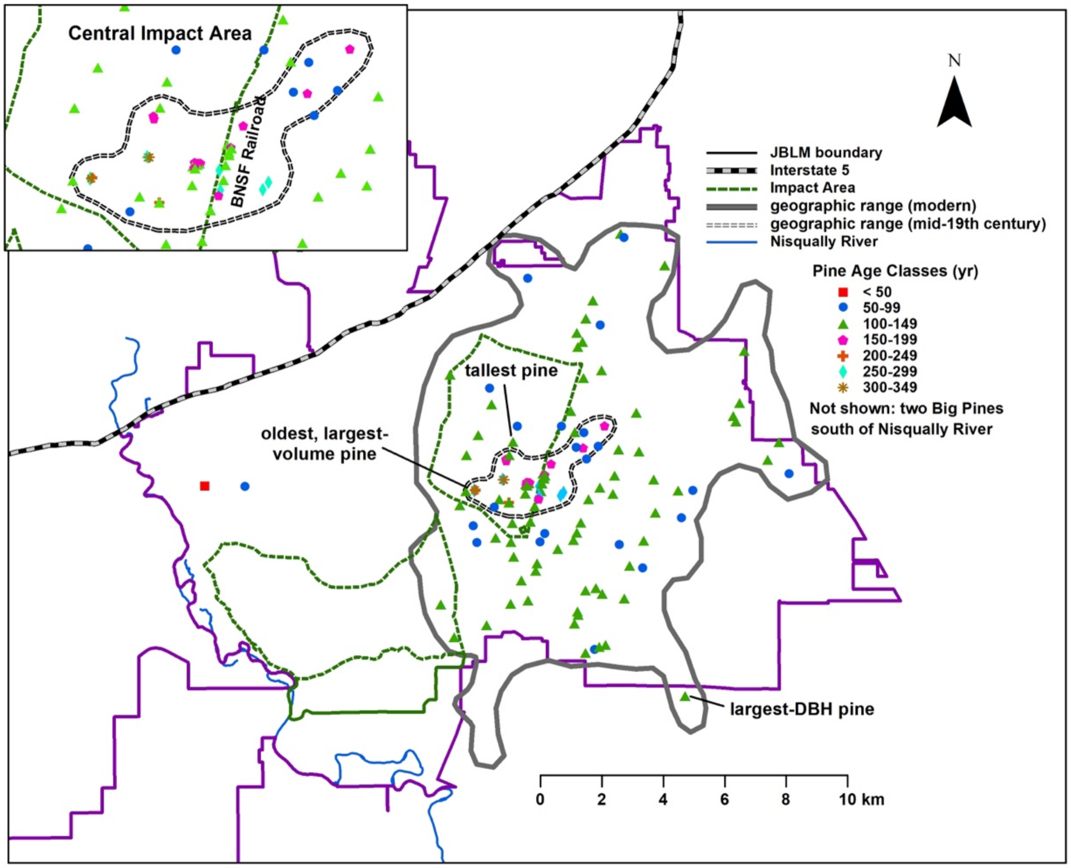

Figure 2. Map of Joint Base Lewis-McChord, WA, showing the locations and 2019 ages of the largest, oldest ponderosa pine trees within the JBLM geographic range. The inset is a magnified view of the core region of the range, with only trees ≥ 150 yr of age shown.

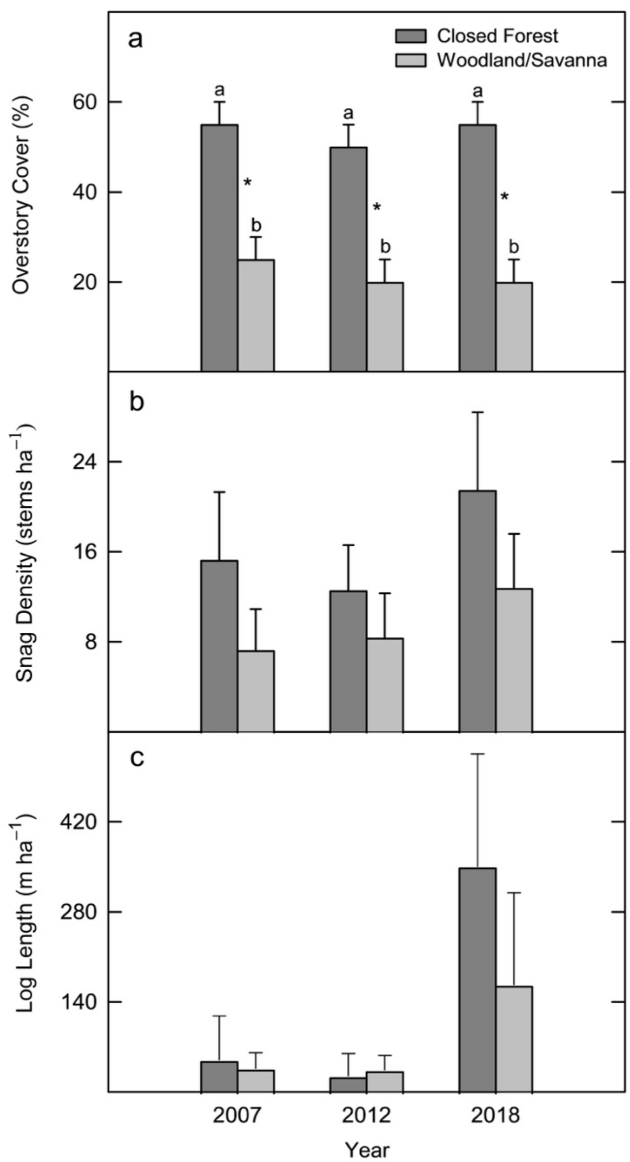

Figure 3. Mean overstory cover (a), snag density (b), and log length (c) ± 95% confidence intervals of Plot-level variables in relation to Year and Forest Type. Means are estimated marginal for overstory cover and observed for snag density and log length. Within each Forest Type, marginal means with the same letter above the error bars are not significantly different ($P > 0.05$), and between Forest Types in each Year, marginal means with an asterisk between them are significantly different, both based on linear mixed model contrasts. No valid model could be fit to the snag or log data.

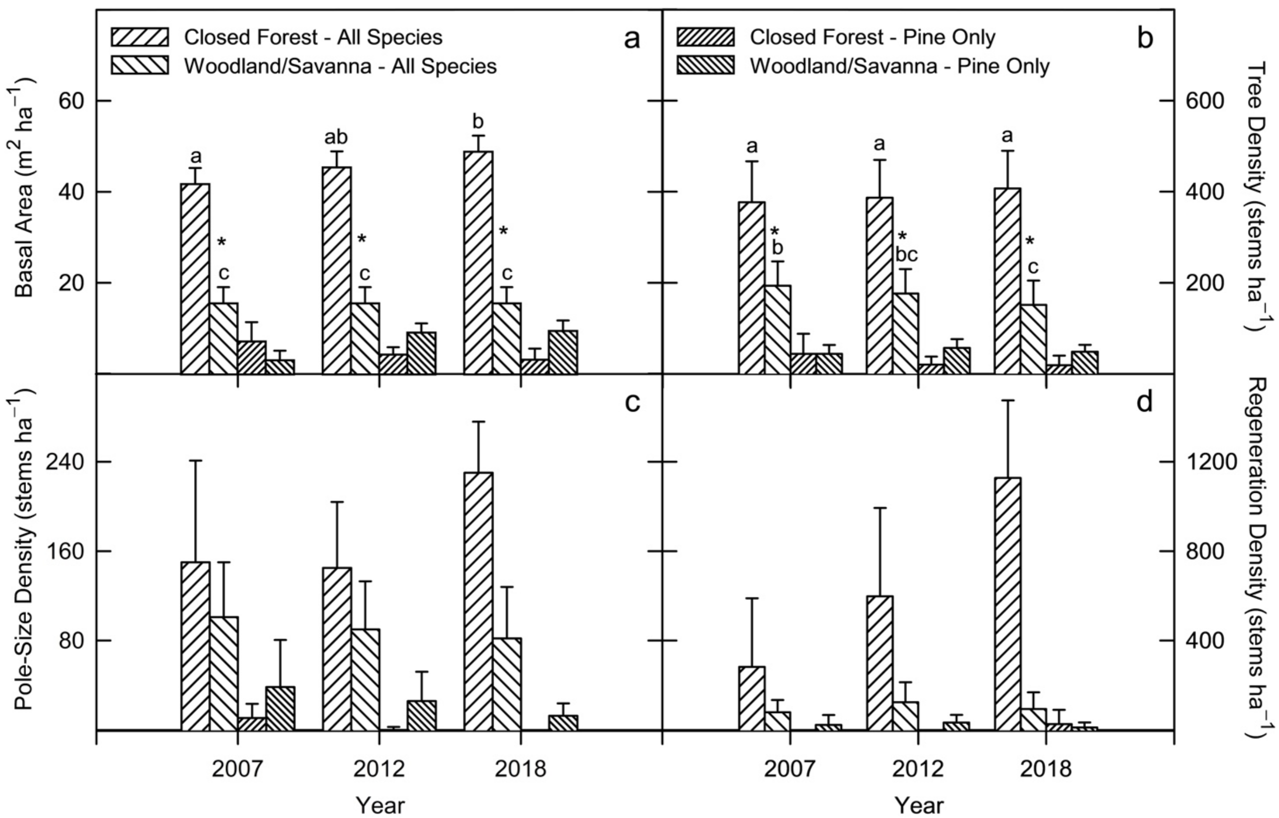

Figure 4. Mean basal area (a), tree density (b), pole-size density (c), and regeneration density (d) ± 95% confidence intervals of Species-level variables in relation to Year, Forest Type, and Species. Means are estimated marginal for basal area and tree density of All Species, and observed for all other variables. Within each Forest Type, marginal means with the same letter above the error bars are not significantly different ($P > 0.05$), and between Forest Types in each Year, marginal means with an asterisk between them are significantly different, both based on linear mixed model contrasts. No valid model could be fit to the data for the other variables.

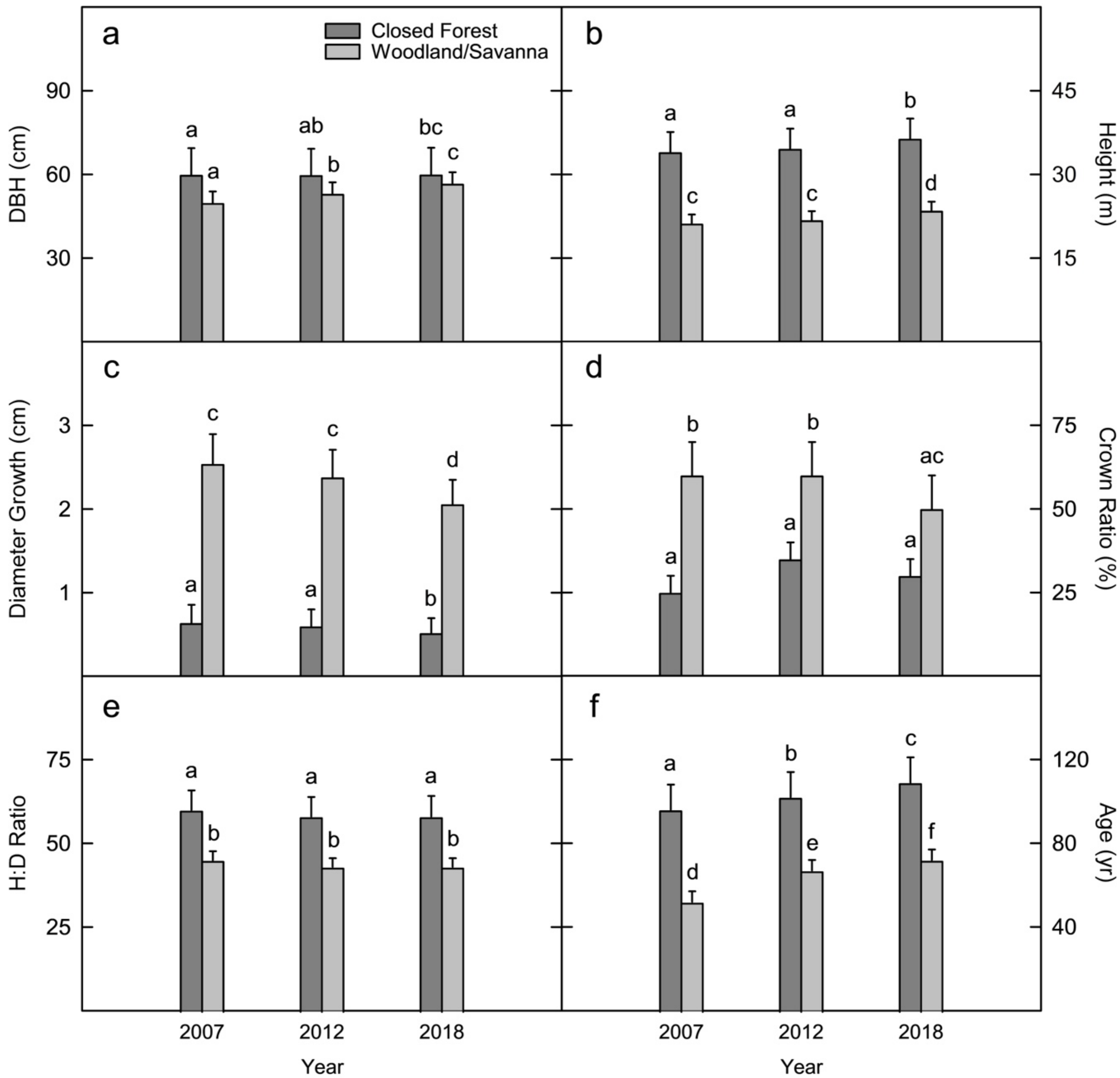

Figure 5. Estimated marginal means ± 95% confidence intervals for Average Pine DBH (a), height (b), diameter growth (c), crown ratio (d), H:D ratio (e), and age (f) in relation to Year and Forest Type. Within each Forest Type, marginal means with the same letter above the error bars are not significantly different ($P > 0.05$), and between Forest Types in each Year, marginal means with an asterisk between them are significantly different, both based on linear mixed model or generalized linear mixed model contrasts. Tree ages are for end of the growing seasons of 2006, 2011, and 2017.

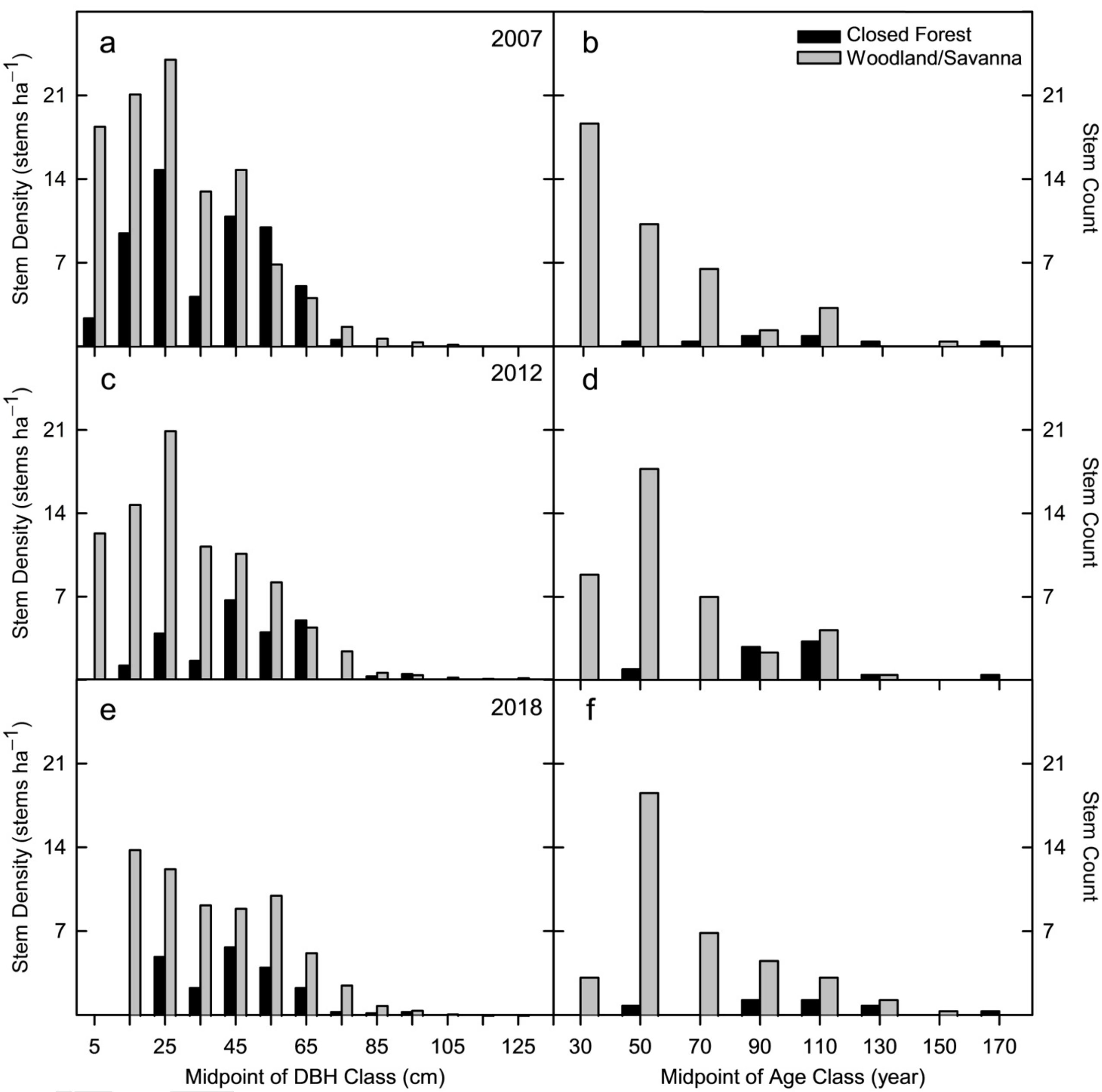

Figure 6. Diameter (DBH) distributions of pines on plots (a) and age distributions of Average Pines (b) in relation to Year and Forest Type. DBH classes are 10 cm wide, age classes are 20 yr wide.

TABLE 1. Big Pine (DBH ≥ 76 cm DBH) characteristics. Values are means ± 95% confidence interval (range). *n* = 125 for DBH, 124 for height, 78 for crown ratio, 124 for H:D ratio, and 120 for age.

DBH (cm)	Height (m)	Crown Ratio (%)	H:D Ratio	Age (yr)
104 ± 3 (79–161)	40.4 ± 1.1 (29–64)	60 ± 5 (15–95)	39 ± 1 (25–57)	137 ± 9 (59–334)

TABLE 2. Linear mixed model results for Plot-level, Species-level, and Average Pine variables whose final model residuals approximately met the normality and homogeneity of variance assumptions. Levels of Year: first sampling (2007–2008) = 1, second sampling (2012–2013) = 2, third sampling (2018–2019) =3. Levels of Forest Type: Closed Forest =1, Woodland/Savanna = 2. Coefficients are means ± 95% confidence intervals. df = degrees of freedom, *t* =*t*-value, *P* = probability that the coefficient differs from zero (α = 0.05), NS = not significant (*P* > 0.05).

Model Term	Coefficient	df	*t*	*P*
	Overstory Cover			
Intercept	8.56 ± 8.30	143	–2.020	0.016
Forest Type	–29.94 ± 6.08	145	12.240	<0.001
	All Species Basal Area			
Intercept	7.32 ± 9.67	239	–1.485	NS
Year	3.41 ± 2.28	257	–2.960	0.003
Forest Type	–22.87 ± 4.91	218	6.185	<0.001
Year x Forest Type	3.47 ± 1.78	258	3.826	<0.001
	All Species Tree Density			
Intercept	–69.2 ± 149.0	256	0.910	0.364
Year	54.65 ± 32.38	257	–2.865	0.005
Forest Type	–146.3 ± 112.3	277	2.533	0.011
Year x Forest Type	34.61 ± 29.11	258	2.331	0.021

	Average Pine DBH			
Intercept	32.56 ± 13.22	129	4.828	<0.001
Year	6.87 ± 1.74	187	7.730	<0.001
Forest Type	–13.51 ± 10.87	132	2.436	0.016
Year x Forest Type	3.41 ± 1.55	187	–4.326	<0.001
	Average Pine Height			
Intercept	6.94 ± 4.96	116	2.746	0.007
Year	1.19 ± 0.33	187	7.174	<0.001
Forest Type	–12.72 ± 4.02	113	6.204	<0.001
	Average Pine Crown Ratio			
Intercept	107.2 ± 16.9	298	12.403	<0.001
Year	–12.19 ± 6.78	203	–3.735	<0.001
Forest Type	40.06 ± 14.63	297	–5.367	<0.001
Year x Forest Type	7.71 ± 5.98	208	2.528	0.012
	Average Pine H:D Ratio			
Intercept	23.91 ± 6.97	113	6.724	<0.001
Forest Type	–19.00 ± 5.73	116	6.498	<0.001
	Average Pine Age			
Intercept	1.62 ± 16.05	110	0.198	0.84
Year	6.49 ± 0.81	186	15.724	<0.001
Forest Type	–43.66 ± 13.08	108	6.542	<0.001

TABLE 3. Generalized linear mixed model results for variables whose final model residuals did not meet the normality and homogeneity of variance assumptions. Levels of Year and Forest Type are the same as for Table 1. Coefficients are means ± 95% confidence intervals. *z* = Wald's z-score, *P* =probability that the coefficient differs from zero (α = 0.05).

Model Term	Coefficient	*z*	*P*
	Pine Tree Density		
Conditional Submodel			
Intercept	0.665 ± 0.021	61.03	<0.001
Year	–0.013 ± 0.0004	–57.65	<0.001
Zero Submodel			
Intercept	–0.112 ± 0.0223	–9.645	<0.001
	Average Pine Diameter Growth		
Conditional Submodel			
Intercept	0.473 ± 0.043	21.755	<0.001
Year	–0.010 ± 0.003	–7.035	<0.001
Forest Type	–0.138 ± 0.035	–7.635	<0.001