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Whitebark and Foxtail Pine in Yosemite, Sequoia, and Kings Canyon National Parks: Initial Assessment of Stand Structure and Condition

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Abstract: The Inventory & Monitoring Division of the U.S. National Park Service conducts long-term monitoring to provide park managers information on the status and trends in biological and environmental attributes including white pines. White pines are foundational species in many subalpine ecosystems and are currently experiencing population declines. Here we present results on the status of whitebark and foxtail pine in the southern Sierra Nevada of California, an area understudied relative to other parts of their ranges. We selected random plot locations in Yosemite, Sequoia, and Kings Canyon national parks using an equal probability spatially-balanced approach. Tree- and plot-level data were collected on forest structure, composition, demography, cone production, crown mortality, and incidence of white pine blister rust and mountain pine beetle. We measured 7899 whitebark pine, 1112 foxtail pine, and 6085 other trees from 2012–2017. All factors for both species were spatially highly variable. Whitebark pine occurred in nearly-pure krummholz stands at or near treeline and as a minor component of mixed species forests. Ovulate cones were observed on 25% of whitebark pine and 69% of foxtail pine. Whitebark pine seedlings were recorded in 58% of plots, and foxtail pine seedlings in only 21% of plots. Crown mortality (8% in whitebark, 6% in foxtail) was low and significantly higher in 2017 compared to previous years. Less than 1% of whitebark and zero foxtail pine were infected with white pine blister rust and <1% of whitebark and foxtail pine displayed symptoms of mountain pine beetle attack. High elevation white pines in the southern Sierra Nevada are healthy compared to other portions of their range where population declines are significant and well documented. However, increasing white pine blister rust and mountain pine beetle occurrence, coupled with climate change projections, portend future declines for these species, underscoring the need for broad-scale collaborative monitoring.

Keywords: *Cronartium ribicola*; *Dendroctonus ponderosae*; five-needle pine; foxtail pine; mountain pine beetle; *Pinus albicaulis*; *Pinus balfouriana*; white pine blister rust; whitebark pine

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1. Introduction

Forests across North America are experiencing rapid change driven by a combination of factors including outbreaks of native pests and pathogens, introduced exotic species, altered fire regimes, and rapid climate change [1–3]. Increasing temperatures, changes in precipitation regimes (timing, magnitude and type), and changing nutrient loads (carbon dioxide, nitrogen, phosphorus) are all significant drivers of ecosystem change in forest ecosystems [4]. Each factor alone can alter forest structure, function, and species composition. Additive or synergistic effects among stressors can lead to abrupt or rapid change and are likely if multiple agents act jointly [5,6]. The changes to forest structure, composition and function in the coming century will likely be unprecedented and have significant consequences for regional and global biodiversity, carbon dynamics, and species distributions [7]. Broad-scale changes such as increased tree mortality rates over the last several decades have already been documented across a large range of latitude and forest types in western North America [8], which may have important consequences for forest stand dynamics and ecosystem functions [9].

Five-needle white pines (Family Pinaceae, Genus *Pinus*, Subgenus *Strobus*), and in particular whitebark pine (*Pinus albicaulis* Engelm.) and foxtail pine (*P. balfouriana* ssp. *austrina* R.J. Mastrog & J.D. Mastrog) are foundational species [10] in upper subalpine and treeline forests of several National Park Service (NPS) Pacific West Region (PWR) parks, including Sequoia and Kings Canyon National Parks (SEKI) and Yosemite National Park (YOSE) (Figure 1). Declines in foundation tree species are a particularly pernicious threat to regional and global biodiversity because trees provide fundamental structure to ecosystems that is not replicated by other organisms [11]. If a foundation tree species is lost from these systems, it can precipitate cascading shifts in biological diversity, ecosystem function and services, and community stability [12].

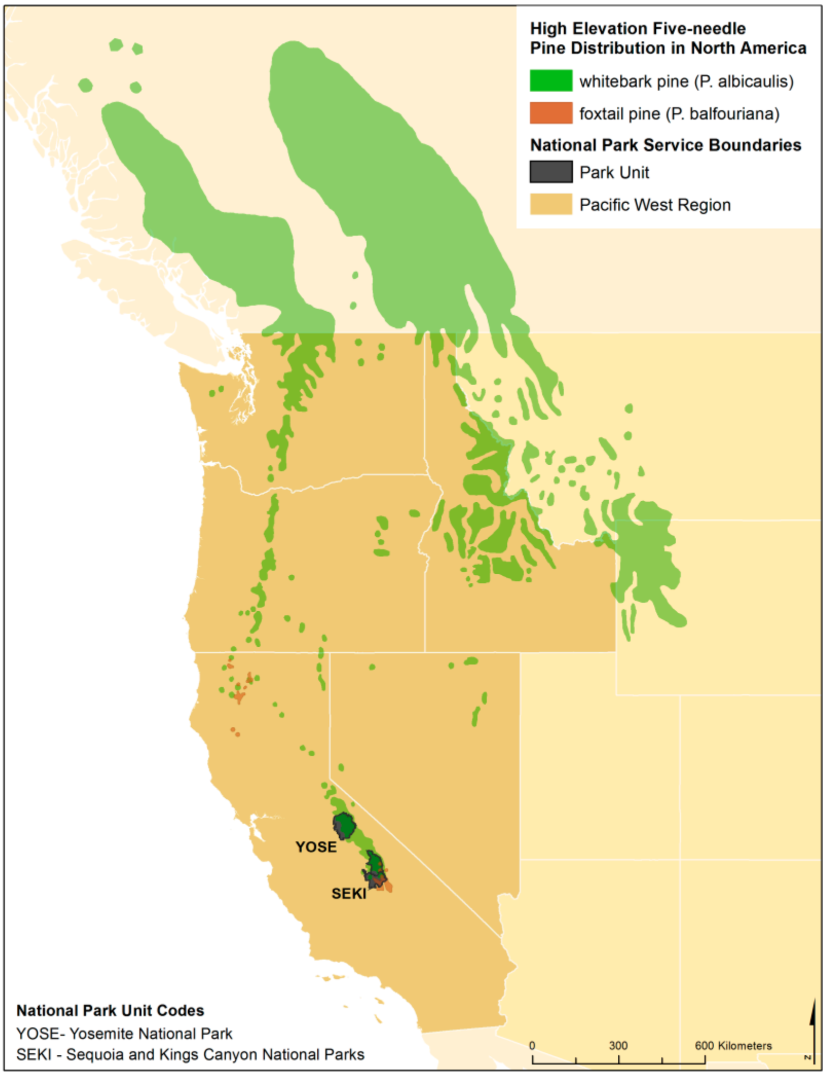

Figure 1. Distribution of whitebark pine and foxtail pine in North America and location of Yosemite, Sequoia, and Kings Canyon National Parks in the Sierra Nevada, California, USA.

High elevation white pines are experiencing declines due to multiple interacting factors including the introduced exotic pathogen *Cronartium ribicola* J.C. Fisch., which causes white pine blister rust, mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks, altered fire regimes, and a rapidly changing climate [13]. Declines of whitebark pine in particular have been so severe that it has been listed as endangered under the Canadian Species at Risk Act [14] and as a candidate species for protection under the U.S. Endangered Species Act [15]. However, these declines have been less severe in the Sierra Nevada [16]. Because high elevation white pines are assumed to be in relatively good condition in the southern Sierra Nevada when compared to other regions within North America, this area has received relatively little attention in terms of research and monitoring. Our study attempts to fill this significant knowledge gap by reporting on the current status of two high elevation white pine species in the southern extent of their range. These populations are of particular importance due to their likely vulnerability to climate change given potential climate-induced range shifts or tipping points at range limits [17]. Also, their potential genetic adaptation to a drier, more Mediterranean climate could serve as an important source for long-distance gene flow to more northern populations under warmer future conditions [18].

1.1. Whitebark Pine

Whitebark pine is a foundation species in high-elevation forests due to its role in shaping community structure, species composition, and regional biodiversity [11,19]. Whitebark pines regulate important ecological processes in high elevation ecosystems, including snowmelt delay, community development following fire, soil erosion abatement, facilitation of the establishment of less hardy species, and food for a variety of sensitive wildlife species including grizzly bears (*Ursus arctos* Linnaeus) and Clarks nutcracker (*Nucifraga columbiana* Wilson) [20,21]. Whitebark pine is a coevolved mutualist with Clark's nutcracker, and is dependent upon nutcrackers for dispersal of its seeds [22,23]. Whitebark pine can be found in subalpine forests and at treeline across western North America, including the southern Sierra Nevada mountains in California, USA where is reaches its southern distribution limit [24,25]. It often occurs as the only tree species on the coldest and driest sites near treeline (Figure 2) or in mixed species stands on protected, lower elevation sites more favorable to its shade-tolerant competitors [26]. In the PWR, whitebark pine is scattered across tens of thousands of hectares (Figure 1), including the high elevations of SEKI and YOSE.

Figure 2. Whitebark pine near Kuna Crest, Yosemite National Park, CA, USA. Photo taken by Sierra Nevada Network forest monitoring crew, 2017.

In the Sierra Nevada, two main threats to high elevation white pines are White pine blister rust (WPBR) and mountain pine beetles (MPB). WPBR was first introduced to western North America in 1910 in British Columbia and has since spread throughout the range of most white pines [10]. Its prevalence on whitebark pine decreases from north to south in the PWR, resembling the trend seen in the Rocky Mountains [27]. WPBR has been relatively rare in high elevation forests in the southern Sierra Nevada when compared to northern portions of the PWR (e.g., North Cascades) [28]. MPB have been abundant in the northern Cascades, but the extent and severity of recent outbreaks have also decreased with latitude [29]. In the Sierra Nevada MPB activity appears to be driven largely by drought events [16,30], which may become more frequent and severe with warming temperature [31].

1.2. Foxtail Pine

Foxtail pine is endemic to two distinct areas in California: the Klamath Mountains in the northwest part of the state and the southern Sierra Nevada [32] (Figure 1). There has been considerably less research on foxtail pine populations compared to whitebark pine. However, the southern population of foxtail pine (subspecies *austrina*) has provided important data used in dendrochronological research focused on paleoclimate [33] due to is remarkable lifespan (>3000 years) and slow growth [34]. Foxtail pine often occurs in single species stands, but it is also commonly associated with whitebark pine, red fir (*Abies magnifica* A. Murray bis var. *magnifica*), and western white pine (*P. monticola* Douglas ex D. Don) [35]. Foxtail and whitebark pine overlap in some portions of their southern Sierra Nevada distribution. However, south of the Kings-Kern divide, which separates the Kings River basin to the north from the Kern River basin to the south (36.7° N latitude), foxtail pine is the major (sometimes exclusive) subalpine and treeline tree species (Figure 3). Foxtail pine provides important habitat and food resources for birds and mammals, and influences snow melt and soil erosion. Recent impacts of WPBR and MPB on foxtail pine in the southern Sierra Nevada have been minimal [28].

Figure 3. Foxtail pine near Rock Creek ranger station, Sequoia National Park, CA, USA. Photo taken by Jenny Cribbs (NPS), 2017.

1.3. Objectives

Several NPS parks the PWR identified white pine species as targets for long-term monitoring [36–38]. NPS scientists collaborated to devise a common set of monitoring objectives and procedures which are documented in a shared white pine monitoring protocol [39]. Fieldwork was initiated in 2011 and summaries of annual monitoring results are available from the Sierra Nevada Network website [40]. The anticipated impacts from WPBR, MPB, and climate change on high-elevation pines were primary factors considered for monitoring. Key demographic parameters within white pine forest communities are also estimated by monitoring individual trees within permanent plots. Specific objectives as outlined in McKinney et al. [39] are to quantify the status and trend in:

- Trees species composition and structure
- Tree species birth, death, and growth rates
- Incidence of white pine blister rust and level of crown mortality
- Incidence of bark beetles
- Cone production of white pine species

Information gathered from this monitoring project will be integral to providing a more comprehensive understanding of high elevation white pine populations within PWR parks, as well as allowing for comparisons across broader geographic areas. It will also allow early detection of important changes in populations that may precipitate management intervention. This paper describes the current status of whitebark pine and foxtail pine within YOSE and SEKI based on survey data collected from a newly established permanent plot network. It is the first comprehensive status report that documents the current stand structure and condition of whitebark and foxtail pine forests within these parks.

2. Materials and Methods

2.1. Plot Establishment

This study was conducted in YOSE and SEKI and data from 2012 through 2017 were analyzed for this paper. Sampling methods are described in great detail in McKinney et al. [39] and the following text has been adapted from the descriptions in that protocol. The sample frames for each species-park population (SEKI-whitebark pine, SEKI-foxtail pine, and YOSE-whitebark pine) were based on the distribution of whitebark and foxtail pine as identified in the YOSE and SEKI vegetation maps [41] (Figures 4–6). The whitebark pine sample frame in YOSE covered 30,820 ha (10% of the total park area), while the whitebark pine sample frame from SEKI occupied 26,867 ha (7.7% of the total park area) and the foxtail pine sample frame in SEKI occupied 27,654 ha (7.9% of the total park area). There was a 3598 ha (7.1% of the combined distribution) overlap of the foxtail pine and whitebark pine sample frames in SEKI, primarily in the northeastern area of Sequoia National Park where the two species co-occur.

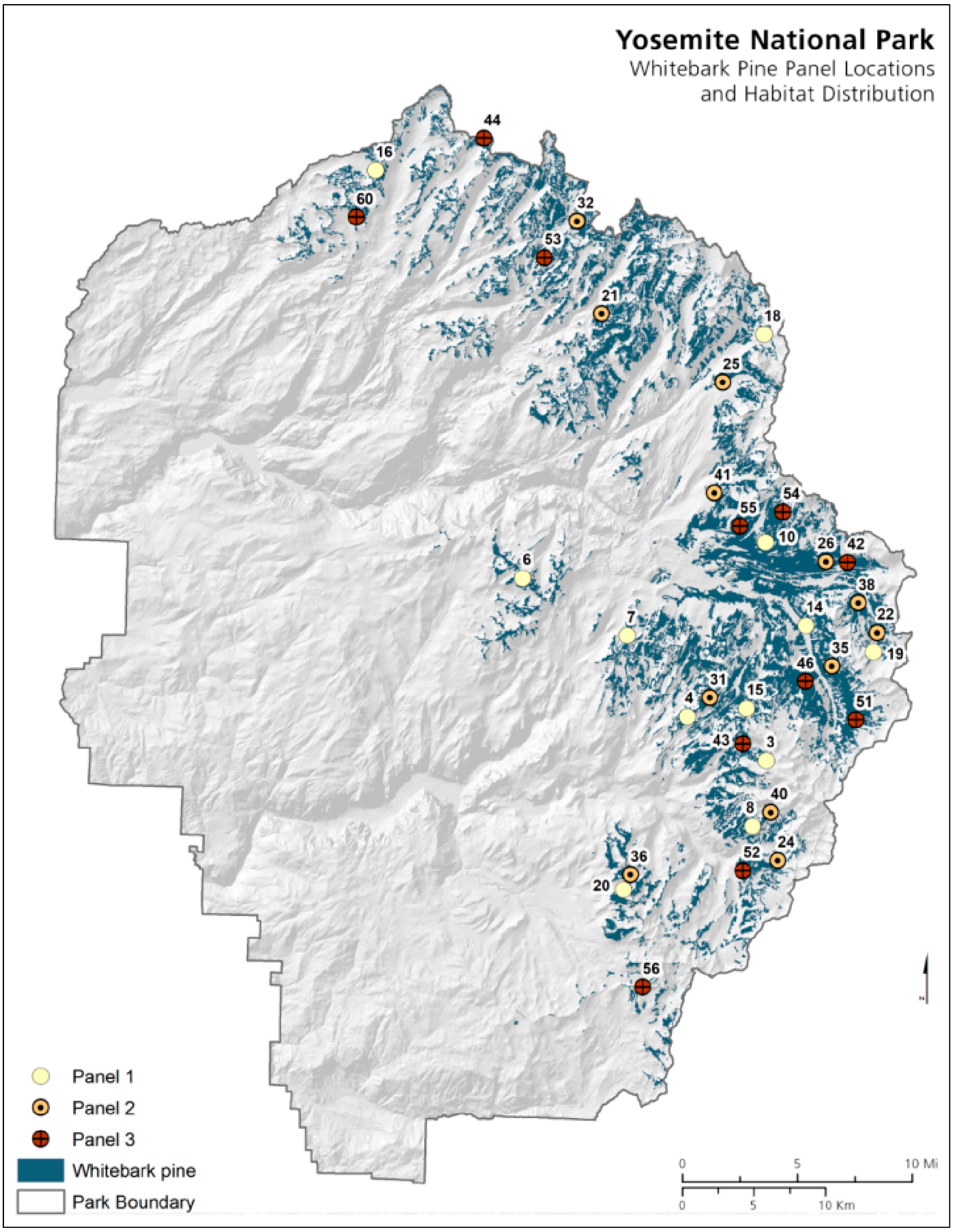

Figure 4. Whitebark pine distribution and plot locations in Yosemite National Park, CA, USA. Plots are assigned to one of three panels (12 plots each) and are sampled using a rotating re-visit design. Thirty-five of the planned 36 plots had been installed at time of publication.

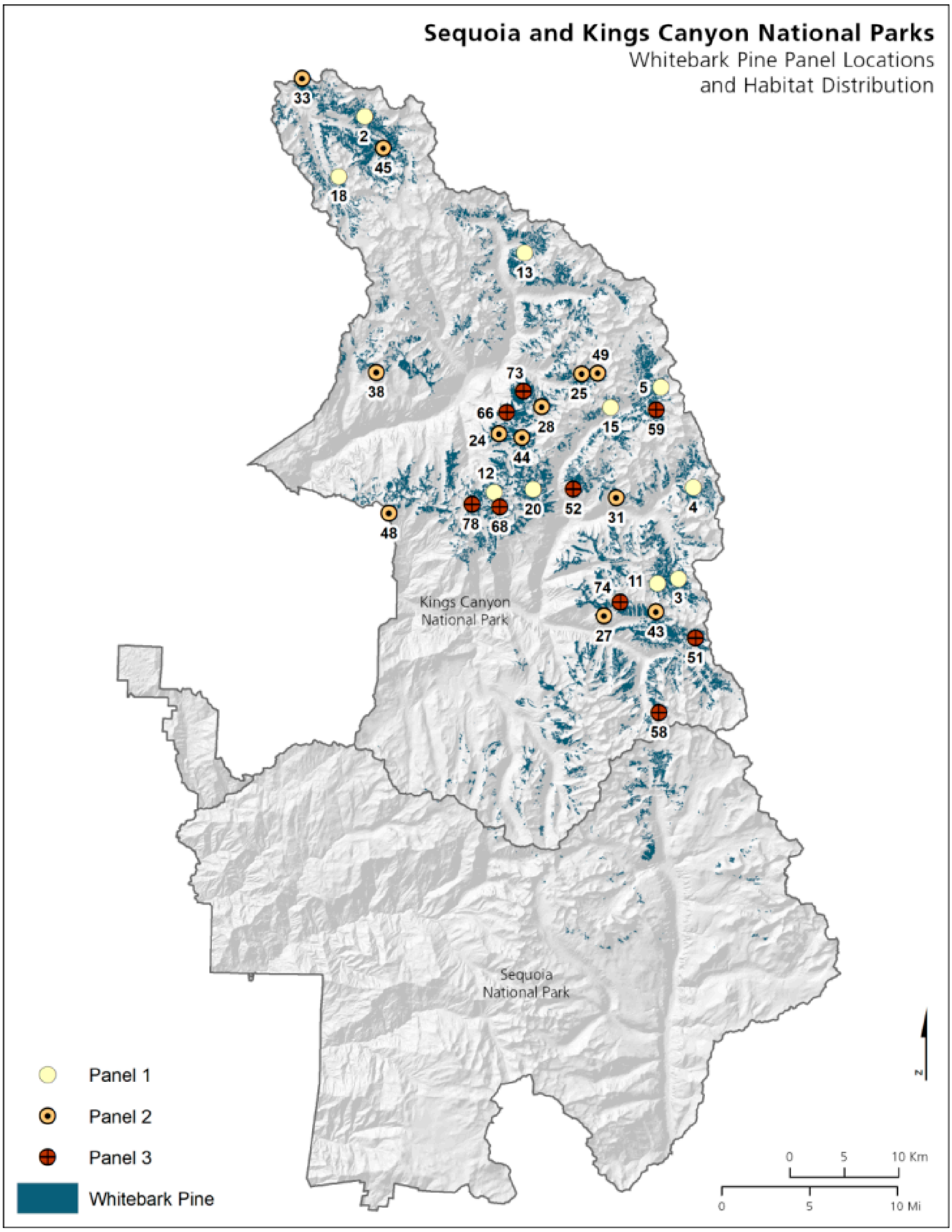

Figure 5. Whitebark pine distribution and plot locations in Sequoia and Kings Canyon National Parks, CA, USA. Plots are assigned to one of three panels (12 plots each) and are sampled using a rotating re-visit design. Thirty-one of the planned 36 plots had been installed at time of publication.

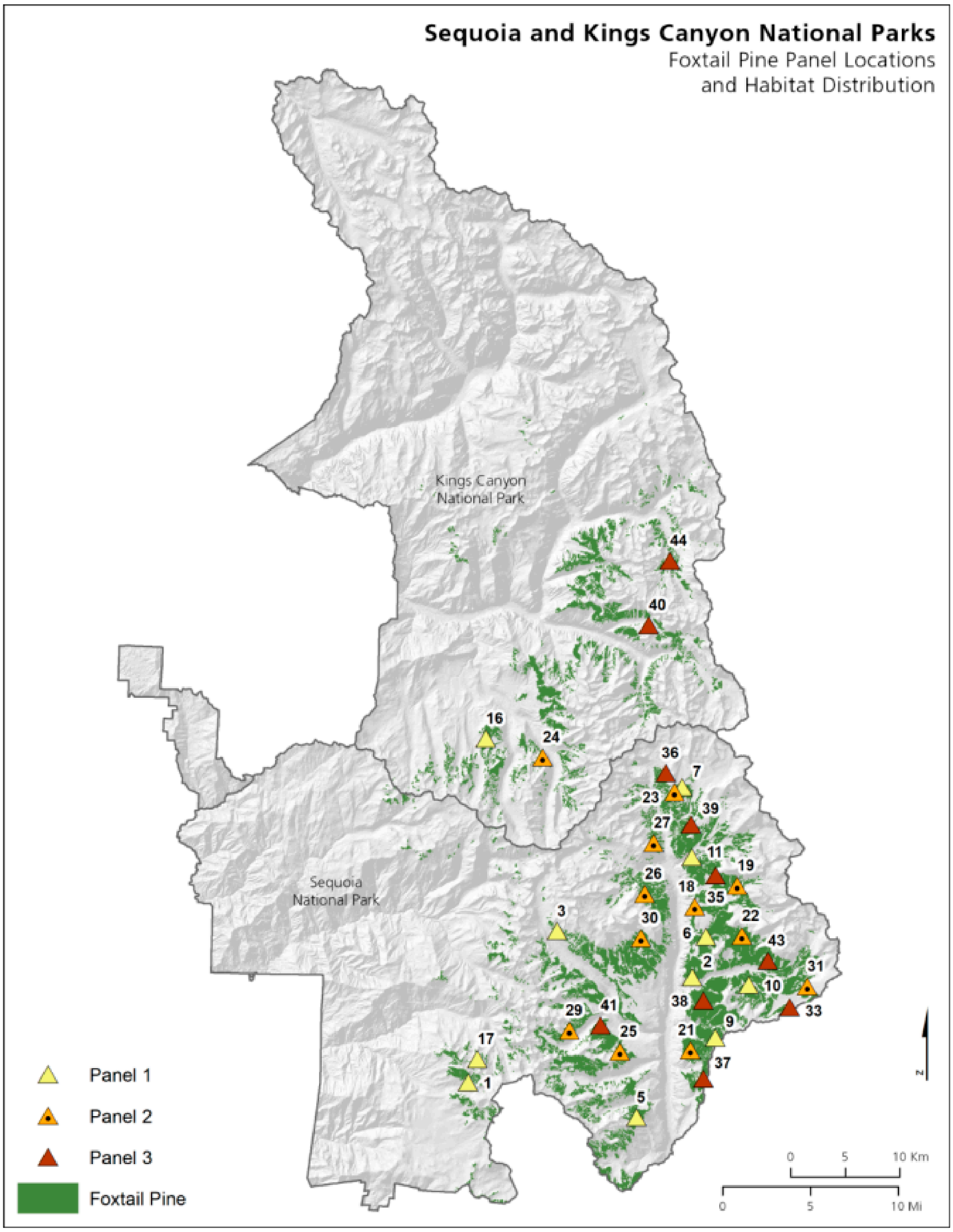

Figure 6. Foxtail pine distribution and plot locations in Sequoia and Kings Canyon National Parks, CA, USA. Plots are assigned to one of three panels (12 plots each) and are sampled using a rotating re-visit design. Thirty-three of the planned 36 plots had been installed at time of publication.

We used a geographic information system (GIS) to generate all sampling points using a Generalized Random Tessellated Stratified (GRTS) algorithm [42], including a selection of oversampling points in case potential sites did not meet the sampling criteria or safety constraints. A GRTS design produces a spatially balanced, probabilistic sample well suited for monitoring natural resources that occur over large areas [43]. Plots in the ordered list were assigned to one of three panels. A panel refers to a group of sample units that are measured on the same occasion (during the same field season in this case). Each panel is sampled on a rotating basis once every three years and plot level data are provided in the Supplementary Materials (Tables S1–S3). Based on this sampling design, our scope of inference extends broadly across mapped stands of whitebark and foxtail pine on <35-degree slopes within YOSE and SEKI. Through the 2017 field season, 99 of the planned 108 long-term monitoring plots have been established; 35 are located in YOSE (Figure 4) and 64 in SEKI. All of the plots in YOSE are in the whitebark pine sample frame, while the plots in SEKI are split between the whitebark (Figure 5) and foxtail pine (Figure 6) sample frames with 31 and 33 plots in each, respectively.

2.2. Plot Layout

Plot design is described in McKinney et al. [39] in detail and a summary is provided below. Quarter hectare (50 × 50 m) macroplots consisting of five subplots are used to measure and track forest demographic parameters, disease, and insect occurrence, and the magnitude of their impact (Figure 7). The response design is compatible with the *Interagency Whitebark Pine Monitoring Protocol for the Greater Yellowstone Ecosystem* (GYWPMWG) [44] but differs in some respects; most notably, plot size. The 10 × 50 m plot size from the Yellowstone protocol has been increased to accommodate the often sparse or patchy distribution of white pines in our PWR parks and to adequately address forest demographic objectives. This design effectively represents five parallel 10 × 50 m subplots as used in the GYWPMWG and as proposed by the Whitebark Pine Ecosystem Foundation [45].

A total of nine square regeneration plots (3 × 3 m) were established within each macroplot to measure seedling regeneration (Figure 7). Regeneration plots are located at each corner, at each midpoint between corners, and in the middle of the macroplot.

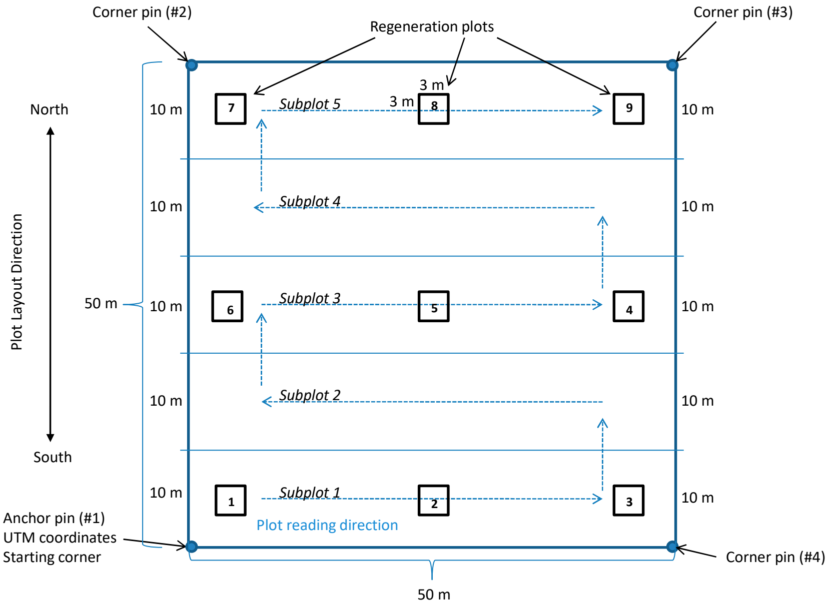

Figure 7. 50 × 50 m permanent plot layout. Smaller 3 × 3 m regeneration plots (numbered one through nine) are where seedlings are measured (Figure from McKinney et al. [39]).

2.3. Tree Measurements

Within each plot, each live tree taller than a vertical distance of 1.37 m from its base was affixed with a uniquely numbered metal tag; its species identified, and diameter at 1.37 m (breast height, DBH) and tree height measured. Standing dead trees ≥5 cm DBH and ≥1.37 m height were also affixed with a metal tag and recorded as either recently dead or dead. Recently dead trees have needles present (but no green needles) and dead trees have no needles present. For plots that were re-measured, recently dead trees were defined as those that were alive during the previous visit but were dead at the time of the re-survey and dead trees were those that were already dead. Trees that were recorded as dead and down in re-measured plots (n = 2) were excluded from the analysis, as were missing trees that were alive during the previous visit ($n = 3$). WPBR infection was assessed for all living white pine trees. The bole and branches of white pine trees were each vertically divided into thirds (upper, middle, and bottom) and each third assigned to one of three rust condition classes: (1) absent–no sign of rust infection, (2) aeciospores present, or (3) no aeciospores, but presence of at least three of the following five indicators of infection: rodent chewing, flagging, swelling, roughened bark, and oozing sap. If either aeciospores or at least three symptoms of WPBR were observed, the tree was considered to be infected. MPB occurrence was recorded for all pine trees (live and dead) using three indicators of beetle activity: pitch tubes, frass, and J-shaped galleries, which are characteristic of MPB in the Sierra Nevada. The presence of galleries was only determined for dead trees because bark needs to be removed for this assessment (unless bark is already missing and galleries can be observed on the live tree). The level of canopy kill in live trees was determined by dividing the tree's canopy (all the main branches, encompassing all foliage and supporting twigs and side branches) into thirds and recording an ocular estimate of the percentage of each third of the canopy that was dead. Cone production was recorded based on whether female cones were present or absent on each live whitebark or foxtail pine tree. Live seedlings were counted by species and assigned to a height class in regeneration plots. Height classes were: (1) 20 to <50 cm, (2) 50 to <100 cm, and (3) 100 to <137 cm. Seedlings <20 cm were not measured.

2.4. Data Analysis

Summary statistics for each sample frame related to stand health and structure were calculated. These included average DBH, height, basal area, crown mortality, WPBR infection, MPB activity, and cone production by species. For three plots in the SEKI whitebark sample frame, we did not sample all five 10 × 50 m subplots in the first year of sampling. In these plots, we completed the sampling for any subplot not sampled during the first sample year in a subsequent sampling period. In these cases, we adjusted plot area to reflect the actual area sampled for any area-dependent calculations, such as stems or basal area per ha. We removed all trees with missing DBH records ($n = 29$) or where DBH was recorded as zero ($n = 126$) due to factors like becoming pinned or leaning from any analyses requiring diameter measurements.

We performed separate analyses to estimate the effects of both tree- and site-level factors on both ovulate cone production and the average proportion of tree-level crown mortality. We included plot-level elevation, universal transverse mercator coordinate system (UTM) easting for the southwest plot corner, target species basal area, non-target species basal area, and tree-level DBH for both analyses. The basal area of both target and non-target species was included to characterize interspecific and intraspecific competition and/or facilitation. Tree level metrics, such as DBH and average crown mortality (included in the cone production analysis only) were included due to previously demonstrated relationships with mortality [46] and cone production [27]. Sample year was also included as a categorical variable in the cone production models, but if its inclusion did not improve model fit ($\Delta\text{AIC} < 2$) it was not retained in the final model. This was done to investigate the occurrence of mast seed years during the sampling period. Because MPB activity and WPBR infection were so rare, neither metric was analyzed to examine potential associations with tree- or site-level factors.

We used generalized linear mixed effects models (GLMMs) to estimate the effects of tree- and stand-level factors on ovulate cone production and the average proportion of crown mortality in live trees. The presence or absence of ovulate cones is a binary variable (i.e., 0 or 1), so we used logistic GLMMs with a logit link function (lme4 package version 1.1-13 [47]) in R version 3.5.1 [48]. We used beta regression to model average crown mortality, which was the average of the crown mortality measurements for each tree, converted to a proportion ranging between 0 and 1 (glmmADMB package version 0.8.5 [49]). Beta regression requires that proportions are never exactly 0 or 1, so we transformed the proportions using procedures outlined in Smithson and Verkuilen [50], which constrained the values between 0 and 1.

When possible, we estimated marginal and conditional r^2 values for each model, which is the variance explained by the fixed effects (marginal r^2) and both fixed and random effects combined (conditional r^2, piecewiseSEM package [51,52]). We specified plot as the random effect in all GLMMs, while all other variables were treated as fixed effects. We used the equation

$$1-\frac{\text{residual deviance}}{\text{null deviance}}$$

to estimate a pseudo r^2 for plot-level GLMMs that describes their explained variation relative to the full model [53].

3. Results

3.1. Yosemite National Park

Whitebark Pine

Due to the increasing west to east elevation gradient in YOSE, most of the plots are located in the eastern half of the park, where the elevation is high enough for suitable whitebark pine habitat (Figure 4). On average, the plots in YOSE had the lowest elevation and slope values of the three sample frames, with a mean elevation of 3091 m (standard deviation [sd] = 161 m) and average slope of 15° (sd = 6). The plots were distributed across all aspects, though a slight majority (54%) was located on southwest aspects, between 170 and 270°.

We recorded 7866 live trees across 35 plots in YOSE, including 3772 (48%) whitebark pine, 2898 (37%) lodgepole pine (*Pinus contorta* ssp. *murrayana* (Grev. & Balf.) Critchf.), 1162 (15%) mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière), 31 western juniper (*Juniperus occidentalis* Hook.), two Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and one red fir; the latter three species made up <1% of total stems combined. We recorded an additional 181 snags in the plots, 27 of which were whitebark pine (15%). Sixty-four percent of the standing dead trees (snags) were lodgepole pine (n = 115), while 22 (12%) were mountain hemlock. The remaining 17 snags (9%) could not be identified to species. Twenty-two of the snags (12%) appeared to be recently dead and still had brown needles present. A cause of death was assigned to 19 of the 181 snags (10%). Ten trees appeared to have died from physical damage and included trees with broken stems or trees that were uprooted or crushed. Other mortality agents were rare, such as bark beetle attack (six trees), diseases other than WPBR (two trees), and competition (one tree), and only accounted for nine of the snags. Mortality was not attributed to WPBR for any of the snags.

Live whitebark pine DBH ranged from 0.1–78.3 cm with a plot level average of 7.9 cm (Table 1). Though whitebark pine was the most common species in our study plots, lodgepole pine were larger on average and had an average DBH of 14.5 cm. Thus, they had the highest live basal area at 18.3 m^2/ha (Table 1). In comparison, whitebark pine had an average live basal area of 3.7 m^2/ha, and mostly consisted of trees less than ten cm DBH (Figure 8). Mountain hemlock had the lowest basal area of the commonly found species in the sample frame with an average basal area of 2.8 m^2/ha. In 12 of the 35 plots (34%) the primary growth form of whitebark pine was krummholz with >90% of trees in these plots adopting this form.

Table 1. Summary statistics of whitebark pine plots measured at Yosemite National Park, CA, USA (n = 35). Seedlings were not sampled in one plot, reducing the sample size to 34. DBH = diameter at 1.37 m, WPBR = white pine blister rust, MPB = mountain pine beetle, sd = standard deviation.

Tree Density (trees/ha)	Mean (sd)	Range
P. contorta density	331 (450)	0–1760
T. mertensiana density	133 (338)	0–1376
Other species density	4 (22)	0–132
Snag density	21 (25)	0–100

Table 1. *Cont.*

Tree Density (trees/ha)	Mean (sd)	Range
Tree DBH (cm)		
P. albicaulis	7.9 (5.2)	1.6–29.7
P. contorta	14.5 (9.6)	1.7–34.6
T. mertensiana	10.7 (4.2)	1.7–15.4
Other species	21.6 (12.0)	13.1–30.1
Snags	24.8 (14.3)	0.9–56.2
Tree basal area (m^2/ha)		
P. albicaulis	3.7 (5.1)	<0.1–19.0
P. contorta	18.3 (24.3)	0–76.9
T. mertensiana	2.8 (7.3)	0–32.7
Other species	0.8 (4.8)	0–28.1
Snags	1.7 (2.9)	0–14.7
Seedling regeneration 20–136 cm (seedlings/ha)		
P. albicaulis	853 (2434)	0–13,210
Other species	320 (519)	0–1605
Incidence of stressors		
P. albicaulis crown mortality (%)	8.2 (9.0)	0.7–43.3
P. albicaulis WPBR infection rate (# of infected trees/ha)	1.4 (8.1)	0–48
WPBR occurrence rate (% of infected *P. albicaulis*/plot)	0.1 (0.8)	0–4.8
MPB infestation rate (# of infested trees/ha)	1.0 (2.4)	0–12
P. albicaulis MPB infestation rate (# of infested *P. albicaulis*/ha)	0.2 (0.9)	0–4
P. albicaulis MPB occurrence rate (% of attacked *P. albicaulis*/plot)	<0.1 (0.2)	0–1.0
Female cone production (# of trees with cones/ha)		
P. albicaulis	101 (150)	0–620

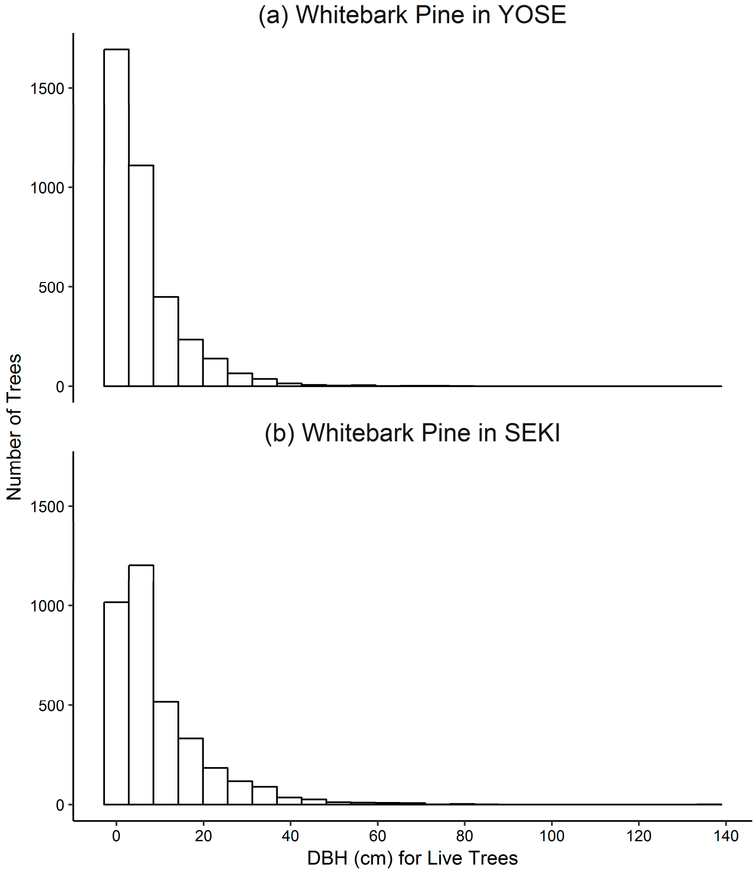

Figure 8. Histogram of all live whitebark pine diameter at 1.37 m (DBH) in Yosemite National Park (YOSE), CA, USA (**a**) and Sequoia and Kings Canyon National Parks (SEKI), CA, USA (**b**). DBH ranged from 0.4 to 78.3 cm in YOSE and 0.4 to 136.5 in SEKI.

Seedling regeneration was sparse and patchy for all species. In fact, six of the 34 plots sampled did not contain any seedlings within the regeneration plots. We found whitebark pine seedlings in 19 of the 34 plots (54%) and they made up 73% of the total seedling count (235 whitebark seedlings). However, only five of the 19 plots contained more than five whitebark pine seedlings. Whitebark pine seedling density averaged 853 per ha, though this value is greatly inflated by a single plot (PINALB_19) that contained 107 whitebark pine seedlings. The next highest number of whitebark seedlings within a plot was 39. If PINALB_19 is excluded from the analysis, the average number of seedlings per ha drops to 478. A total of 41 and 46 lodgepole and mountain hemlock seedlings, respectively, were recorded in the regeneration plots. A single additional western white pine seedling was also recorded. Seedlings per ha averaged 320 (sd = 519) cumulatively for all non-target species.

Whitebark pine generally appeared to be in good health and had low levels (8.2%) of crown mortality (Table 1). Much of this crown mortality was due to environmental factors including wind and ice damage, as well as limited damage from biological agents like brown felt blight (*Neopeckia coulteri* (Peck) Sacc. or *Herpotrichia juniper* (Duby) Petr.) and insect damage. The average proportion of crown mortality in live whitebark pine trees increased with DBH (Table 2) and was significantly higher in 2017 (Figure 9a) compared to other years. There was not strong evidence for consistent effects due to the other variables in the model, which included elevation, UTM easting at the SW plot corner, whitebark pine basal area, and non-whitebark pine basal area. The estimates for all of these terms were not significant at the $\alpha = 0.1$ level (Table 2).

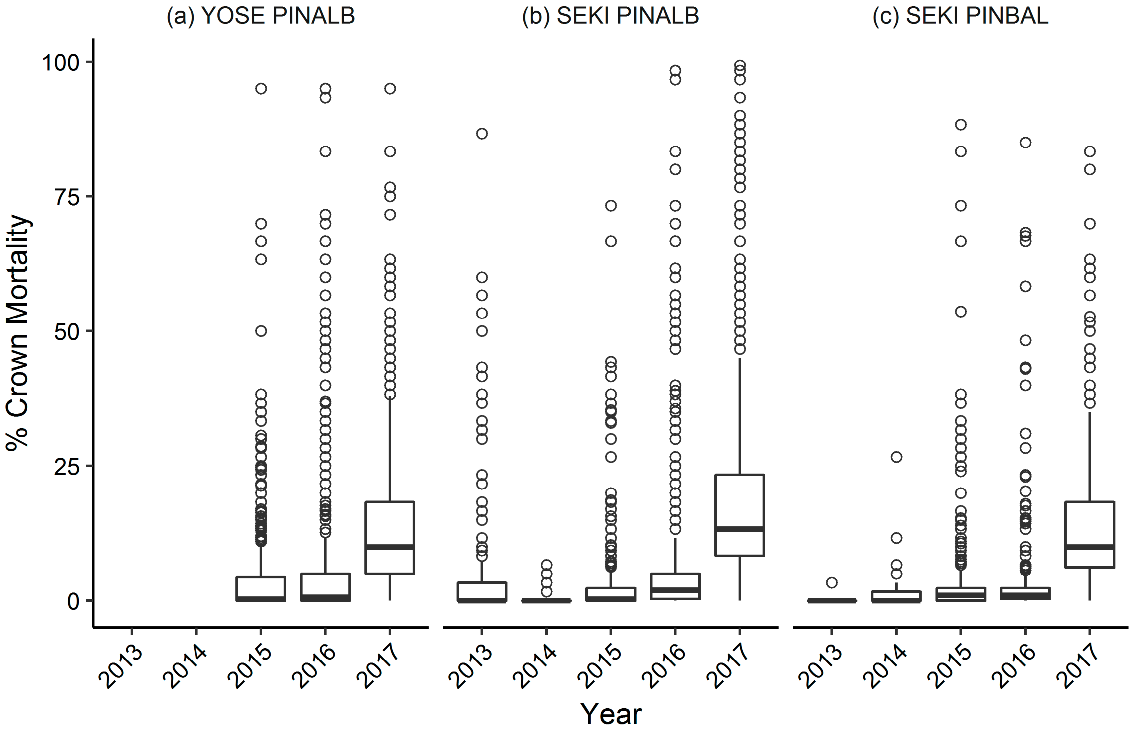

Figure 9. Individual tree percent crown mortality by year in (**a**) Yosemite National Park whitebark pine sample frame (YOSE PINALB), (**b**) Sequoia and Kings Canyon National Parks whitebark pine sample frame (SEKI PINALB), and (**c**) Sequoia and Kings Canyon National Parks foxtail pine sample frame (SEKI PINBAL).

Table 2. Standardized regression estimates (Est), standard errors (SE), *p*-values, and 95% confidence intervals (CI) from the Generalized Linear Mixed Model of the proportion of average crown mortality for all sample frames. YOSE = Yosemite National Park, CA, USA. SEKI = Sequoia and Kings Canyon National Parks, CA, USA. BA = basal area (m^2/ha), DBH = diameter at 1.37 m, Easting = UTM E, NAD83.

Sample Frame	Term	Est	SE	*p*-Value	CI (95%)
Whitebark pine YOSE	Intercept	−3.264	0.127	<0.001	−3.513, −3.014
	Elevation (m)	0.016	0.106	0.880	−0.193, 0.225
	Easting	0.005	0.099	0.960	−0.188, 0.198
	PINALB BA	−0.130	0.096	0.179	−0.319, 0.059
	Other BA	−0.034	0.100	0.735	−0.229, 0.161
	DBH (cm)	0.031	0.017	0.076	−0.003, 0.065
	2016	0.202	0.175	0.248	−0.141, 0.546
	2017	1.443	0.198	<0.001	1.055, 1.830
Whitebark pine SEKI	Intercept	−3.286	0.133	<0.001	−3.546, −3.026
	Elevation (m)	−0.044	0.045	0.328	−0.133, 0.044
	Easting	−0.065	0.040	0.105	−0.144, 0.014
	PINALB BA	0.135	0.039	<0.001	0.059, 0.212
	Other BA	−0.003	0.036	0.923	−0.074, 0.067
	DBH (cm)	0.027	0.016	0.099	−0.005, 0.059
	2014	−0.084	0.194	0.664	−0.464, 0.296
	2015	0.141	0.16	0.380	−0.174, 0.455
	2016	0.443	0.135	0.001	0.177, 0.708
	2017	1.804	0.147	<0.001	1.515, 2.093
Foxtail pine SEKI	Intercept	−3.657	0.560	<0.001	−4.756, −2.559
	Elevation (m)	−0.003	0.084	0.969	−0.168, 0.162
	Easting	−0.019	0.076	0.801	−0.168, 0.130
	PINBAL BA	0.176	0.080	0.028	0.019, 0.332
	Other BA	0.023	0.075	0.755	−0.123, 0.170
	DBH (cm)	0.136	0.032	<0.001	0.073, 0.199
	2014	0.047	0.641	0.941	−1.209, 1.303
	2015	0.482	0.564	0.393	−0.623, 1.587
	2016	0.640	0.558	0.251	−0.454, 1.734
	2017	1.645	0.591	0.005	0.486, 2.804

WPBR was rare in YOSE. Across all 35 plots, only one plot had trees that were infected and infection rates averaged 0.1% overall for whitebark pine. Within the one plot, 12 individual trees were infected by WPBR out of a total of 251 live whitebark pine, resulting in an infection rate of 3.9% for the plot. This translated into an average of 1.4 infected trees per ha across the sample frame (Table 1). The low level of WPBR infection prohibited us from running models on the presence or absence of WPBR. However, the plot with WPBR present had the highest overall whitebark pine basal area in YOSE (19.0 m^2/ha), with relatively low basal area for other species (1.4 m^2/ha). There were no obvious topographic or geographic differences between this plot and plots without WPBR. MPB incidence was even more rare than WPBR in YOSE, with observed beetle activity recorded in <0.1% of whitebark pine. Signs of beetle attack were recorded on six dead trees and three live trees resulting in an average of one tree per ha with observed signs of bark beetle attack. All of the dead trees were lodgepole pine and the live trees consisted of two whitebark pine and one lodgepole pine.

We found 883 whitebark pine (23%) with ovulate cones in YOSE, for an average of 101 cone-bearing trees per ha (Table 1). The probability of ovulate cone production in YOSE increased with increasing elevation and individual tree DBH, but decreased with increasing average proportion of crown kill and longitude (Table 3). Neither basal area of whitebark pine nor basal area of other species had a significant effect on ovulate cone production. The model had relatively high prediction accuracy, classifying 87% of observed cases correctly (AUC = 0.913, error rate = 0.129). The model had a marginal r^2 of 0.474, and a conditional r^2 of 0.567.

Table 3. Standardized regression estimates (Est. log-odds), standard errors (SE), *p*-values, and 95% confidence intervals (CI) from the Generalized Linear Mixed Model of the probability of producing cones (no = 0, yes = 1) for all sample frames. YOSE = Yosemite National Park, CA, USA. SEKI = Sequoia and Kings Canyon National Parks, CA, USA. BA = basal area (m^2/ha), DBH = diameter at 1.37 m, Easting = UTM E, NAD83, Avg. Crown Mort. = average crown mortality.

Sample Frame	Term	Est	SE	*p*-Value	CI (95%)
Whitebark pine YOSE	Intercept	−1.889	0.266	<0.001	−2.410, −1.368
	Elevation (m)	1.775	0.447	<0.001	0.899, 2.651
	Easting	−1.075	0.342	0.002	−1.745, −0.406
	PINALB BA	0.331	0.305	0.278	−0.267, 0.929
	Other BA	0.21	0.334	0.529	−0.444, 0.864
	DBH (cm)	2.427	0.111	<0.001	2.210, 2.644
	Avg. Crown Mort.	−0.571	0.093	<0.001	−0.753, −0.388
Whitebark pine SEKI	Intercept	−2.852	0.592	<0.001	−4.013, −1.690
	Elevation (m)	0.086	0.205	0.676	−0.316, 0.488
	Easting	0.139	0.178	0.436	−0.210, 0.488
	PINALB BA	−0.242	0.168	0.151	−0.572, 0.088
	Other BA	−0.430	0.164	0.009	−0.751, −0.108
	DBH (cm)	2.295	0.091	<0.001	2.116, 2.473
	Avg. Crown Mort.	−0.531	0.077	<0.001	−0.681, −0.380
	2014	1.055	0.849	0.214	−0.609, 2.718
	2015	2.002	0.702	0.004	0.625, 3.378
	2016	0.808	0.624	0.195	−0.415, 2.030
	2017	1.793	0.671	0.008	0.477, 3.109
Foxtail pine SEKI	Intercept	2.117	0.195	<0.001	1.734, 2.500
	Elevation (m)	0.146	0.155	0.347	−0.158, 0.450
	Easting	0.135	0.143	0.346	−0.145, 0.415
	PINBAL BA	−0.234	0.166	0.159	−0.559, 0.091
	Other BA	−0.130	0.144	0.366	−0.413, 0.152
	DBH (cm)	3.267	0.247	<0.001	2.782, 3.751
	Avg. Crown Mort.	−0.963	0.124	<0.001	−1.206, −0.72

3.2. Sequoia and Kings Canyon National Parks

3.2.1. Whitebark Pine

The plots in the whitebark pine sample frame in Sequoia & Kings Canyon National Parks are located primarily in the eastern half of Kings Canyon National Park (Figure 5). The average elevation is 3,284 m (sd = 136) with an average slope of 17° (sd = 9). Plots are evenly distributed across aspects, although southwest aspects were slightly more common.

We recorded 5038 live trees within 31 plots in SEKI, including 3563 (71% of live trees) whitebark pine, 1421 (28%) lodgepole pine, 41 foxtail pine, 12 western white pine, and one mountain hemlock; the latter three species comprised 1% of total stems combined. Whitebark pine were more common, but smaller than lodgepole pine in the sample frame. Whitebark pine averaged 442 trees per ha, with an average DBH of 10.1 cm (Table 4). Lodgepole pine averaged 181 trees per ha with an average DBH of 19.7 cm. Whitebark pine DBH ranged between 0.4 to 136.5 cm (Figure 8). The larger size of lodgepole pine led to a pattern similar to what we observed in YOSE where it had the highest basal area at 11.3 m^2/ha, compared to 7.4 m^2/ha for whitebark pine (Table 4). The remaining species combined averaged seven trees per ha and had an average basal area of 0.5 m^2/ha. There was a total of 125 snags in the sample frame resulting in an average density of 16 stems per ha with an average DBH of 27.1 cm, and basal area of 1.9 m^2/ha. Whitebark pine growing as krummholz was more rare in SEKI compared to YOSE as krummholz was the primary growth form (>90% of whitebark within a plot adopting this form) in only two of the 35 plots (6%).

We were able to identify the species for 115 of the 125 snags, most of which (83 trees, 66%) were whitebark pine. We also recorded 31 dead lodgepole pine and one western white pine. Though we could not identify a mortality agent for a majority (74%) of the snags, MPB was the most common identifiable cause of death, accounting for 26 (21%) of the dead individuals in the sample frame. The remaining six snags were killed by lighting or physical damage, such as broken stems or being crushed. Cause of mortality was not attributed to WPBR for any of the snags.

Table 4. Summary statistics of whitebark pine plots measured at Sequoia and Kings Canyon National Parks, CA, USA (*n* = 31). DBH = diameter at 1.37 m, WPBR = white pine blister rust, MPB = mountain pine beetle, sd = standard deviation.

Tree Density (trees/ha)	**Mean (sd)**	**Range**
P. albicaulis	442 (386)	32–1568
P. contorta	181 (335)	0–1516
Other species	7 (22)	0–116
Snag density	16 (23)	0–112
Tree DBH (cm)		
P. albicaulis	10.1 (5.4)	1.9–30.2
P. contorta	19.7 (11.8)	2.6–47.3
Other species	18.0 (10.7)	4.2–31.2
Snags	27.1 (13.2)	8.9–50.8
Tree basal area (m^2/ha)		
P. albicaulis	7.4 (7.5)	<0.1–23.0
P. contorta	11.3 (16.6)	0–56.5
Other species	0.5 (2.0)	0–10.9
Snags	1.9 (3.9)	0–20.3
Seedling regeneration 20–136 cm (seedlings/ha)		
P. albicaulis	785 (2226)	0–11,605
Other species	147 (269)	0–988
Incidence of stressors		
P. albicaulis crown mortality (%)	8.2 (7.1)	<0.1–23.8
P. albicaulis WPBR infection rate (# of infected trees/ha)	0.8 (2.2)	0–8
WPBR occurrence rate (% of infected *P. albicaulis*/plot)	0.1 (0.4)	0–1.4
MPB infestation rate (# of infested trees/ha)	4.2 (15.2)	0–84
P. albicaulis MPB infestation rate (# of infested *P. albicaulis*/ha)	3.7 (15.2)	0–84
MPB occurrence rate (% of *P. albicaulis*/plot with MPB activity)	1.0 (3.5)	0–17.6
Female cone production (# of trees with cones/ha)		
P. albicaulis	134 (130)	0–524

New seedling recruitment in the SEKI whitebark pine sample frame was similar to what we found in YOSE in that seedlings were generally sparse, but density was highly variable. Eight of the 31 plots did not contain seedlings of any species and we recorded a total of 234 seedlings within the remaining plots. Whitebark pine seedlings were found in 19 of the 31 plots (61%) and was the dominant species (197 seedlings), accounting for 84% of all seedlings observed. Average seedling density was 785 seedlings per ha (Table 4), though this number was greatly inflated by a single plot (PINALB_43) where 94 of the 197 whitebark seedlings were observed. In fact only one additional plot had more than ten whitebark pine seedlings. When PINALB_43 was removed from the analysis, average seedling density dropped to 424 seedlings per ha. Lodgepole pine was the next most abundant species with a total of 26 seedlings observed, followed by foxtail pine (two seedlings) and Jeffrey pine (one seedling). There were an additional eight seedlings that were not identified to species within one of the plots. Cumulative seedling density for non-target species was 147 seedlings per ha (Table 4).

Average crown mortality was low for whitebark pine in SEKI, averaging 8.2% across plots (Table 2). Crown mortality was significantly higher in 2016 and 2017 compared to 2013–2015 (Figure 9b). Whitebark pine basal area also had a positive relationship with crown mortality. The effect of DBH was marginally positive at an $\alpha = 0.1$ level (Table 2). There was not strong evidence for consistent effects due to the other variables in the model, which included elevation, UTM easting at the SW plot corner, and non-whitebark pine basal area. The estimates for all of these terms were not significant at the $\alpha = 0.1$ level (Table 2).

At least three symptoms of WPBR or live aecia, were observed on six whitebark pine within four different plots in the whitebark pine sample frame in SEKI, translating to an average infection rate of 0.1% (Table 4). One infected tree was found in a plot near Taboose Pass (PINALB_5), one was by the Bench ranger station (PINALB_59), and several were near Charlotte Dome (PINALB_27) and Kearsarge Lake (PINALB_51). This resulted in an estimated average infection rate of 0.8 trees per ha across the sample frame (Table 4). All observations of WPBR within the monitoring plots were in Kings Canyon National Park. The low level of WPBR infection prohibited us from running models on the presence or absence of blister rust. However, similar to YOSE, the plots with WPBR in SEKI had higher than average basal area estimates of whitebark pine. The average incidence of beetle attack on whitebark pine in SEKI was 1.0% (Table 4). Bark beetle activity overall was rare, as signs of beetle attack were recorded on a total of 33 trees within eight plots. Beetle activity was concentrated within a single plot in Arrow Basin in Kings Canyon National Park (PINALB_52), where 21 whitebark pine (17.6%) showed signs of beetle attack. Overall, 29 of the attacked trees were whitebark pine (four live, 25 dead) and four were lodgepole pine (two live, two dead) translating to an average of 4.3 trees per ha that displayed signs of MPB attack (Table 4).

We recorded 992 live whitebark pine (28%) with ovulate cones, which resulted in an average of 134 live whitebark with ovulate cones per ha (Table 4). As in YOSE, the likelihood of trees producing ovulate cones increased with DBH, but also was higher in 2015 and 2017 compared to 2013, 2014, or 2016 (Table 3). The proportion of trees with cones decreased with the average proportion of crown killed and the basal area of other species. The model did not indicate that ovulate cone production varied significantly with elevation, longitude, or whitebark pine basal area. The model classified 85% of observed cases correctly (AUC = 0.901, error rate = 0.154) and had a marginal r^2 of 0.51, and a conditional r^2 of 0.55 (Table 3).

3.2.2. Foxtail Pine

The plots in the foxtail pine sample frame in SEKI are located primarily in the eastern half of Sequoia National Park (Figure 6). The average elevation is 3232 m (sd = 167) with an average slope of 19° (sd = 7). Plots are distributed across all aspects, although northern aspects were slightly more common.

We recorded 2192 live trees in the foxtail pine sample frame, including 1071 foxtail pine (49%), 564 whitebark pine (26%), 547 lodgepole pine (25%), seven western white pine, two red fir, and one Jeffery pine; the latter three species comprised 1% of total stems combined. Foxtail pine was the most abundant, as well as largest species, and averaged 130 trees per ha with a basal area of 26.0 m^2/ha (Table 5). DBH ranged between 0.4 and 182.3 cm (Figure 10) and averaged 48.1 cm across plots. Whitebark pine and lodgepole pine were equally abundant, but lodgepole pine had a much higher average basal area compared to whitebark pine due to its larger average size (Table 5).

Table 5. Summary statistics of foxtail pine plots measured at Sequoia and Kings Canyon National Parks, CA, USA ($n = 33$). DBH = diameter at 1.37 m, WPBR = white pine blister rust, MPB = mountain pine beetle, sd = standard deviation.

Tree Density (trees/ha)	Mean (sd)	Range
P. balfouriana	130 (107)	4–436
P. albicaulis	68 (137)	0–520
P. contorta	66 (108)	0–376
Other species	1 (3)	0–12
Snags	23 (22)	0–92

Table 5. *Cont.*

Tree Density (trees/ha)	Mean (sd)	Range
Tree DBH (cm)		
P. balfouriana	48.1 (32.3)	3.6–182.3
P. albicaulis	19.7 (28.1)	3.0–94.6
P. contorta	28.1 (15.2)	7.2–58.7
Other species	23.3 (21.2)	2.4–54.4
Snags	58.7 (24.2)	6.2–119.0
Tree basal area (m^2/ha)		
P. balfouriana	26.0 (18.1)	<0.1–72.5
P. albicaulis	1.2 (2.5)	0–10.6
P. contorta	6.7 (11.3)	0–41.1
Other species	0.2 (0.8)	0–4.3
Snags	6.6 (6.9)	0–31.4
Seedling regeneration 20 – 136 cm (seedlings/ha)		
P. balfouriana	45 (106)	0–494
Other species	37 (133)	0–741
Incidence of stressors		
P. balfouriana crown mortality (%)	6.2 (7.0)	0–25.5
P. balfouriana WPBR infection rate (# of infected trees/ha)	0	0
P. albicaulis WPBR infection rate (# of infected trees/ha)	0.1 (0.7)	0–4
WPBR occurrence rate (% of infected *P. balfouriana*/plot)	0	0
MPB infestation rate (# of infested trees/ha)	0.6 (1.5)	0–4
P. balfouriana MPB infestation rate (# of infested *P. balfouriana*/ha)	0.1 (0.7)	0–4
MPB occurrence rate (% of *P. balfouriana*/plot with MPB activity)	0.1 (0.7)	0–4
Female cone production (# of trees with cones/ha)		
P. balfouriana female cone production (# of trees with cones/ha)	90 (69)	0–284

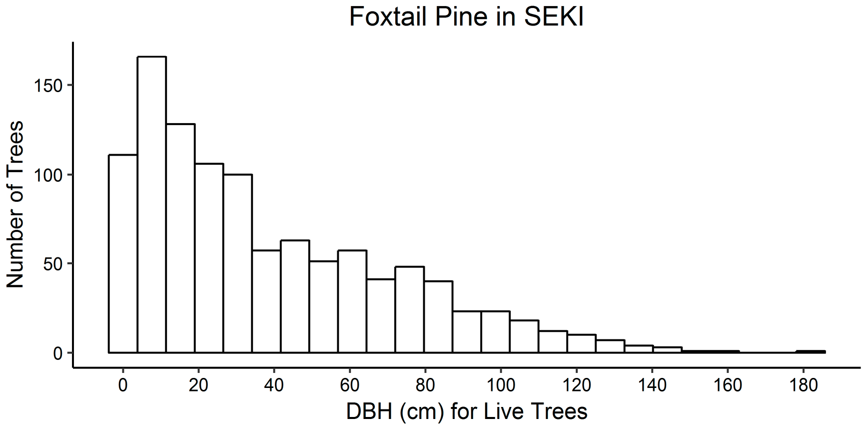

Figure 10. Histogram of all live foxtail pine diameter at 1.37 m (DBH) in Sequoia and Kings Canyon National Parks (SEKI), CA, USA. DBH ranged from 0.4 to 182.3 cm.

There were an additional 191 snags (8% of all stems), most of which (95 trees, 50%) were foxtail pine. Snag density averaged 23 stems per ha and had an average basal area of 6.6 m^2/ha (Table 5). Snag DBH averaged 58.7 cm across all plots. Very few of the snags had an identifiable cause of death. Of the six individuals (3% of all snags) where the mortality agent could be identified, physical damage was most common, accounting for four of the six cases. Two lodgepole pine were killed by MPB, and one additional tree was killed by lightning.

Seedling density in the SEKI foxtail pine sample frame was remarkably sparse, as only 22 seedlings (12 foxtail pine, eight whitebark pine, two lodgepole pine) were recorded. No seedlings were observed in 21 of the 33 plots. Average foxtail pine seedling density was 44.9 seedlings per ha (Table 5) and foxtail pine seedlings were found in only seven of 33 plots (21%). Cumulative seedling density for the other species was 37.4 seedlings per ha.

Average crown mortality was quite low, averaging 6% of the crown for foxtail pine (Table 5). Crown mortality increased with DBH and foxtail pine basal area, and was also higher in 2017 compared to 2013–2016 (Table 2, Figure 9c). No other covariates in the model were significant at the $\alpha = 0.1$ level.

Symptoms of WPBR were not observed on any foxtail pine within the monitoring plots, though one whitebark pine within PINBAL_40 was found to be infected (Table 5). This plot is located in Kings Canyon near the Charlotte ranger station and is in an area where WPBR had been observed in the whitebark pine monitoring plots. MPB was rare and we only found five trees (four lodgepole pine [two live, two dead], one live foxtail pine) among five plots with evidence of MPB. This translated to an average incidence of 0.1% of foxtail pine displaying symptoms of MPB attack.

We found 743 living foxtail pine (69%) with ovulate cones in the sample frame for an average density of 90 cone bearing trees per ha. This is the lowest density of cone bearing trees per ha among all three sample frames, but it is the highest percentage of trees by far. Ovulate cone production in foxtail pine was positively associated with DBH and negatively associated with the average proportion of crown killed in plots (Table 3). No other predictors in the model showed a relationship to ovulate cone production that was significant at the $\alpha = 0.1$ level. The model was able to correctly classify the presence of cones 87% of the time (AUC = 0.916, error rate = 0.127), and had marginal and conditional r^2 values of 0.663 and 0.677, respectively.

4. Discussion

Overall, high elevation white pines in YOSE and SEKI appear to be relatively healthy, especially when compared to other portions of their range [10,21]. WPBR infection rates were low in both parks. No foxtail pine were observed with symptoms of WPBR and well below 1% of whitebark pine were infected, averaging around one infected tree per ha in both YOSE and SEKI. WPBR did not appear to be a strong driver of tree mortality in subalpine forests in the southern Sierra Nevada at this time, as no dead trees were assessed to have died from WPBR. However, 18 of 19 whitebark pine infected by WPBR were discovered in the last two years of sampling, which may suggest that while WPBR is not currently widespread, it could become a more important driver of mortality in the future given the likely continued spread of WPBR within subalpine forests in the Sierra Nevada.

MPB activity was also quite rare, averaging less than five attacked trees per ha, representing less than one percent of all white pines. This is in stark contrast to lower elevation forests in the Sierra Nevada that have experienced dramatic mortality driven by the recent severe drought [54,55] and associated MPB outbreak [56]. Successful attacks were observed primarily on whitebark pine and lodgepole pine and were often limited to single trees or very small clumps. Whitebark pine has experienced significant mortality from MPB in other areas of the southern Sierra Nevada [16,30] and other parts of its range [57,58], but we did not observe this pattern in subalpine forests in YOSE or SEKI during the course of this study.

Crown mortality was low (<10%) in both whitebark pine and foxtail pine, though it appears to have increased in more recent years (Figure 9). The only factor that displayed a significant relationship with the average proportion of crown mortality in YOSE was sample year, as crown mortality was higher in 2017 compared to earlier years, though the effect size was relatively small (Figure 9a). Crown mortality for whitebark pine in SEKI was higher in 2016 and 2017 and also increased in plots with higher whitebark pine basal area. In both YOSE and SEKI, crown mortality was marginally higher in larger trees than smaller ones. For foxtail pine in SEKI, crown mortality was higher for larger trees, in plots with a greater foxtail pine basal area, and in 2017. Recent crown mortality anecdotally appears to be driven primarily by environmental factors like wind and frost damage as opposed to biological factors like WPBR or beetles. The low snow pack in 2015 may have contributed to the higher levels of crown mortality (due to frost and wind damage) observed the following two summers compared to previous years. Conversely, the high snow year of 2017 may have caused an increase in physical damage, resulting in higher crown mortality. Environmental factors appeared to be the driving factor of tree mortality as well, as most of the snags where we were able to assign a cause of death were attributed to environmental or physical causes. Standing dead basal area was low in general, indicating that there has not been any extensive mortality in these areas in recent history.

The proportion of cone-bearing trees was quite different across species as roughly 25% of whitebark pine trees had female cones (23% and 28% in YOSE and SEKI, respectively) compared to 69% for foxtail pines. The proportion of cone bearing trees increased with tree size and decreased with crown mortality across all sample frames (Table 3). The positive relationship we observed between tree size and cone production mirrors the findings of previous studies, where the probability of cone production increased with size class [59]. The proportion of cone-bearing foxtail pine was similar to the findings of Maloney [60], who reported an average of 64% for cone-bearing foxtail pine in the Sierra Nevada. The proportion of cone-bearing whitebark pine was also similar to proportions given by Meyer et al. [30], who found that the percentage of cone-bearing trees ranged from 6.8 to 31.0% in their study area in the southern Sierra Nevada. Maloney [61], however, has reported the percentage of cone-bearing whitebark pine to be as high as 80% farther north in the Lake Tahoe area of the Sierra Nevada. This may be a reflection of asynchronous mast years, as whitebark pine cone production is thought to be somewhat periodic with large cone crops generally occurring every three to five years, though this varies geographically [61,62]. Whitebark pine crown mortality has also been shown to be a strong predictor of cone production in other studies [29], as most of whitebark pine cone production occurs in the upper third of the crown [24,63]. Therefore, when this portion of the crown dies, the ability of the tree to produce ovulate cones is greatly reduced or eliminated [29]. In Yosemite, whitebark cone production decreased with longitude and increased with elevation. In SEKI, whitebark pine cone production decreased with basal area of other species in the plots and increased in 2015 and 2017 relative to the other sample years.

Stand structure for whitebark pine was quite variable and illustrates the multiple habitats and growth forms of this species. The number of whitebark pine encountered within a plot ranged from a single stem to 588 in one of the krummholz dominated plots. Whitebark pine occurred in both pure stands, often at treeeline growing as krummholz, and as a rare component of stands dominated by other species. In Yosemite, the most commonly encountered other species with whitebark pine were mountain hemlock and lodgepole pine. In SEKI, lodgepole pine was the most common co-occurring species. It was not uncommon for basal area and trees per ha of these other species to exceed that of whitebark pine within the plots where they co-occurred. Foxtail pine stand structure was less variable and it tended to occur at lower stem densities (though with higher basal area) compared to whitebark pine. The most common co-occurring species were whitebark pine and lodgepole pine.

Whitebark and foxtail pine were the dominant species within the seedling plots in their respective sample frames and the most common other species were mountain hemlock in YOSE and lodgepole pine in SEKI. Seedling recruitment was low but variable for whitebark pine and was consistently low for foxtail pine. Foxtail pine seedling recruitment was roughly half of what has been previously reported in the southern Sierra Nevada by Maloney [60], though it well within the range of reported values (7–227 seedlings/ha). Part of this difference is due to the exclusion of the smallest seedlings (<20 cm tall) in our study and therefore we likely under-estimate total seedling density. Low seedling densities for foxtail pine in the southern Sierra Nevada do not appear uncommon, however, and populations have been estimated to have been stable (recruitment $\approx$ mortality) over the last 1000 years [33]. For whitebark pine, our estimated seedling densities fall within the range of those previously reported by Meyer et al. [30] in the southern Sierra Nevada (433–4716 seedlings per ha). There is some evidence that whitebark pine recruitment has increased over the last century compared to previous rates, driven in part by increases in minimum temperature and precipitation [64].

5. Conclusions

These data provide a solid baseline for assessing current status and evaluating future change in subalpine forests in the southern Sierra Nevada. The plot network and associated information will also provide exciting opportunities to address additional research questions related to the management and conservation of these species, and are already being used to investigate questions related to population genetics, disease incidence and spread, and drought tolerance of whitebark pine in the Sierra Nevada. Managers face multiple challenges related to white pine conservation and conservation due to multiple factors including a rapidly changing climate, existing wide-spread degradation of white pine ecosystems, and conflicting management and policy directives. As the PWR Inventory & Monitoring Program high elevation white pine monitoring plot network is re-sampled its value and utility will continue to grow and help both current and future natural resource managers ensure the persistence of these iconic species.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/10/1/35/s1, Table S1: Location and site characteristics for the whitebark pine sample frame in Yosemite National Park, CA, USA (n = 35). Table S2: Location and site characteristic for the whitebark pine sample frame in Sequoia and Kings Canyon National Parks, CA, USA (n = 31). Table S3: Location and site characteristics for the foxtail pine sample frame in Sequoia and Kings Canyon National Parks, CA, USA (n = 33).

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