Article

Whitebark Pine in the Northern Cascades: Tracking the Effects of Blister Rust on Population Health in North Cascades National Park Service Complex and Mount Rainier National Park

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Abstract: Whitebark pine (*Pinus albicaulis* Engelm.) is a key component of subalpine and alpine ecosystems in the northern Cascades. The species survival is threatened by white pine blister rust, mountain pine beetles, fire exclusion, and climate change. Trees were monitored in permanent plots in two national parks three times between 2004 and 2016. The proportion of trees showing signs of blister rust infection increased in North Cascades National Park Service Complex from 32% in 2004 to 51% in 2016 and from 18% to 38% in Mount Rainier National Park. Mortality increased from 7% to 21% in North Cascades National Park Service Complex and 38% to 44% in Mount Rainier National Park. Annual mortality rates were calculated for three time periods: 2004-2009, 2009-2015/2016, and 2004-2015/2016. Mortality rates, annualized across the entire study period, were 1.47% in Mount Rainier National Park and 2.27% in North Cascades National Park Service Complex; these rates decreased between the first time period and the second, which could reflect blister rust resistance. Signs of mountain pine beetle were rare and limited to a few trees in individual plots. Although reproductive trees were found in most stands, densities were low and regeneration was dominated by subalpine fir.

Keywords: *Pinus albicaulis*; whitebark pine; blister rust; national park; subalpine; Cascades; mountain pine beetle

1. Introduction

The silhouettes of dead whitebark pine (*Pinus albicaulis* Engelm.) are scattered across the subalpine landscape of North Cascades National Park Service Complex and Mount Rainier National Park. In the northern Cascades, whitebark pine is patchily distributed in the dry, cold subalpine areas typical of the eastern slopes of North Cascades National Park Service Complex and Mount Rainier National Park. Whitebark pine is often referred to as a keystone species in high-elevation areas of western North America due to its influence on biodiversity, ecosystem structure, and hydrologic cycles [1, 2]. The species' survival is threatened by the introduced white pine blister rust (*Cronartium ribicola* J. C. Fisch) which was first documented in western North America in 1910 [3, 4]. Over the last 100 years, precipitous declines and widespread mortality have been documented in whitebark pine across the western United States and northwest Canada [5-9].

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Historical accounts of the spread of white pine blister rust from the area of North Cascades National Park Service Complex are limited to one 1913 report of a potential pine infection near Newhalem, Washington on the west edge of the park [4]. In contrast, Mount Rainier National Park was a center of activity from the late 1920s through the 1960s. In 1928, white pine blister rust was found on Gooseberries (*Ribes spp.)* in low-elevation forests (approximately 800 meters (m)) in the southwest corner of Mount Rainier National Park. By 1930, surveys by the US Department of Agriculture's (USDA) Bureau of Plant Industry documented it on western white pine (*Pinus monticola*) [10]. Although surveys initially focused on the commercially important western white pine, memos from USDA foresters noted that the value of white pines in the park was aesthetic and surveys should focus on areas where mortality would be visible to the park visitors, marring the views. In 1931, O.A. Tomlinson, Superintendent of Mount Rainier National Park, met with pathologists from the Bureau of Plant Industry. The meeting focused on current status, future surveys, and control efforts. At the meeting, lead pathologist Dr. E.P. Meinecke urged park managers to protect whitebark pine populations in the Sunrise area, stating that it would be a calamity if whitebark pine were lost from the picturesque quality of the barren areas below the glaciers [11]. By 1951-52, surveys in the Sunrise area documented that 52-55% of whitebark pines were infected with blister rust, despite widespread programs that removed *Ribes* to protect white pines. In the late 1950s and 1960s, work in Mount Rainier National Park turned to fungicides and surveys of western white pine for genetically resistant trees. Although the scenic value of whitebark pine was repeatedly mentioned in park memos, blister rust control efforts were terminated around 1964 when it was determined that the fungicide treatments were not effective [12, 13].

Between 1994 and 1999, national park staff conducted inventories, in both parks, to quantify the extent of blister rust and mountain pine beetles (*Dendroctonus ponderosae* Hopkins) [14]. Surveys revealed that about one third of all trees surveyed were dead, blister rust infection rates were highly variable (0-70%), and observations of mountain pine beetle were rare. We realized that long-term monitoring plots with marked trees were needed to accurately attribute the cause of mortality and to track long-term trends in population health [5, 6, 9, 15]. In 2004, we established permanent plots in each park to monitor trends in whitebark pine population health and to provide data to initiate discussion on adaptive management or restoration. Specifically, our objectives were: 1) quantify status and trends in infection and mortality rates in trees and saplings; 2) quantify the incidence of mountain pine beetles; 3) describe status and trends in seedling density; 4) evaluate landscape patterns of white pine blister rust infection and mortality; and 5) describe the current composition and structure of whitebark pine stands.

2. Materials and Methods

2.1. Study Area

The study was conducted in the subalpine parklands of North Cascades National Park Service Complex and Mount Rainier National Park in the northern Cascade Mountains of Washington state (Figure 1). North Cascades National Park Service Complex actually encompasses three areas administered by the National Park Service: North Cascades National Park, Ross Lake National Recreation Area, and Lake Chelan National Recreation Area. North Cascades National Park Service Complex extends from the Canadian border southeast along the Cascade Crest for about 82 kilometers (km) encompassing 276,815 hectares (ha) with an elevation range of 199-2,806 m. Straddling the Cascade Crest, North Cascades National Park Service Complex spans two very different biogeographic zones. The west slopes of the Cascades experience a wet, temperate maritime climate with annual precipitation of up to 897 centimeters (cm), while the drier eastern slopes have a more continental climate with annual precipitation of about 76 cm. Mount Rainier National Park encompasses 95,781 ha from low-elevation old-growth forests at 490 m in elevation to the summit of Mount Rainier at 4,392 m.

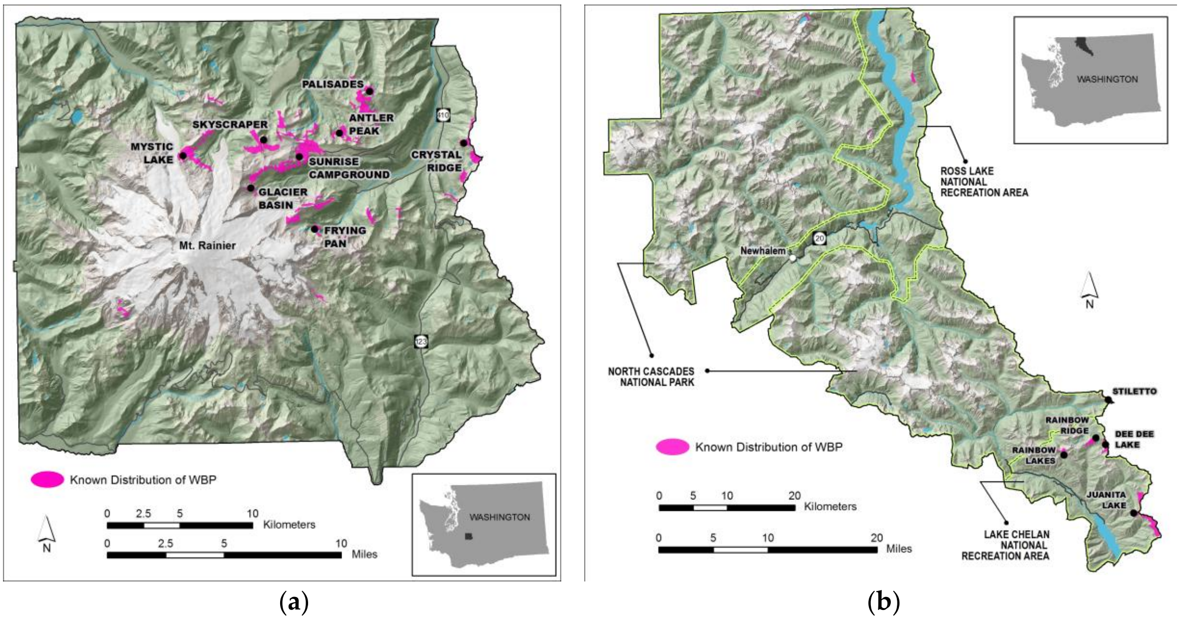

Figure 1. Study sites and whitebark pine distribution in (**a**) Mount Rainier National Park and (**b**) North Cascades National Park Service Complex.

2.2. Field Methods

We used a two-stage sample design with primary units (stands/polygons) and secondary units (0.4 ha plots) sampled from the primary units. Based on a previous inventory, we anticipated surveying up to eight stands in Mount Rainier National Park and five in North Cascades National Park Service Complex during one field season [14] (Rochefort 2008). Using inventory data, we calculated the number of plots needed per stand to estimate the proportion of dead trees and proportion of infected trees with precision within the range of 0.1-0.2 [16]. Stands and plots were randomly selected from whitebark pine distribution maps assembled from historic maps and more recent vegetation surveys [14, 16, 17, 18]. These maps delineated 66 polygons or tree stands in Mount Rainier National Park totaling 1,433 ha and 12 polygons or stands in North Cascades National Park Service Complex encompassing 923 ha.

Circular 0.4 ha plots were randomly located in each stand in 2004 and then resurveyed in 2009 and 2015-2016. Two stands in North Cascades National Park Service Complex were surveyed in 2016 because we could not complete the 2015 surveys before snowfall (Table 1). Plot centers were marked with rebar and the locations were recorded with a global positioning system unit. Within each plot, all trees greater than or equal to 2.54 cm diameter at breast height (dbh), living and dead, were identified to species and measured (dbh and height). All whitebark pine trees within the plot were tagged with aluminum tags and examined for signs of blister rust (e.g., cankers present on bole or branch or signs of gnawing), crown kill, cones, fire scars, mountain pine beetle, and mistletoe. Saplings (greater than or equal to 50 cm in height and less than 2.54 cm dbh) and seedlings (less than 50 cm in height) were identified to species and tallied. Whitebark pine saplings were examined for presence of blister rust (e.g., cankers, chlorotic needles).

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Table 1. Sample sites (primary sample units) and plots (secondary sample units) established at Mount Rainier National Park and North Cascades National Park Service Complex.

Stand	Mean Elevation (meters)	Number of Plots Sampled		
		2004	2009	2015/16[1]
Mount Rainier National Park				
Antler Peak	1,858	4	4	4
Crystal Ridge	1,927	5	5	5
Frying Pan	1,817	3	3	3
Glacier Basin	2,033	5	5	5
Mystic Lake	1,872	3	3	3
Skyscraper	1,962	2	2	2
Sunrise Campground	1,940	5	5	5
Palisades	1,883	2	2	2
North Cascades National Park Service Complex				
Dee Dee Lake	1,976	7	7	7
Juanita Lake	2,084	7	7	7
Rainbow Lakes	1,870	7	7	7
Rainbow Ridge	1,987	7	7	7
Stiletto	1,938	7	7	7

[1] Rainbow Lakes and Stiletto were sampled in 2016.

2.3. Data Analysis

2.3.1. Population Health

We described whitebark pine population health by calculating the mean percent of trees that were dead, live, and uninfected at each time period. To provide inference to the entire whitebark pine population for each park, percentages for each park were constructed using means for each stand weighted by the size of the stand [19]. All analyses were conducted using R version 3.4.2 [20].

Population health was examined in two ways: cumulatively and progressively. Cumulative estimates of blister rust infection included all dead trees documented during each of the three monitoring periods. Progressive analyses removed previously dead trees from subsequent analysis (e.g., if a tree was recorded as dead in 2004, it was removed from the data set for 2009 and 2015). Our reason for doing this was twofold: first, cumulative analysis describes the image one sees (scientists and the visiting public) when visiting a whitebark pine site because standing dead trees persist for years. Progressive analysis provides insight into the movement of blister rust through the stands by examining changes in mortality rates across the monitoring time period. In progressive analyses, we removed one Mount Rainier National Park stand (Frying Pan) from our analysis because two of the three plots had no live trees remaining after 2004, and we could not obtain stand level averages.

Saplings were summarized by mean percent dead, uninfected, and infected. Live seedlings were simply tallied and average density calculated.

2.3.2. Landscape Patterns of Population Health

Landscape level patterns of whitebark pine health were summarized in terms of infection, mortality, and prevalence. Tree mortality and infection patterns were investigated using stand level data and linear mixed effect models based on the normal distribution. Repeated observations for a stand across each of the three study years were accommodated by including a random stand effect in the intercept. A sample unit was a stand, and 13 stands across three years represented the sample size used to fit the models (n = 39). Models were fit with combinations of the covariates elevation, slope, northness, eastness, x location, y location, dbh, and park, summarized at the stand level. Northness was calculated as the cos(aspect) with values of 1 indicating north facing slopes and values

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of -1 indicating south facing slopes. Eastness was calculated as the sine(slope) with values of 1 indicating east facing slopes and values of -1 indicating west facing slopes.

Blister rust prevalence was defined as the proportion of infected or dead whitebark pine trees across all plots and stands. We used the cumulative data on repeated whitebark pine health to fit generalized linear mixed effects models to predict blister rust prevalence at the landscape level. The sample unit was an individual tree, and a total sample size of 1,661 whitebark records across 2004, 2009 and 2015/2016 survey years from legacy plots was available for model fitting. We fit a linear mixed effect model with a binomial distribution and logit link incorporating a random effect of tree in the intercept to address the lack of independence among repeated tree measurements across years. The Frying Pan stand was dropped from this analysis because dbh data were not collected for most of the trees in 2009.

2.3.3. Stand Composition and Structure

Community composition of trees, saplings, and seedlings was examined for each study site by comparing basal area of trees species and densities of trees, saplings, and seedlings.

3. Results

3.1. Population Health

3.1.1. Trees

We established 64 plots within our 13 study sites and monitored 1,661 trees (649 dead and 1,012 live) over the course of our study. During each survey effort, we surveyed between 249 and 312 trees (live and dead) in each park with plot densities ranging from one to 86 trees; each year, nine to 13 plots had only one to two trees (Table 2). Blister rust occurred in all but two of our study plots, and mountain pine beetle was only found in five plots in Mount Rainier National Park and seven plots in North Cascades National Park Service Complex at very low incidences (i.e. generally one or two trees per plots or 0.4-6.7% of trees surveyed per year).

Table 2. Number of whitebark pine trees sampled by year at Mount Rainier National Park and North Cascades National Park Service Complex.

Park	Year	Stands (n)	Plots	Trees	Trees per plot
Mount Rainier	2004	8	29	249	1-43
National Park	2009	8	29	260	1-40
	2015	8	29	258	1-39
North Cascades	2004	5	35	287	1-79
National Park	2009	5	35	295	1-82
Service Complex	2015/2016	5	35	312	1-86

Tree mortality and blister rust infection rates were highest in Mount Rainier National Park. Cumulative mortality increased from 37.79% in 2004 to 43.76% in 2015; average proportion of live infected trees increased from 18.48% to 38.8% (Figure 2, Table 3). In North Cascades National Park Service Complex, average mortality in 2004 was 6.74% and rose to 21.37% in 2015/2016 while the proportion of live infected trees increased from 32.33% to 43.61%. Infection rates are conservative and based on presence of bole or stem cankers or animal gnawing on stems. In our initial surveys (2004), it was often difficult to determine the cause of mortality because many trees had been dead for so long, but in 2009 and 2015/2016 surveys blister rust was frequently listed as the cause since cankers were visible or had been noted in previous surveys.

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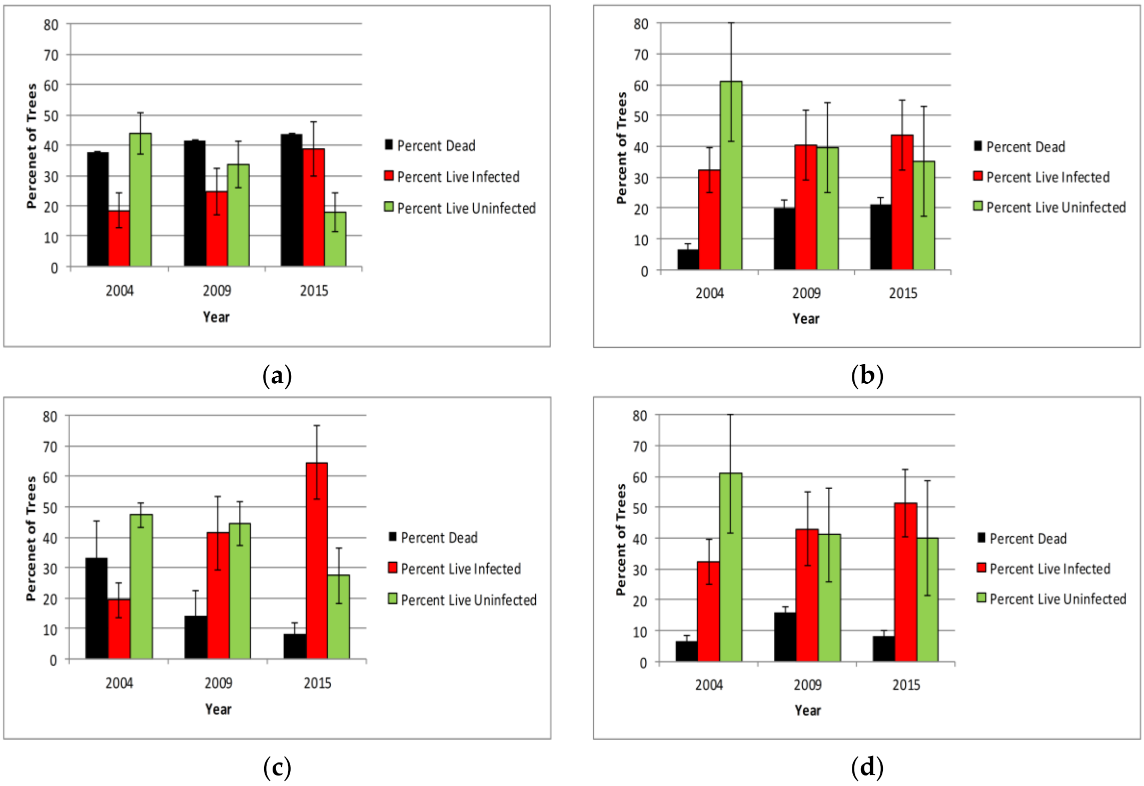

Figure 2. Percent of whitebark pine trees that are dead, infected live, and uninfected live trees in Mount Rainier National Park and North Cascades National Park Service Complex in 2004, 2009, and 2015/2016. Figures (**a**) and (**b**) are cumulative calculations in (**a**) Mount Rainier and (**b**) North Cascades and figures (**c**) Mount Rainier and (**d**) North Cascades are progressive (i.e. previously dead trees are removed from 2009 and 2015/2016).

Table 3. Cumulative and progressive[1] average percent or whitebark pine trees that were recorded as dead, live infected, and live uninfected by park and year.

		Cumulative			Progressive		
Park	**Year**	**% Dead**	**% Live Infected (SE[2])**	**% Live Uninfected (SE)**	**% Dead Mean (SE)**	**% Live Infected Mean (SE)**	**% Live Uninfected Mean (SE)**
Mount Rainier National Park	2004	37.79 (11.28)	18.48 (5.56)	43.73 (6.85)	33.31 (12.14)	19.39 (5.77)	47.30 (3.92)
	2009	41.68 (11.34)	24.66 (7.53)	33.66 (7.76)	14.31 (7.99)	41.36 (12.18)	44.33 (7.18)
	2015	43.76 (11.45)	38.27 (8.86)	17.96 (6.39)	7.99 (3.68)	64.63 (12.25)	27.38 (9.01)
North Cascades National Park Service Complex	2004	6.74 (1.70)	32.33 (7.22)	60.93 (19.38)	6.74 (1.70)	32.33 (7.22)	60.93 (19.38)
	2009	19.89 (2.61)	40.48 (11.38)	39.62 (14.72)	15.92 (1.79)	42.92 (11.99)	41.16 (15.26)
	2015/2016	21.37 (2.20)	43.61 (11.37)	35.02 (17.86)	8.43 (1.53)	51.39 (10.82)	40.17 (18.65)

[1]In progressive calculations, previously dead trees were removed from 2009 and 2015/2016 event years. One stand was dropped from Mount Rainier National Park progressive analysis because all trees in two of three stands were dead in 2004.

[2] SE = standard error

When we looked at the progression of blister rust infection, the trends in mortality and infection were similar among parks despite higher baseline mortality (2004) at Mount Rainier National Park. By 2009, mortality was 14.31% at Mount Rainier National Park and 15.92% in North Cascades

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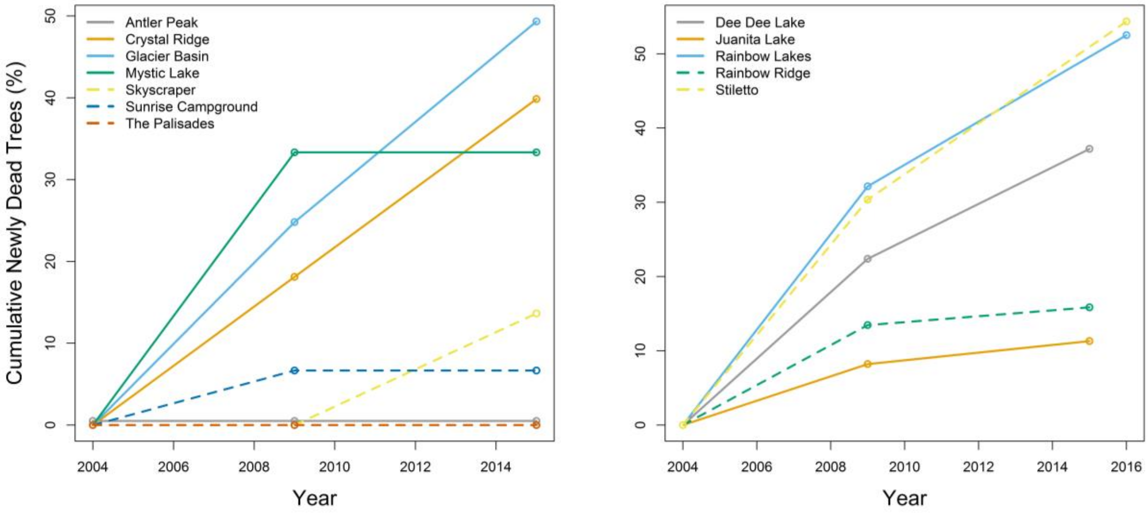
National Park Service Complex and 7.99% and 8.43%, respectively in 2015/2016. Infection rates were also similar, but still higher in Mount Rainier National Park (Figure 3, Table 2).

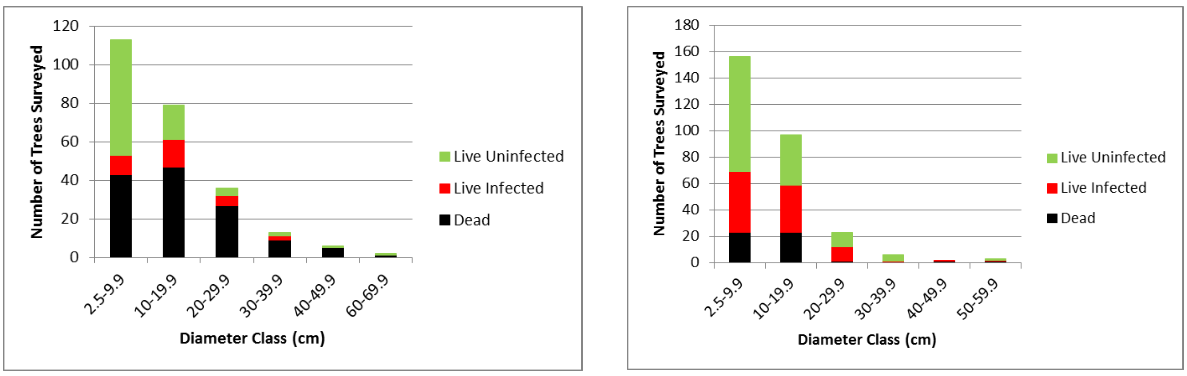


(**a**) (**b**)

Figure 3. Percent newly dead trees across the study period for stands in (**a**) Mount Rainier National Park and (**b**) North Cascades National Park Service Complex. 2004 is graphed at zero to indicate the baseline.

To compare trends in mortality between parks and time periods, we annualized mortality rates for three time periods: 2004 to 2009, 2009 to 2015/2016, and 2004 to 2015/2016 (Figure 3). The number of intervening years was used to standardize the percent newly dead estimate. The averages across stands were calculated for a naïve form of annualized mortality rate. Mortality rates in each park decreased from the 2004-2009 time period to the 2009-2015/2016 time period. At Mount Rainier National Park, the annual mortality rate went from 2.37% (95% confidence interval (CI) ±1.73) to 1.43% (95% CI ±1.18). At North Cascades National Park Service Complex, the annual mortality rate went from 4.26% (95% CI ±1.82) to 1.94% (95% CI ±0.89) during 2004 to 2009, and 2009 to 2015/2016. When the period from 2004 to 2015/2016 was evaluated, using no information from sampling in 2009, the annual mortality rate for Mount Rainier National Park was 1.47% (95% CI ±0.85) and for North Cascades National Park Service Complex was 2.27% (95% CI ±0.96).

In each park, the majority of uninfected whitebark pine trees were in the smaller diameter classes (Figure 4).



(**a**) (**b**)

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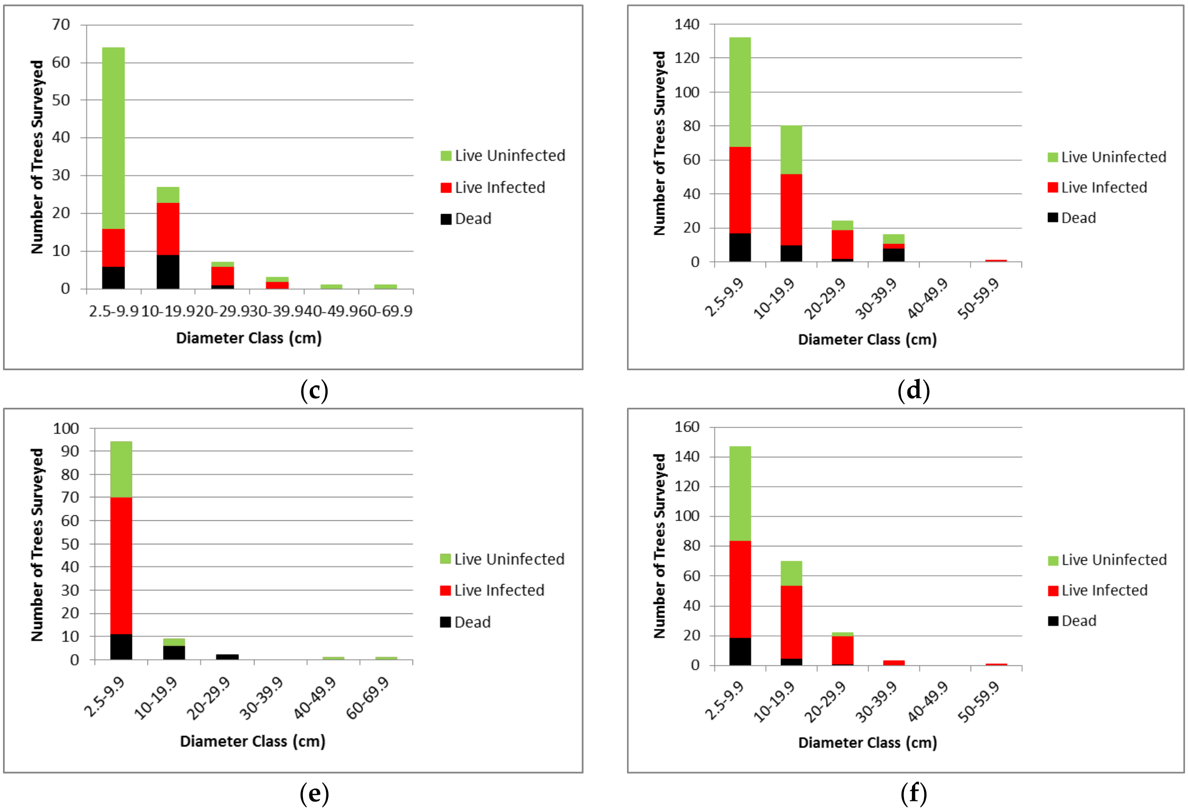

Figure 4. Number of whitebark pine trees surveyed by diameter class and health over the three survey periods: (**a**) Mount Rainier 2004, (**b**) North Cascades 2004, (**c**) Mount Rainier 2009, (**d**) North Cascades 2009, (**e**) Mount Rainier 2015, (**f**) North Cascades 2015/2016.

3.1.2. Saplings

Whitebark pine saplings were documented in every stand but in only 58-75% of study plots, depending on the year. Mortality was generally very low: 0.92 – 8.11% in North Cascades National Park Service Complex and 2.7-3.7% in Mount Rainier National Park. However, infection rates were higher in Mount Rainier National Park (24.6-50.8 %) than in North Cascades National Park Service Complex (17.1-24.8%) (Figure 5). A total of 429 live whitebark pine saplings were counted in Mount Rainier National Park and 588 in North Cascades National Park Service Complex over the three survey periods. A total of 7,721 saplings of eight additional species were counted in Mount Rainier National Park with density ranges of 520-843 stems/ha/year and 5,948 saplings of eight species with densities of 290-321 stems/ha/year in North Cascades National Park Service Complex.

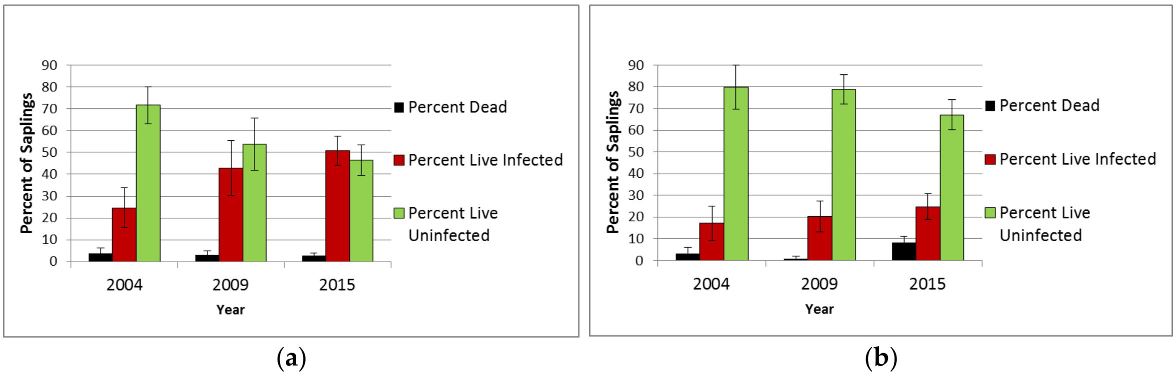

Figure 5. Mean proportions of dead, live infected, and healthy (uninfected) saplings in (**a**) Mount Rainier National Park and (**b**) North Cascades National Park Service Complex.

3.1.3. Seedlings

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We counted 111 whitebark pine seedlings in Mount Rainier National Park and 352 seedlings in North Cascades National Park Service Complex over the three survey periods. Whitebark pine seedlings occurred in all stands in North Cascades National Park Service Complex and all stands except for Frying Pan in Mount Rainier National Park, but seedlings were patchily distributed and only 43% of plots had whitebark pine seedlings. Seedlings of eight other species did occur in all stands for a total of 19,021 seedlings.

3.2 Landscape Patterns of Mortality, Infection and Prevalence

3.2.1. Tree Mortality

The best model for percent dead, based on the lowest Akaike Information Criterion (AICc), included effects of northness, eastness and park (Table 4). The model contained a random stand intercept and was of the form:

$$\text{Dead (\%)} = 39.8 - 6.3 \times \text{Northness} + 23.5\ \text{Eastness} - 19.6 \times \text{Park} + u_j.$$

The p-values associated with each parameter from the model were 0.72, 0.32, and 0.16 for northness, eastness and park, respectively. Though none of these p-values was individually significant, the model was the most likely given the data. The model indicated the percent of dead trees decreased with northness and increased with eastness, indicating more dead trees on south-east facing slopes. The percent of dead trees was lower at North Cascades National Park Service Complex than Mount Rainier National Park.

Table 4. Top five linear mixed effect models for predicting percent dead trees; the selected model is in bold.

Model Form	AICc	DeltaAICc
Percent Dead ~ Northness + Eastness + Park	**309.35**	**0.00**
Percent Dead ~ Slope + Northness + Eastness + Park	310.07	0.73
Percent Dead ~ Elevation + Northness + Eastness + Park	310.73	1.38
Percent Dead ~ Northness + Eastness + Park + dbh	311.10	1.76
Percent Dead ~ Elevation + Slope + Northness + Eastness + Park	311.60	2.26

We also looked at the third-best model, including northness, eastness, park and elevation, to evaluate the relationship between elevation and mortality. This model was less than two delta AIC values from the best model and could be considered equally likely given the data [21]. The interpretation of the model coefficients for northness, eastness, and park did not change with the addition of an elevation parameter, though the park coefficient became less significant due to the correlation between park and elevation. The direction of the model coefficient for elevation indicated the percent of dead trees decreased with increased elevation.

3.2.2. Infection

The best model for percent live infected included effects of northness, eastness and park (Table 5). The model parameters and form with random stand intercept u_j were:

$$\text{Live Infected (\%)} = 28.8 - 14.0 \times \text{Northness} + 10.1 \times \text{Eastness} + 9.8 \times \text{Park} + u_j.$$

The p-values associated with each parameter from the model are 0.25, 0.52, and 0.30 for northness, eastness and park, respectively. Though none of these p-values was individually significant, the model was the most likely given the data. The model indicated the percent of live infected trees decreased with northness and increased with eastness, indicating more infected trees on south-east facing slopes. The percent of live infected trees was also greater at North Cascades National Park Service Complex than Mount Rainier National Park.

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Table 5. Top five linear mixed effect models for predicting percent live infected trees; the selected best model is in bold.

Model Form	AICc	DeltaAICc
Percent Infection ~ Northness + Eastness + Park	**321.93**	**0.00**
Percent Infection ~ Slope + Northness + Eastness + Park	322.63	0.70
Percent Infection ~ Northness + Eastness + Park + dbh	323.76	1.83
Percent Infection ~ Slope + Northness + Eastness + Park + dbh	324.65	2.72
Percent Infection ~ Northness + Eastness	326.53	4.60

3.2.3. Prevalence

Models were fit with combinations of the following covariates: dbh, dbh^2, park, stand, year, the interaction between stand and year (Stand:Year), and the interaction between dbh and year (dbh:Year), as well as the intercept-only model. Model forms were restricted so that both main effects were included if the interaction term was in the model. In addition, models with the quadratic term for dbh (dbh^2) also contained the linear term. Correlated covariates, such as stand and park, were not fit in a model together. Models were chosen based on the corrected AICc for finite populations, where the smaller AICc indicated a more likely model given the data. The results of the model selection process for the top five models are presented in Table 6.

Table 6. Relative rating for top five models for prevalence; selected model is in bold.

Model Form	AICc	DeltaAICc
Prevalence ~ dbh + Stand + Year + dbh:Year	1007.2	0.0
Prevalence ~ Stand + Year + Stand:Year	1017.6	10.4
Prevalence ~ dbh + dbh^2 + Stand + Year + Stand:Year	1025.0	17.7
Prevalence ~ dbh + Stand + Year + Stand:Year	1030.2	23.0
Prevalence ~ Year	1035.6	28.4

The best model that predicted blister rust prevalence at Mount Rainier National Park and North Cascades National Park Service Complex included main fixed effects of dbh, stand, and year, and the interaction of dbh and year (dbh:Year). The model indicates the relationship between dbh and prevalence was different for each year. The inclusion of stand in the model as a factor allows us to predict this relationship for each stand as management purposes dictate (Figure 6, Table 7). In addition, we fit the same model with an effect of park, rather than stand, to visualize the relationship of dbh and prevalence by year for each park (Figure 7). In general, prevalence was greater at Mount Rainier National Park than at North Cascades National Park Service Complex for any given tree size.

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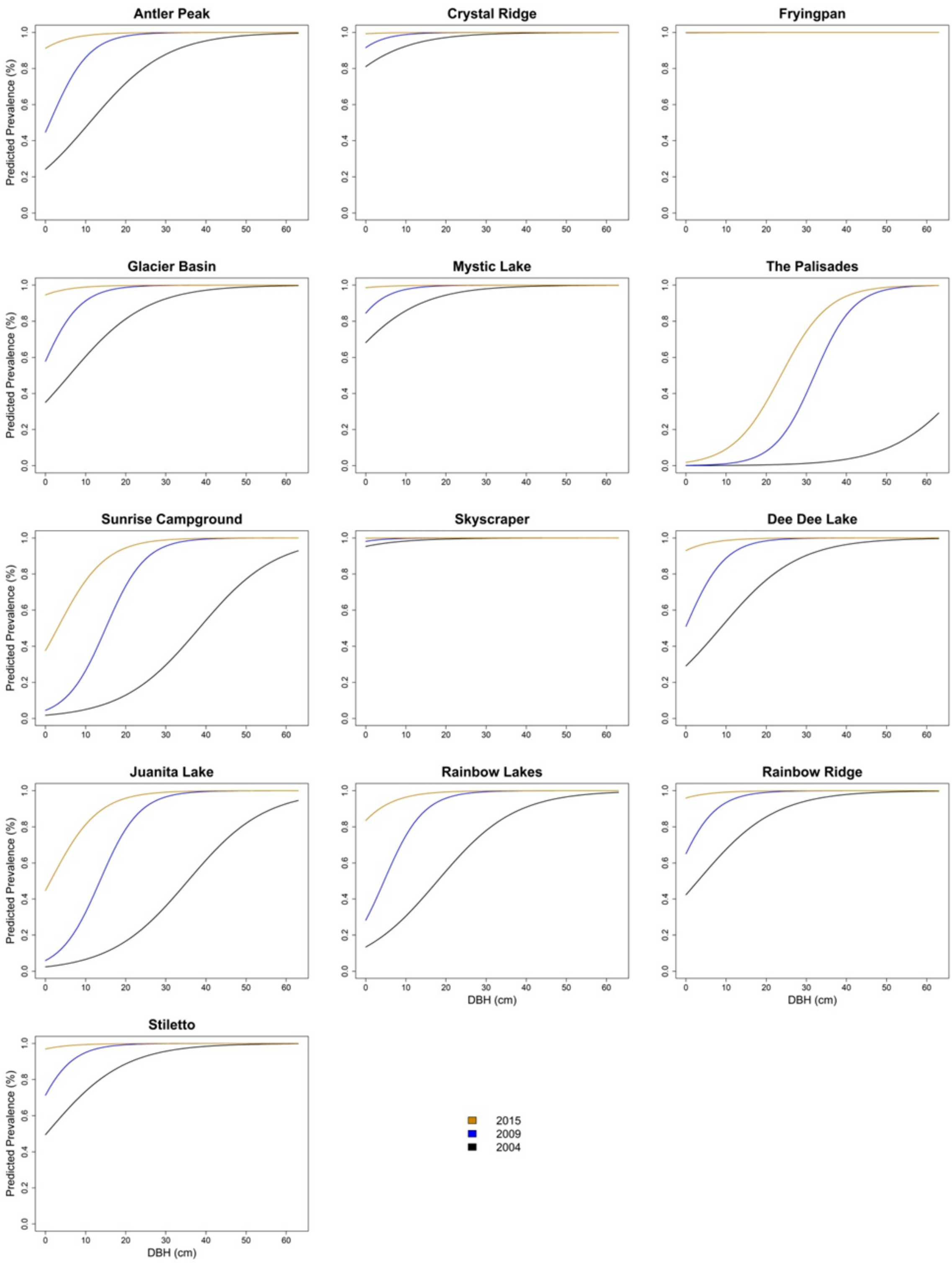

Figure 6. Model predicted prevalence across range of tree diameters (dbh in cm) for each stand.

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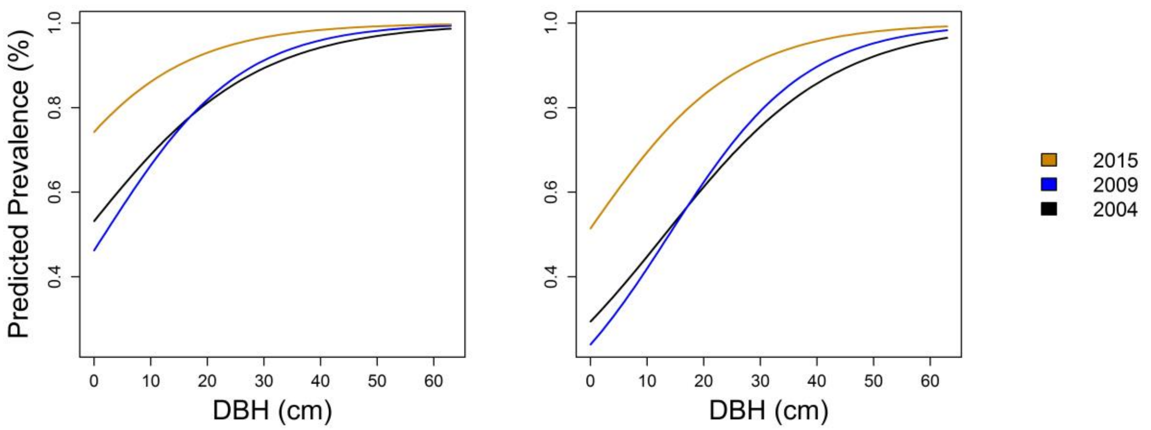
Table 7. Prevalence model parameters for the selected model

Parameter	Coefficient
dbh	-1.144
Stand: Crystal Ridge	2.597
Stand: Frying Pan	7.601
Stand: Glacier Basin	0.530
Stand: Mystic Lake	1.906
Stand: The Palisades	-6.301
Stand: Sunrise Campground	-2.844
Stand: Skyscraper	4.153
Stand: Dee Dee Lake	0.254
Stand: Juanita Lake	-2.550
Stand: Rainbow Lakes	-0.718
Stand: Rainbow Ridge	0.836
Stand: Stiletto	1.124
Year: 2009	0.932
Year: 2015	3.483
dbh: Year 2009	0.995
dbh: Year 2015	0.634



(**a**) (**b**)

Figure 7. Model predicted prevalence across range of tree diameters (dbh in cm) in (**a**) Mount Rainier National Park and (**b**) North Cascades National Park Service Complex.

3.2. Current Composition Status of Whitebark Pine Stands

We documented nine tree species in our study sites, eight in Mount Rainier National Park and six in North Cascades National Park Service Complex (Figure 8 (a) and (b)). Subalpine fir (*Abies lasiocarpa*), silver fir (*Abies amabilis*), Engelmann spruce (*Picea engelmannii*), mountain hemlock (*Tsuga mertensiana*), and whitebark pine were recorded in both parks. Subalpine larch (*Larix lyallii)* grows only in North Cascades National Park Service Complex and Alaska yellow cedar (*Chamaecyparis nootkatensis*), ponderosa pine (*Pinus ponderosa*), and lodgepole pine (*Pinus contorta*) were only recorded in Mount Rainier National Park plots. In all stands except Juanita Lake, subalpine fir was the dominant species, and whitebark pine contributed less than 20% of the total basal area in all stands in Mount Rainier and in two stands in North Cascades National Park Service Complex (Rainbow Ridge and Rainbow Lakes) (Figure 8). In Mount Rainier National Park, Glacier Basin had the highest percent of whitebark pine (17.4%). In North Cascades National Park Service Complex, whitebark pine comprised 43% and subalpine larch comprised 33% of basal area in the Juanita Lake

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area. In 2015/2016, basal area ranged from 9-45 square meters (m^2)/ha in Mount Rainier National Park and 6-16 m^2/ha in North Cascades National Park Service Complex stands.

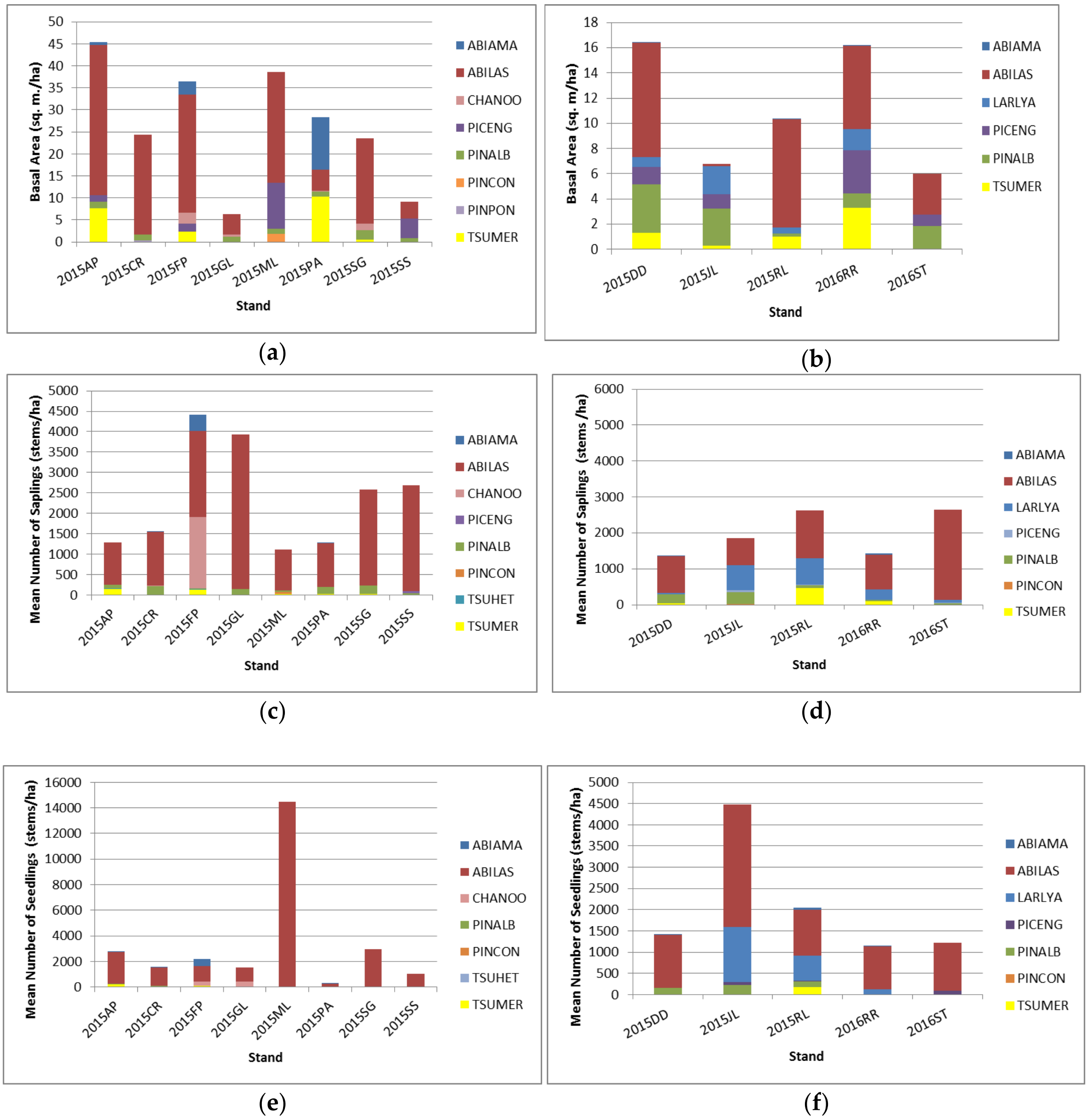

Figure 8. Stand composition in 2016/2016 for trees, saplings and seedlings. Mean tree basal area by species in (**a**) Mount Rainier National Park and (**b**) North Cascades National Park Service Complex. Mean sapling density by stand in (**c**) Mount Rainier National Park and (**d**) North Cascades National Park Service Complex. Mean seedling density by stand in (**e**) Mount Rainier National Park and (**f**) North Cascades National Park Service Complex. Species abbreviations are as follows: ABIAMA = silver fir (*Abies amabilis*), ABILAS = subalpine fir (*Abies lasiocarpa*), CHANOO = Alaska yellow cedar (*Chamaecyparis nootkatensis*), LARLYA = subalpine larch (*Larix lyallii*), PICENG = Engelmann spruce (*Picea engelmannii*), PINALB = whitebark pine (*Pinus albicaulis*), PINCON= lodgepole pine (*Pinus contorta*), PINPON = ponderosa pine (*Pinus ponderosa*), TSUHET = western hemlock (*Tsuga heterophylla*), and TSUMER = mountain hemlock (*Tsuga mertensiana*).

We recorded nine tree species in sapling and seedling surveys (Figure 8 (c), (d), (e), (f)). Ponderosa pine was not found in regeneration in either park. Western hemlock (*Tsuga heterophylla*) was recorded only in the Antler Peak stand in Mount Rainier National Park. Sapling density ranged from 1,120-4,413 stems/ha and whitebark pine was present in all stands, but contributed less than 19% of total stems with densities ranging from 25-343 stems/ha. Subalpine fir was generally the most numerous species comprising greater than 75% of all stems and densities of 755-2,594 stems/ha. Whitebark pine densities were highest in North Cascades National Park Service Complex in Juanita Lake (343 stems/ha) and Dee Dee Lake (243 stems/ha). Subalpine larch comprised 37% and 28% of Juanita Lake (685 stems/ha) and Rainbow Lakes (727 stems/ha), respectively. In Frying Pan in Mount Rainier National Park, subalpine fir comprised 48%, Alaska yellow cedar 39%, and whitebark pine less than 1% (25 stems/ha).

Seedling densities ranged from 247-14,465 stems/ha, but whitebark pine seedling density only ranged from 3-204 stems/ha, and no seedlings were found in two stands: Palisades (Mount Rainier National Park) and Stiletto (North Cascades National Park Service Complex). Subalpine fir was the most numerous in all stands, but Frying Pan had high densities of Alaska yellow cedar (17%) and silver fir (25%). Subalpine larch comprised 29% of all seedlings in Juanita Lake and Rainbow Lakes in North Cascades National Park Service Complex, where subalpine fir was 65% and 52% of stems density, respectively. Whitebark pine density was highest in Dee Dee Lake (141), Juanita Lake (204), and Rainbow Lakes (145).

4. Discussion

Over the 12 years of our study, white pine blister rust infection and mortality continued to increase in all of our study stands. Today, only 18% of whitebark pine trees in Mount Rainier National Park appear free of blister rust infection, 38% are infected, and 44% of all whitebark pines are dead. In North Cascades National Park Service Complex, 35% of all trees are uninfected, 44% are infected, and 21% of trees are dead. Although annualized mortality rates decreased between monitoring periods (2004-2009 and 2009-2015/2016), they remained higher in North Cascades National Park Service Complex (2.27%) than Mount Rainier National Park (1.47%). Smith et al [9] reported a decreasing annual mortality rate in the Canadian Rockies and hypothesized this could be indicative of natural selection. Optimistically, this seems a plausible explanation for the parks in our study, especially since resistance screening at the USDA Forest Service Dorena Genetic Resource Center found high levels of genetic resistance in Mount Rainier National Park families and high genotypic diversity in samples from both parks [22]. Progeny of parent trees from Mount Rainier National Park have shown among the highest levels of genetic resistance to white pine blister rust of any geographic sources to date as shown [23]. Resistance was assessed using cones collected from canker-free trees in 2007 and results of screening indicate that a percentage of remaining non-rust affected trees at Mount Rainier have genetic resistance to white pine blister rust. However, mortality is still increasing, the number of reproductive trees is decreasing, and predicted prevalence is higher in larger trees.

In both parks, regeneration (saplings and seedlings) was dominated by subalpine fir. Whitebark pine sapling densities generally ranged from 25-343 stems/ha, with the highest densities in two stands in North Cascades National Park Service Complex at Juanita Lake (343 stems/ha) and Dee Dee Lake (243 stems/ha). Seedlings densities were even lower, ranging from 3-204 stems/ha. The highest seedling densities occurred in North Cascades National Park Service Complex at Dee Dee Lake (141 stems/ha), Juanita Lake (204 stems/ha), and Rainbow Lakes (145 stems/ha). In some stands, fire exclusion may have resulted in lower densities of whitebark pine regeneration [24]. Whether these seedling and sapling densities are high enough to perpetuate these stands seems doubtful. McCaughey et al. [25] recommended planting hardy seedlings from potentially rust-resistant trees at a density of 479 stems/ha, based on an assumption of 50% survival.

National parks are charged with protecting naturally evolving levels of biodiversity. Loss of whitebark pine, from an introduced fungus, threatens to change the trajectory of these ecosystems [1, 2]. Our surveys paint a bleak picture of trends in whitebark pine population health and persistence, but there are enough unknowns to remain optimistic. Annualized mortality rates are decreasing, and genetic studies indicate high genotypic diversity in the two seed zones covering the parks and recommend these sites as candidates for selection of elite seed families based on potential adaption to pathogens [22]. In our surveys, we noted cones on trees greater than or equal to 10.0 cm dbh, but most of the uninfected trees surveyed in our most recent survey were less than 10 cm dbh. Additionally, our record of cone production is limited, and as reproductive trees decrease, low densities of trees and cone production could reach thresholds too low to attract Clark's nutcrackers, limiting dispersal [26, 27, 28]. In fact, Ray et al [29] recently documented that abundance of Clark's nutcrackers is strongly decreasing in Mount Rainier National Park and appears to be decreasing in North Cascades National Park Service Complex. Patterns in prevalence, mortality, infection, and regeneration are highly variable across our landscapes, pointing toward the need for increased monitoring, more genetic resistance screening, and development of stand specific restoration plans that include active management alternatives such as planting.

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