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Interactions of management and white pine blister rust on *Pinus strobiformis* regeneration abundance in southwestern USA

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Modelling natural regeneration is complex, and both natural and anthropogenic disturbances can alter forest trajectories. *Pinus strobiformis* (southwestern white pine, SWWP) is an important component of mixed conifer forests in the Southwest and management recommendations related to natural and planted regenerations are needed to guide conservation of SWWP in the face of an invasive disease (white pine blister rust, WPBR). Regeneration was surveyed across six mountain ranges, three silviculture treatments and two levels of disease severity in the Southwest US. Key findings were: (1) SWWP regeneration in stands with no recent management (<20 years) and high disease severity had unsustainable WPBR infection, (2) SWWP regeneration was less abundant but less likely to be infected in stands with recent management, (3) stands with high disease severity had fewer SWWP seedlings than stands with no or low disease severity and (4) SWWP regeneration densities were best predicted by other understory species abundance. We recommend silviculture treatments that reduce basal area to 9–10 $m^2\,ha^{-1}$ and leave large canopy openings to enhance natural SWWP regeneration. Without creating conditions for disease-free regeneration to reach reproductive maturity, some stands may lose SWWP as an overstory component. Results may help refine SWWP management guidelines and expand conservation efforts in forests threatened by WPBR.

Introduction

Natural regeneration is a complex, stochastic process and understanding the dynamics associated with tree regeneration is critical to forest sustainability (Nyland, 1996; Puhlick *et al.*, 2012; Bataineh *et al.*, 2013). Regeneration abundance can be difficult to predict because it may be directly or indirectly influenced by abiotic factors, biotic factors or interactions between both (Puhlick *et al.*, 2012; Fisichelli *et al.*, 2013). Abiotic factors such as geology, soils, climate and fire influence the potential for germination, establishment and survival of regeneration, and also influence the current biotic conditions of overstory and understory species composition and structure (Paluch, 2005; Puhlick *et al.*, 2012; Fisichelli *et al.*, 2013). Biotic disturbances, such as disease or insect outbreaks, or anthropogenic disturbances including previous silviculture treatments, can alter the trajectory of stand dynamics by creating establishment sites and increasing resource availability to regeneration (Gray *et al.*, 2005; Waring and O'Hara, 2005; Bataineh *et al.*, 2013). However, disease or insect outbreaks may also cause infection and mortality to regeneration, so the affected species may not be able to take advantage of increased resources.

Currently, forest structure in many dry mixed conifer forests of the Western US is considered dense and overcrowded with novel species mixtures due to disruption of historical fire regimes and intense logging practices (Gray *et al.*, 2005; Korb *et al.*, 2012; Rodman *et al.*, 2016). Silviculture treatments (reducing basal area (BA) through regeneration treatments or intermediate treatments, such as thinning) may be effective tools for successful regeneration of desired species (e.g. Stoddard *et al.*, 2015) but disease and insect disturbances can alter desired outcomes of such treatments and should be considered in order to create the most resilient future forest structures (Waring and O'Hara, 2005; Zald *et al.*, 2008). Anticipating changes, realignment of disturbed systems and promoting resilience are all important tools in adaptive management in the face of invasive pests and a changing climate (Waring and O'Hara, 2005; Millar *et al.*, 2007; O'Hara and Ramage, 2013; DeRose and Long, 2014). More effective silviculture treatments may be developed when primary abiotic and biotic factors, and regulatory patterns that govern natural regeneration success have been identified. Understanding the baseline ecology of natural regeneration is essential when species sustainability is threatened by an invasive pest (Schoettle and Sniezko, 2007; Loo, 2009; Goodrich and Waring, 2017).

Southwestern white pine (*Pinus strobiformis* Engelm., SWWP) is a five-needle pine species that occurs across mixed conifer forests throughout Mexico and more disjunctly in the Southwest

US (Arizona, New Mexico, southwestern Colorado and western Texas) (Little, 1971; Steinhoff and Andresen, 1971; Looney and Waring, 2013). Like all North American five-needle pine species, SWWP is susceptible to infection by *Cronartium ribicola* (J.C. Fisch.), the invasive fungal pathogen that causes white pine blister rust (WPBR). WPBR is a canker-causing disease that can lead to branch dieback, topkill and mortality of all sizes of SWWP (Conklin *et al.*, 2009; Looney *et al.*, 2015). Although SWWP is generally a minor species component in southwestern US, this species contributes to biodiversity and ecosystem resiliency as a food and habitat resource for wildlife and through the ability of mature trees to survive fire (Grissino-Mayer *et al.*, 1995; Samano and Tomback, 2003; Mattson and Arundel, 2013).

High rates of WPBR mortality, delayed forest recovery and loss of ecosystem services in other North America five-needle pine systems threatened by WPBR preview what may occur in some Southwest ecosystems with no proactive conservation and management strategies in place (Schoettle, 2004; Schoettle and Sniezko, 2007; Tomback and Achuff, 2010; Keane and Schoettle, 2011). Conservation strategies for other five-needle pines include mechanical cutting and prescribed burning to reduce competition and enhance natural regeneration and promoting rust resistance through planting genetically resistant seedlings (Schoettle and Sniezko, 2007; Keane and Schoettle, 2011; Schoettle *et al.*, 2012; Keane *et al.*, 2017). Genetic resistance to *C. ribicola* has been found in SWWP and current work is in progress to quantify the frequency of resistance across the SWWP range (Conklin *et al.*, 2009; Sniezko *et al.*, 2011; Waring *et al.*, 2017; Goodrich *et al.*, in press). The suitable distribution range for SWWP is expected to contract across southwestern US by 2090 in most future climate predictions (Crookston and Rehfeldt, 2008; Shirk *et al.*, 2018), furthering the need to enhance resiliency in SWWP forests.

Silviculture treatments best suited to stimulate and encourage SWWP regeneration are not well-defined, in part because we lack knowledge of the species' ability to grow and compete under different light regimes, amongst different species and across various stand conditions. Retaining overstory SWWP in silviculture prescriptions to increase SWWP regeneration is recommended, as is removing competing vegetation in intermediate treatments (Conklin *et al.*, 2009; Looney and Waring, 2012). Recent work illustrates that SWWP seedlings grow most quickly in open conditions created by regeneration treatments (Goodrich and Waring, 2017). There is a lack of published SWWP regeneration density data across both managed and non-managed southwestern US forests (Jones, 1971; Looney and Waring, 2013, but see Ffolliott and Gottfried, 1991; Looney and Waring, 2012; Goodrich and Waring, 2017).

A gradient of WPBR incidence exists across southwestern mixed conifer forests (Conklin, 2004; Fairweather and Geils, 2011; Looney *et al.*, 2015), creating opportunities to study SWWP regeneration dynamics with both the presence and absence of the disease. Our overarching goal was to survey for regeneration within non-managed stands and recently (<20 years) managed stands with a range of previous silviculture treatments and WPBR severities in order to provide better management recommendations to sustain SWWP through enhanced regeneration success. Results may be helpful in guiding conservation and management strategies of SWWP in the face of an invasive pathogen by providing direction on site selection and prescriptions for a variety of objectives (e.g. intermediate treatments, regeneration treatments and seedling outplanting efforts) when restoration is warranted (Schoettle and Sniezko, 2007; Keane and Schoettle, 2011). Our research questions were the following:

(1) What are average overstory and regeneration densities and proportions of SWWP compared with co-occurring species across six mountain ranges in southwestern US?
(2) What are average regeneration densities of SWWP across past silviculture treatments and two levels of WPBR severity?
(3) What between- and within-stand variables are associated with SWWP regeneration abundance?
(4) Do differences in SWWP size class distributions occur across silviculture treatments or WPBR severity levels?

Methods

Study area

We sampled mixed conifer forests with SWWP as a substantial overstory component across Arizona and New Mexico National Forest and Native American tribal land in 2012–13 (Figure 1; Goodrich and Waring, 2017). Our surveys included National Forests (NF) land, the Fort Apache Indian Reservation (owned by the White Mountain Apache tribe) in Arizona and the Mescalero Apache Indian Reservation (owned by the Mescalero Apache tribe) in New Mexico. We grouped stands by the mountain ranges (hereafter referred to as sites) in which they occurred: San Francisco Peaks (n = 3 stands), Mogollon Rim (n = 6), White Mountains (n = 11), Mt Graham (n = 4), Signal Mountain (n = 3) and Sacramento Mountains (n = 28) (Figure 1). Our sampling represented a range of topographic relative moisture index (TRMI) values, a scalar index ranging from 0 (xeric) to 60 (mesic) and intended to represent site moisture characteristics by combining aspect, slope and topographic variables (Parker, 1982).

Silviculture treatments and WPBR severity

We sampled stands across two current WPBR severity levels and three silviculture treatment categories within ranges of TRMI values. Within categories of low (10–<25), medium (>25–<40) and high (>40–55) TRMI values we attempted to sample two levels of WPBR severity (low and high, defined below), and include at least three stands within each of the following levels of silviculture treatments (representing a gradient of residual BA from high to low): (1) stands with no recent silviculture treatments (no tree removal or prescribed fires) in the past 20 years, (2) recent (<20 years prior) uneven-aged (UEA) regeneration treatments or timber stand improvement treatments and (3) recent (<20 years prior) even-aged (EA) regeneration treatments. UEA structures were generally created through single-tree selection regeneration methods, thinning or a fuels treatment (Supplementary data Table S1). EA structures were created through establishment phase of shelterwood with reserves or clearcut with reserves regeneration methods, leaving two-aged residual structures (Supplementary data Table S1). EA regeneration methods were only found on the Mescalero Apache Indian Reservation in the Sacramento Mountains. We sampled a minimum of three stands per silviculture treatment in every TRMI category with the exception of high TRMI (>40–55), where only two recently-managed UEA stands and one recently-managed two-aged stand were sampled. Stands with high WPBR severity were defined as those with >10% stand incidence of WPBR (percent of overstory trees infected with WPBR, range: 0–88%) and at least 5% mean stand severity (crown dieback due to WPBR cankers, range: 0–25.8%) of infected trees. Stands with no WPBR and low severity WPBR were grouped together because early effects of the disease should not affect overstory or understory composition. Five percent

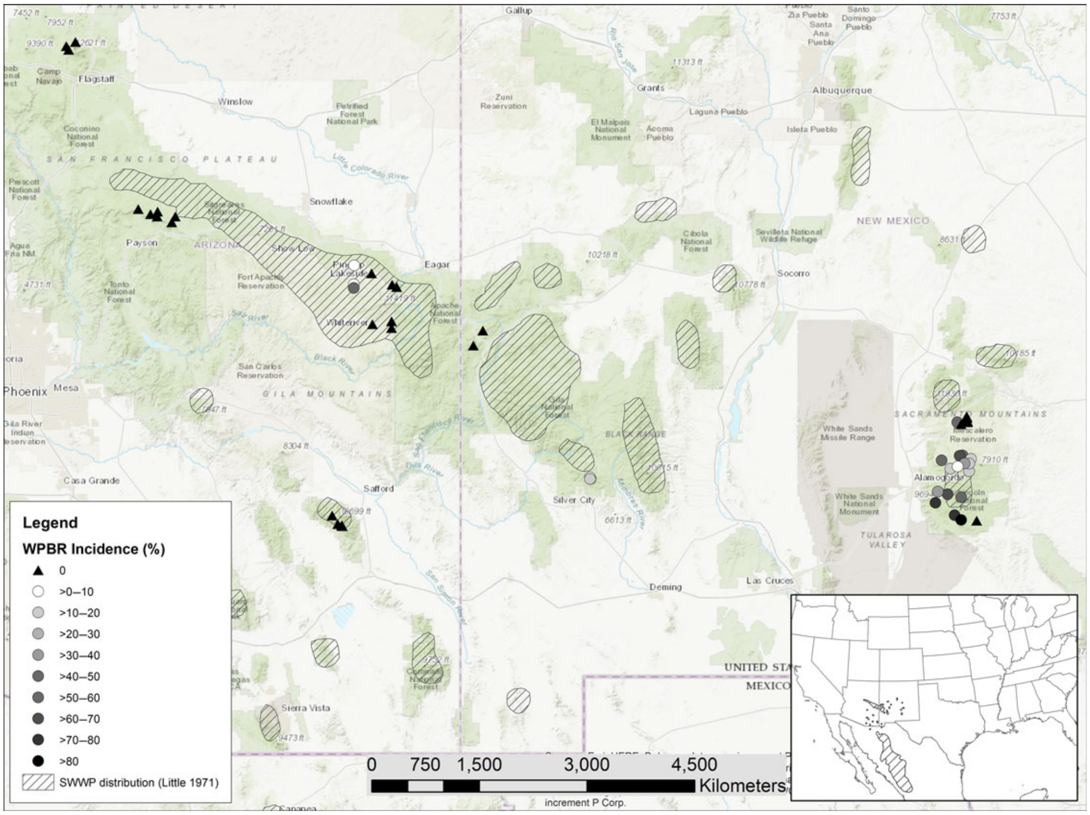

Figure 1 Fifty-five stands sampled for regeneration across six mountain ranges (sites) in Arizona and New Mexico. White pine distribution layer credit of United States Geological Survey (2006) based on Little (1971). WPBR = white pine blister rust.

mean severity was selected as the cutoff point where changes in overstory crown conditions could influence understory conditions and has been used as a cutoff between healthy and declining health at the individual tree level in previous research (Kearns and Jacobi, 2007). There were no pre-treatment SWWP regeneration density data or WPBR severity data available for any surveyed stands.

Stand selection and plot sampling

Stands were defined by stand delineation boundaries on NF lands or treatment boundaries on tribal lands. We followed stand selection methods defined in Looney and Waring (2012) and described in Goodrich and Waring (2017). In brief, we selected stands to scout for suitability by limiting our queries to NF stand exam data that contained $\geq$6.9 $m^2\,ha^{-1}$ BA of SWWP. Permanent plot data were used as scouting information for stands on the Fort Apache Reservation (Looney and Waring, 2012) and local knowledge was used to identify potential reconnaissance stands on the Mescalero Apache Indian Reservation (William Hornsby, pers. comm., Bureau of Indian Affairs Branch of Forestry, 2012–13) where stand exam data were unavailable. Within all potential stands, a random point was generated within the stand boundaries and located in the field using Global Positioning System (GPS). Plots (50 m × 20 m, 0.1 ha) were established if a minimum SWWP overstory density occurred and randomly relocated within the stand if adequate densities did not occur (see Goodrich and Waring, 2017 for details).

Fifty-five stands were surveyed using a combination of 0.1 ha rectangular plots and transects with three 0.0016 ha plots per transect using the same methods as described in Goodrich and Waring (2017). Each 0.1 ha rectangular plot was oriented parallel to slope contour and size corrected for slope. For all overstory trees, we recorded species, diameter at breast height (DBH) and condition (live or dead). Tree height, height to base of live crown, crown widths and damage agents were measured on all overstory SWWP stems. All SWWP were visually inspected using binoculars for signs or symptoms (e.g. aecia, branch flagging, branch swelling, squirrel chewing or roughened bark) of WPBR (Looney *et al.*, 2015). Crown dieback due to WPBR was recorded by tracing tree crowns and dieback (branch flagging and recently killed branches) on transparencies and later estimated using Adobe Photoshop CS5.1 (Millers *et al.*, 1991). If a tree had $\leq$2 branch cankers, an estimate of dieback was visually made, bypassing the transparency sketch (17/83 trees with visual crown dieback estimated). Additional site characteristics measured at each stand included GPS coordinates, percent slope, aspect and topographic and slope positions. Northness (−1 to 1 where −1 represents south and 1 represents north) and eastness (−1 to 1, west to east, respectively) were calculated from aspect (Roberts, 1986). Derived normalized 30-year mean (1961–90) climate variables were estimated from stand coordinates and elevations using thin plate spline surfaces of Rehfeldt (2006).

Three 0.01 ha (10 m × 10 m) subplots were nested within the 0.1 ha plot located at distances of 0–10, 20–30 and 40–50 m above or below the centre line of the rectangular plot. All seedlings (<140 cm height) and saplings ($\geq$140 cm height and $\leq$12.75 cm DBH) were measured for species, height, crown width and condition in each subplot. Within each subplot a line intercept technique (Husch, 2002) was used by placing a ground cover transect across the diagonal of the plot and ground cover type (i.e. grass, forb, shrub, litter, rock, bare, other) was recorded every 0.3 m. Canopy closure was averaged over four cardinal directions at each subplot centre with a spherical densiometer held at 1.2 m above the ground.

A random azimuth and distance from the plot corner were used to start an additional 50 m transect with three additional 4 m × 4 m (0.0016 ha) regeneration subplots at 0, 25 and 50 m. A variable radius plot using an angle gauge with a BA factor of 2.3 $m^2\,ha^{-1}$ was used to record overstory species BA in each subplot. All overstory and understory measurements were similar to those made in the 0.1-ha rectangular plot in the first transect, but overstory SWWP stems were not tagged and severity was not estimated with transparencies. In each subplot ground cover was estimated using a 1m × 1 m square and crown closure was estimated using a spherical densitometer at 1.2 m above the ground at subplot centre.

Statistical analyses

All statistical analyses were completed in *R* statistical programing environment (v. 3.1.1, R Core Team, 2014). We used Kruskal–Wallis (K–W) one-way analysis of variance by ranks tests, which are non-parametric tests to assess whether independent samples originate from the same distribution, to compare regeneration densities and probabilities across sites (n = 6 sites), silviculture treatment and WPBR severity levels (n = 3 levels of silviculture treatment and two levels of WPBR severity). Kendall's τ correlation analyses were used to compare SWWP seedling and sapling densities to between- and within-stand variables. Subplot-level densities were compared with subplot-level factors (e.g. other species densities, BA and percent canopy closure) and mean stand densities relationship with between-stand variables (e.g. climate variables, percent slope and aspect) were assessed. Because of the wide geographic area that was sampled, common species varied between stands. Regeneration (with seedlings and saplings separated as they may occupy different niche spaces) and overstory species were grouped into (1) common shade-tolerant species: white fir (*Abies concolor* (Gord. & Glend.) Lindl. Ex Hildebr), corkbark fir (*Abies lasiocarpa* (Hook.) Nutt. var. *arizonica* (Merriam) Lemmon), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and blue spruce (*Picea pungens* Engelm.) and (2) common shade-intolerant species: trembling aspen (*Populus tremuloides* Michx.), Gambel or other oak species (*Quercus gambelii* Nutt. or various species of *Quercus*), alligator juniper (*Juniperus deppeana* Steud.), Utah juniper (*Juniperus osteosperma*), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) and New Mexico locust (*Robinia neomexicana* A. Gray). SWWP were neither grouped nor were Douglas-fir (DF; *Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (PP; *Pinus ponderosa* Dougl. ex Laws) due to their common occurrence across our study areas.

Hierarchical, mixed-effects models were used to compare SWWP regeneration densities across silviculture and WPBR severity levels and build predictive models. Normally, discrete count data are modelled using Poisson regression, so we modelled our seedling and sapling data as stem counts per subplot. Counts within the three smaller subplots were scaled to 0.01 ha counts and the three nested 0.01 ha subplots were averaged (four total subplots per stand). Regeneration count data often exhibit overdispersion (i.e. the variance is greater than the mean) and in such cases a negative binomial (NB) model is more appropriate where the mean and variance can be independently estimated (Ridout *et al.*, 2001; Li *et al.*, 2011; Crotteau *et al.*, 2014). We confirmed SWWP seedling and sapling data were overdispersed by using the 'dispersiontest' function in package 'AER' (Supplementary data Table S2). Regeneration data also tend to contain more zeros than would be expected under a normal Poisson or NB distribution (zero-inflation) (Crotteau *et al.*, 2014). We confirmed SWWP seedling and sapling data were zero-inflated by comparing the observed and expected proportions of zeros in each data set under a Poisson distribution (Supplementary data Table S2). Zero-inflation is typically accounted for by jointly modelling the zero/non-zero component (using logistic regression) and count component (which can include zeros under a Poisson or NB distribution) (Li *et al.*, 2011). The zero-inflated NB (ZINB) distribution provides flexibility in the variance assumptions and accounts for overdispersion, so we modelled the data with a ZINB probability mass function (Supplementary data equations (S1) and (S2)). Because our data were hierarchical, with subplots nested within stands and stands clustered within sites, we used a mixed-effects modelling approach, which allows for the inclusion of both fixed and random effects (Supplementary data equation (S3)). Models included nested random effects of 'site' and 'stand within-site' and were fitted using the 'glmmADMB' package in *R* (Skaug *et al.*, 2011). To answer our research questions, we developed two ZINB models for both SWWP seedling and sapling counts that included the following explanatory variables:

- Silviculture treatment, WPBR severity and an interaction term included as fixed effects (research question 2).
- Silviculture treatment, WPBR severity, an interaction term and between- and within-stand variables included as fixed effects and reduced to retain best models (research question 3).

We chose other potential between- and within-stand variables if they were significant ($P \leq 0.05$) in the Kendall's τ correlation analyses. We then took all potential covariates and reduced them further by viewing all possible ZINB univariate models and only keeping variables that were significantly related to SWWP seedling or sapling counts at $P \leq 0.10$. We then built predictive ZINB models by modelling all combinations of the significant variables and compared the models with Akaike's information criteria (AIC) (Akaike, 1974), the change in AIC value for each model relative to the best model (ΔAIC) and Akaike's weights (AIC_w) ('qpcR' package, akaike.weights function, Spiess, 2014) (Burnham and Anderson, 2002). We chose the best candidate model as the model with the lowest AIC and in which all covariates were significant at $P \leq 0.05$. We assessed the predictive ability of the top candidate models by examining plots of observed and predicted seedling and sapling frequencies (Li *et al.*, 2011; Auty *et al.*, 2014) and calculated the root mean square error (RMSE) from the predicted and observed values for each candidate model.

Kolmogorov–Smirnov (K–S) bootstrap tests (1000 replicates) were used to compare SWWP diameter distributions (in 10-cm DBH classes) between WPBR severities within each silviculture treatment level ('Matching' package, ks.boot function, Sekhon, 2011). We also compared distributions of WPBR-infected SWWP between silviculture treatments in high WPBR severity stands with K–S tests. We used diameter distributions to calculate ratios of each diameter size class to the next largest size class. The average ratio across size classes in none/low WPBR and non-managed stands within each site was used to calculate the number of seedlings needed to regenerate a stand if one tree per hectare (TPH) of SWWP was desired in the largest size class (≥62.7 cm DBH). The number of seedlings needed in high WPBR stands was calculated by taking this value and dividing it by the average incidence of WPBR-infected TPH to account for WPBR-induced mortality.

Results

SWWP seedlings occurred in 86% and SWWP saplings occurred in 84% of the 55 stands sampled, and densities ranged from 0 to 3 931 seedlings ha^{-1} and from 0 to 1 304 saplings ha^{-1} per stand. There were differences in mean ranks for SWWP seedling densities but not SWWP sapling densities across sites (Table 1 and Figure 2a,c). The San Francisco Peaks had the highest SWWP seedling and sapling densities (Figure 2a,c). The proportion of SWWP seedlings to total seedling densities varied across sites (Table 1) and ranged from 2.7% in the Sacramento Mountains to 42.5% on the San Francisco Peaks (Figure 2a). The ratio of SWWP saplings to total sapling densities also varied widely, from 7.1% on Mount Graham to 60.6% on the San

Table 1 Kruskal–Wallis' (K–W) Chi-squared *H* statistics, degrees of freedom (df) and *P*-values for common species regeneration densities (trees per hectare, TPH), proportions and overstory basal areas (BA, $m^2\ ha^{-1}$) amongst six sites and six silviculture treatment/WPBR disease severity levels. Kruskal–Wallis' *H* statistics significant at $P \leq 0.05$ (bolded *P*-values) indicate differences in the distribution of ranks.

	Kruskal–Wallis mean ranks by site ($n = 6$)		Kruskal–Wallis mean ranks in silviculture treatment/disease severity levels ($n = 6$)	
	K–W Chi-squared	*P*-value (df = 5)	*K–W Chi-squared*	*P*-value (df = 5)
SWWP[a] seedlings	18.79	**0.002**	9.440	0.093
SWWP saplings	5.69	0.337	10.420	0.064
SWWP seedlings/total seedlings	23.95	<**0.0001**	9.370	0.100
SWWP saplings/total saplings	8.03	0.155	10.970	0.052
DF[b] seedlings	6.38	0.271	16.540	**0.005**
DF saplings	2.18	0.824	3.500	0.623
PP[c] seedlings	34.31	<**0.0001**	20.770	**0.001**
PP saplings	7.82	0.166	2.680	0.750
Shade-intolerant seedlings	63.66	<**0.001**	24.280	**0.0002**
Shade-intolerant saplings	10.51	0.062	9.180	0.102
Shade-tolerant seedlings	28.02	<**0.001**	8.440	0.134
Shade-tolerant saplings	23.63	**0.0002**	2.350	0.799
Live SWWP BA	22.91	**0.0003**	15.240	**0.009**
Dead SWWP BA	29.87	<**0.0001**	11.830	**0.037**
Live SWWP BA/Live total BA	13.37	**0.020**	11.84	**0.037**
Live DF BA	16.77	**0.005**	57.230	**0.0001**
Live PP BA	76.36	<**0.0001**	24.730	**0.0002**
Live shade-intolerant BA	84.75	<**0.0001**	25.370	**0.0001**
Live shade-tolerant BA	41.71	<**0.0001**	6.530	0.258

[a]SWWP = southwestern white pine.
[b]DF = Douglas-fir.
[c]PP = ponderosa pine.

Francisco Peaks (Figure 2c), although mean ranks were not significantly different (Table 1). Mean ranks did not differ between sites for DF seedlings or saplings, but there were site-to-site differences in PP seedlings, shade-intolerant seedlings/suckers and shade-tolerant seedlings and saplings (Table 1 and Figure 2a,c). Mean overstory BA ranks differed between sites for live SWWP, dead SWWP, live DF, live PP, live shade-tolerant and live shade-intolerant species (Table 1 and Figure 3a). In general, the San Francisco Peaks had the highest SWWP live BA and Mount Graham had the highest total BA (Table 1 and Figure 3a). The proportion of SWWP BA significantly varied across sites (Table 1) and ranged from 16.3% on Signal Peak to 50.8% on the San Francisco Peaks (Figure 3a). Mean rank differences of some between-stand variables occurred among sites, including elevation, climate variables (mean annual temperature, mean annual precipitation and the proportion of mean annual precipitation that occurs in July, August and September) and percent canopy closure (Supplementary data Table S3).

There was considerable variation in densities of several species of regeneration across the six levels of silviculture treatments and WPBR severity but there were no differences in mean ranks in SWWP seedling or SWWP sapling densities (P = 0.06 and 0.09, respectively) or the proportions of SWWP seedlings and saplings to total seedling and sapling densities (P = 0.10 and 0.052, respectively) across the six levels in the non-parametric analyses (Table 1 and Figure 2b,d). However, we found significant effects of both silviculture treatment and WPBR severity on SWWP regeneration abundance with the ZINB models that supported trends in non-parametric analyses. A significant effect of silviculture treatment occurred on SWWP seedling counts (P = 0.041) where SWWP seedling counts were greater in non-managed and recently-managed two-aged stands compared with recently-managed UEA stands (Figure 4). There was also a significant effect of WPBR on seedling counts; they were lower in high WPBR severity stands compared with none/low WPBR severity stands across all silviculture treatments (P = 0.032) (Figure 4). SWWP sapling counts were higher in non-managed stands compared with recently-managed two-aged and UEA stands in low/none WPBR severity areas (P = 0.034, Figure 4). There was no effect of WPBR severity alone on sapling counts (P = 0.99) but the interaction between management and WPBR severity was significant (P = 0.027). There were higher SWWP sapling counts in high WPBR severity stands in recently-managed two-aged residual structures compared with none/low severity stands with a two-aged structure (Figure 4, P = 0.03).

Overstory species composition and mean BA varied significantly across silviculture treatment and WPBR severity levels (Table 1 and Figure 3b). Live SWWP, dead SWWP, live DF, live PP and live shade-intolerant species BA all varied across levels; non-managed stands had the highest total BA (>25 $m^2\ ha^{-1}$), recently-managed two-aged structures had the lowest total BA

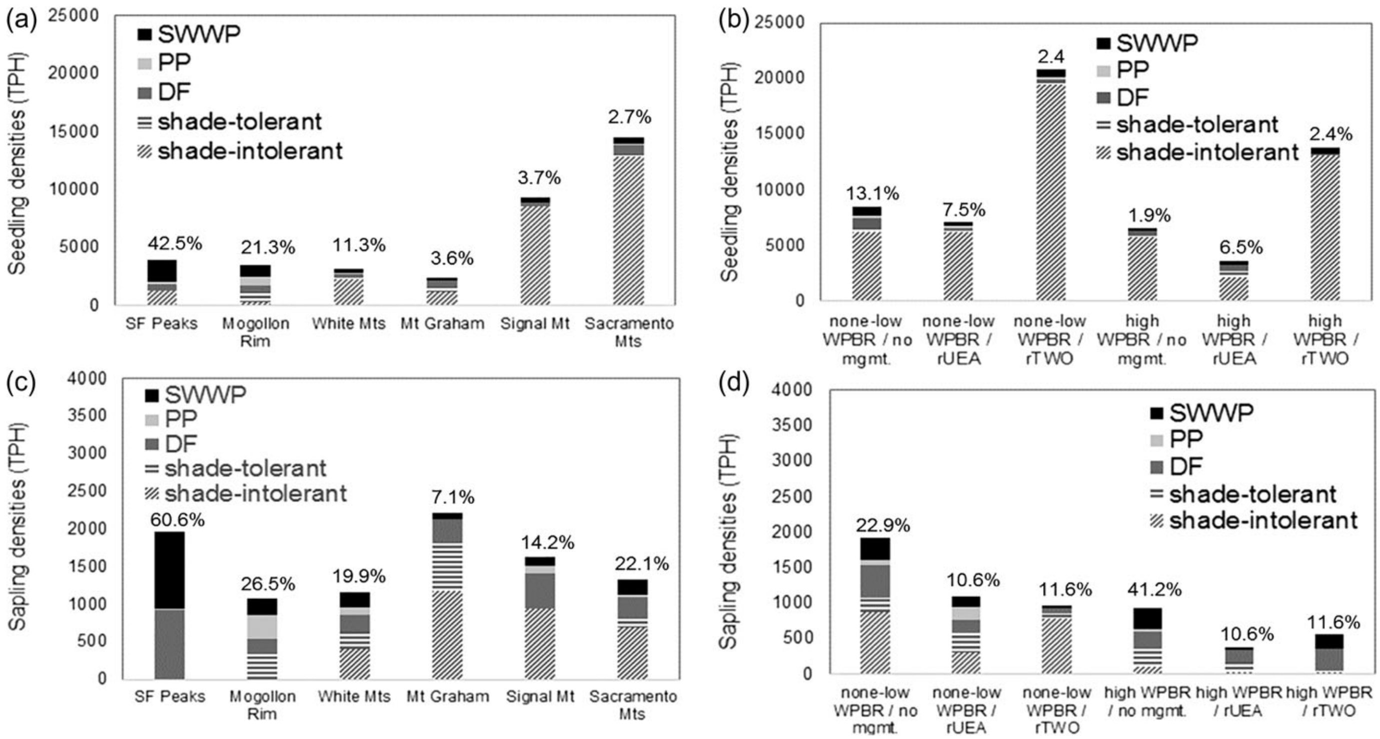

Figure 2 (a–d) Mean southwestern white pine (SWWP), ponderosa pine (PP), Douglas-fir (DF), shade-tolerant and shade-intolerant regeneration densities across six sites in Arizona and New Mexico (a. seedlings and c. saplings) and across six silviculture treatment/white pine blister rust (WPBR) severity levels (b. seedlings and d. saplings). Percentages indicate proportion of SWWP as total regeneration TPH at the subplot level (Note: subplots without regeneration were calculated as 'NA' and not zero, so subplot-level percentages are slightly different than strata-level means in the graph). Silviculture treatments: no recent mgmt (20 years), recent (20 years) uneven-aged (rUEA) treatments and recent (20 years) two-aged (rTWO) treatments. Sites ordered by longitude (west–east).

(<10 m^2 ha^{-1}) and recently-managed UEA structures had total BA between these values (~20 m^2 ha^{-1}) (Figure 3b). The proportion of SWWP BA to total BA varied across levels and was generally highest in recently-managed two-aged stands (Table 1 and Figure 3b). Mean ranks of between-stand attributes were commonly variable; factors that varied between management and disease levels were eastness, percent slope, percent canopy closure and proportion of mean annual precipitation that occurs July–September (Supplementary data Table S3). Stands with high WPBR severity were more east-facing than the stands with none/low WPBR severity (Supplementary data Table S3). Recently managed stands were less steep than non-managed stands and two-aged stands had lower percent canopy closure than non-managed or recently-managed UEA stands (Supplementary data Table S3).

Non-managed stands had the largest proportion of WPBR-infected SWWP regeneration stems in high severity stands (30% of regeneration infected), 4.0% were infected in recently-managed UEA stands and two-aged structures had no regeneration infected in high severity areas (Table 2). Incidence of WPBR in overstory trees and mean crown dieback of infected trees were highest in non-managed, high severity stands but high across all silviculture treatments in stands with high severity WPBR (Table 2). There were no significant differences in mean ranks of *Ribes* species densities (the most common alternate host in the WPBR disease cycle in the Southwest) across silviculture treatment/WPBR severity levels, although the highest densities occurred in UEA stands and lowest in recently-managed two-aged structures (Table 2).

Most factors significantly associated with SWWP seedling and sapling densities varied within stands, and several of these variables were other species' regeneration abundance. An increase in both DF and PP seedling densities was significantly correlated with an increase in SWWP seedlings (τ = 0.292 and 0.289, respectively; Supplementary data Table S4). Increases in shade-tolerant sapling densities, shade-tolerant BA and downed-woody debris ground cover were associated with decreases in SWWP seedlings (τ = −0.304, −0.269 and −0.19, respectively; Supplementary data Table S4). The only climate variable that correlated significantly with SWWP seedling densities was the proportion of mean annual precipitation that occurs in July through September (τ = −0.221; Supplementary data Table S4). There were no significant correlations between SWWP sapling densities and any climate or between-stand variables. An increase in DF sapling densities was significantly correlated with increasing SWWP sapling densities (τ = 0.394; Supplementary data Table S4). SWWP sapling densities were also significantly correlated with an increase in canopy closure (τ = 0.35), live SWWP BA (τ = 0.242) and live DF BA (τ = 0.185) (Supplementary data Table S4).

The top candidate ZINB model predicted a decrease in SWWP seedling counts in high WPBR severity stands, with higher

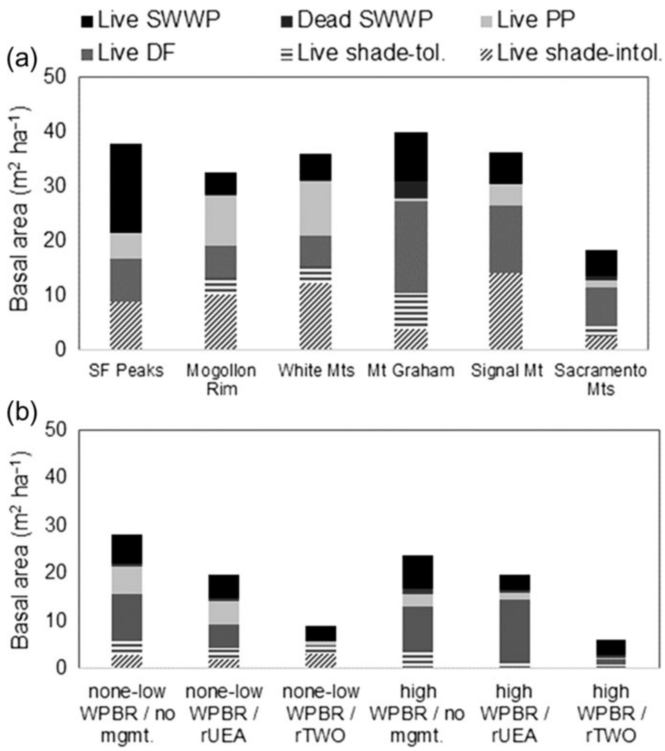

Figure 3 (a and b) Southwestern white pine (SWWP), ponderosa pine (PP), Douglas-fir (DF), shade-tolerant and shade-intolerant overstory basal areas (BA, $m^2\ ha^{-1}$) across six sites in Arizona and New Mexico (a) and six silviculture treatment/white pine blister rust (WPBR) severity levels. Percentages indicate proportion of SWWP as total BA at the subplot level (Note: subplots without overstory trees were calculated as 'NA' and not zero, so subplot-level percentages are slightly different than strata-level means in the graph). Silviculture treatments: no recent mgmt, recent uneven-aged (rUEA) treatments and recent two-aged (rTWO) treatments. Sites ordered by longitude (west–east).

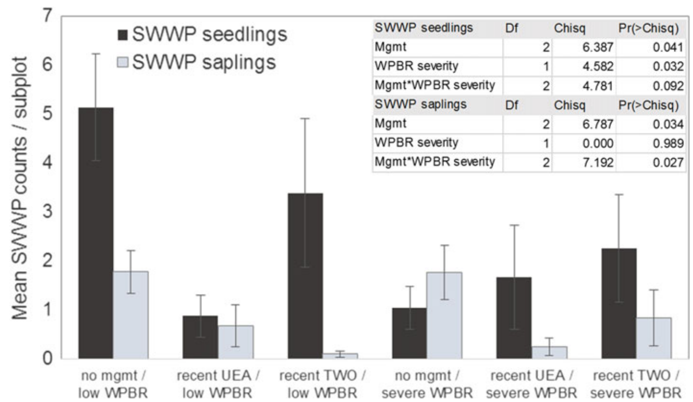

Figure 4 Seedling and sapling zero-inflated negative binomial mixed effect model estimations (seedling and sapling counts per subplot) for the interaction of silviculture treatment (no mgmt, recently treated uneven-aged residual structure (rUEA) and recently treated two-aged residual stand (rTWO) and WPBR severity (none/light and heavy) levels. df = degrees of freedom; Chisq = Chi-square; Pr(Chisq) = P-value. Error bars represent ±1 SE.

percent ground cover of downed-woody debris and in recently-managed UEA stands (Tables 3 and 4). A significant interaction between WPBR severity and DF seedling count indicated that the relationship between SWWP seedling counts and DF seedling count varied between disease levels (Tables 3 and 4). This model had a ΔAIC = 9.0 compared with the saturated model, indicating a better fit (Table 3). The RMSE of the top model was 2.55 seedlings (the range of SWWP seedlings was 0–69 seedlings per subplot). The top candidate SWWP sapling count ZINB model predicted higher SWWP sapling counts in recently-managed, two-aged stands and with increasing canopy closure (Tables 3 and 4). A significant interaction between two-aged stands and canopy closure indicates the relationship between SWWP sapling count and canopy closure varied between management levels. The top model had an AIC value 8.4 lower than the saturated model and a RMSE of 1.21 saplings (range of SWWP saplings from 0 to 31 saplings per subplot; Table 3). The best ZINB models predicted zero counts extremely well but were less accurate in predicting regeneration counts above six stems per subplot (Supplementary data Figure S1).

WPBR severity was not associated with a change in the shape of diameter distributions within any silviculture treatment (Figure 5a–c). There was no difference between diameter distributions of SWWP TPH between none/low and high WPBR severity levels in non-managed stands, (Figure 5a; K–S test D = 0.25, p_{ks} = 0.98), recently-managed UEA stands (Figure 5b; D = 0.25, p_{ks} = 0.98) or recently-managed two-aged stands (Figure 5c; D = 0.375, p_{ks} = 0.63). Management did not affect the diameter distributions of WPBR-infected SWWP either between non-managed stands and recently-managed, two-aged stands (D = 0.625, p_{ks} = 0.061; Figure 5a,c) or between non-managed stands and recently-managed UEA stands (D = 0.5, p_{ks} = 0.18; Figure 5a,b).

In non-managed stands, there were large ratios between sapling-sized trees and the 12.7–22.7 cm DBH class, indicating most sapling-sized trees are not likely to reach the next size class in these stands (Figure 5a). Seedling densities necessary to maintain one TPH of SWWP ≥62.7 cm DBH in none/low WPBR severity, non-managed stands were calculated (mean ratio = 2.04). In order to maintain one SWWP TPH >62.7 cm DBH on average, there need to be approximately ≥150 SWWP seedlings per hectare. Trees in non-managed, high severity stands averaged 46% WPBR infection (range = 19.6–63% across diameter classes; Figure 5a), so in order to maintain one TPH of SWWP ≥62.7 cm DBH in non-managed, high severity WPBR stands there should be ≥300 SWWP seedlings ha^{-1} to account for potential mortality. Sixty percent of stands (n = 33/55) in this study met the >150 TPH criteria; five were recently-managed UEA stands and six were recently-managed two-aged stands. Eighteen stands met the >300 TPH seedling criteria, and four were recently-managed. The mean ratio and minimum seedling density (without accounting for WPBR infection) for non-managed, none/low WPBR severity stands for each site were as follows: San Francisco Peaks ratio = 2.8, minimum seedlings ha^{-1} = 170; Mogollon Rim ratio = 2.1, minimum seedlings ha^{-1} = 40; White Mountains ratio = 2.1, minimum seedlings ha^{-1} = 40; Mt Graham ratio = 3.1, minimum seedlings ha^{-1} = 290; Signal Peak ratio = 3.1, minimum seedlings ha^{-1} = 290 and Sacramento Mountains ratio = 2.5, minimum seedlings ha^{-1} = 100.

Table 2 Disease related variable means and standard deviation (SD) and Kruskal–Wallis' one-way analysis of variance by rank test for differences in ranks among disease and silviculture treatment levels. Kruskal–Wallis' Chi-squared (*H* statistic) significant at $P \leq 0.05$ (bolded values) indicate differences in the distribution of ranks between silviculture treatments and disease levels (*n* = number of stands in each level).

Silviculture treatment[a]	Disease levels[b]	*n*	SWWP regeneration WPBR incidence (%)		SWWP overstory WPBR incidence (%)		SWWP crown dieback from WPBR (%)		Ribes density (SPH[c])	
			Mean	SD	Mean	SD	Mean	SD	Mean	SD
No mgmt	None/low severity	26	0.02	0.13	0.06	0.38	0.37	0.98	64.8	144.7
rUEA		9	0.00	0.00	0.01	0.46	0.25	0.67	81.0	153.8
rTWO		6	0.00	0.00	0.06	0.16	0.38	0.80	28.6	75.6
No mgmt	High severity	8	0.30	0.38	0.50	0.20	13.41	6.64	58.3	101.9
rUEA		3	0.04	0.09	0.49	0.04	9.76	3.02	244.4	234.1
rTWO		3	0.00	0.00	0.15	0.25	11.44	8.94	0.0	0.0
Kruskal–Wallis Chi-squared, P-value (df[d] = 5 for all)			**H = 55.8, P < 0.0001**		**H = 72.16, P < 0.0001**		**H = 76.34, P < 0.0001**		*H = 6.18, P = 0.289*	

[a]Silviculture treatments: rUEA = recently-managed, uneven-aged; rTWO = recently-managed, two-aged, disease levels.
[b]WPBR severity level (none/low severity and high severity).
[c]Stems per hectare.
[d]Degrees of freedom.

Table 3 Zero-inflated negative binomial (ZINB) models predicting southwestern white pine (SWWP) seedling and sapling counts (per subplot). Shaded value indicates the top candidate model based on AIC and all covariates significant at $P < 0.05$.

Dependent variable	Model name	Parameters	AIC[a]	ΔAIC[b]	AIC_w[c]	RMSE[d]
SWWP seedling count	$ZINB_{seed1}$	WPBR severity* DF seedling count + Management + DWD[e]	718	0.0	0.67	2.55
	$ZINB_{seed2}$	WPBR severity* DF seedling count + Management	721.3	3.3	0.13	2.14
	$ZINB_{seed3}$	WPBR severity* DF seedling count + DWD	721.4	3.4	0.12	2.15
	$ZINB_{seed4}$	WPBR severity+ DF seedling count + DWD	723.1	5.1	0.05	2.98
	$ZINB_{seed5}$	DF seedling count + DWD	724.3	6.3	0.03	2.46
	$ZINB_{seed\text{-}saturated}$	Mgmt * WPBR severity + propJAS[f] + DF seedling count + PP seedling count + shade-tolerant sapling count + DWD + Live SWWP BA[g] + Live shade-tolerant BA	727	9.0	–	4.69
SWWP sapling count	$ZINB_{sap1}$	canopy closure * Management	499.0	0.0	0.29	1.33
	$ZINB_{sap3}$	canopy closure * Management + litter[h]	499.9	0.9	0.19	1.45
	$ZINB_{sap4}$	canopy closure * Management + litter + DF sap count	500.3	1.3	0.15	1.39
	$ZINB_{sap5}$	Management*litter + canopy closure	503.4	4.4	0.03	1.74
	$ZINB_{sap\text{-}saturated}$	Management * WPBR severity + DF sapling count + canopy closure + litter + Live SWWP BA + Live DF BA	507.3	8.3	–	0.52

[a]AIC = Akaike's Information Criterion.
[b]ΔAIC = change in AIC in comparison to the best model.
[c]AICw = Akaike's weights.
[d]RMSE = root mean square error.
[e]DWD = percent ground cover of downed-woody debris.
[f]propJAS = proportion of mean annual precipitation that occurs July–September.
[g]BA = live overstory tree basal area (m^2 ha^{-1}).
[h]litter = percent ground cover litter/duff.

Discussion

SWWP regeneration was more prolific at the northwestern edge of the range in the San Francisco Peaks and along the Mogollon Rim. Density increases in SWWP and other more shade-tolerant species compared with historical reconstructions prior to fire exclusion have been documented in these areas before (Cocke *et al.*, 2005; Huffman *et al.*, 2015; Rodman *et al.*, 2016). The northwestern distribution of SWWP has no WPBR and stands appear fully stocked, but these areas are also potential hybridization zones where SWWP and limber pine (*P. flexilis*) ranges

Table 4 Final zero-inflated negative binomial (ZINB) model parameter estimates, standard errors (SE), z-values and Pr(z) values for top SWWP seedling and sapling count per subplot models.

	Estimate	SE	z Value	Pr (lzl)
SWWP seedling ($ZINB1_{seed}$)				
Intercept	2.17	0.36	6.04	< 0.0001
WPBR severity	−1.48	0.50	−2.97	0.003
DF seedling count	0.02	0.02	1.19	0.2334
rUEA[a]	−1.39	0.60	−2.34	0.0195
rTWO[b]	0.43	0.49	0.87	0.3818
DWD[c]	−2.89	1.24	−2.34	0.0195
WPBR severity * DF seedling count	0.12	0.04	2.87	0.0041
SWWP sapling ($ZINB1_{sap}$)				
Intercept	−2.40	1.58	−1.52	0.129
rUEA	−2.69	2.91	−0.92	0.356
rTWO	3.96	1.89	2.10	0.036
canopy closure	0.04	0.02	2.36	0.018
rUEA*canopy closure	0.03	0.04	0.78	0.433
rTWO*canopy closure	−0.10	0.04	−2.72	0.007

[a]rUEA = recently-managed uneven-aged stands.
[b]rTWO = recently-managed two-aged stands.
[c]DWD = percent ground cover of downed-woody debris.
$ZINB1_{seed}$ = Site (random) variance = 0.000000021 (SD = 0.00045), stand within-site (random) variance = 0.5847 (SD = 0.765), negative binomial dispersion parameter = 1.864 (SE = 0.763), zero-inflation = 0.532 (SE = 0.054). $ZINB1_{sap}$ = Site (random) variance = 0.000000021 (SD = 0.00045), stand within-site (random) variance = 0.1677 (SD = 0.410), negative binomial dispersion parameter = 0.698 (SE = 0.471), zero-inflation = 0.534 (SE = 0.121).

overlap (Little, 1971; Steinhoff and Andresen, 1971; Menon et al., 2018). In other sites across the range, SWWP was in lower proportions compared with total regeneration, but not as rare as PP regeneration. This supports other surveys that have quantified SWWP as a minor understory component (generally <5% of total regeneration densities) in stands both pre- and post-treatment (Jones, 1971; Ffolliott and Gottfried, 1991; Looney and Waring, 2013).

Co-occurrence with other species was a consistent predictor of SWWP regeneration in our study area, along with silviculture treatments, WPBR and other within-site factors related to ground cover and canopy openness. Site conditions appropriate for DF regeneration appear to be similar to those necessary for SWWP, and shade-tolerant regeneration and overstory BA were negatively related to SWWP seedling densities. SWWP pine occupies a range of community types from xeric, PP-dominated stands to more mesic communities, but appeared to regenerate best in open, drier, mixed conifer stands compared with higher elevation stands where more shade-tolerant species are prolific (Goodrich and Waring, 2017). Many factors can interact with and influence regeneration species and densities (Gray *et al.*, 2005; Puhlick *et al.*, 2012; Bataineh *et al.*, 2013), making mixed species regeneration particularly difficult to predict (Fisichelli *et al.*, 2013; Crotteau *et al.*, 2014). Other studies on related five-needle pine species including *P. albicaulis*, *P. monticola* and *P. strobus* have identified source strength (overstory BA, number of cones), climate variables, light, soils (Dovciak *et al.*, 2003; Maloney, 2014), elevation and aspect (Larson and Kipfmueller, 2010) as good predictors of regeneration. Our analyses suggest that understory and overstory environments were more important in predicting SWWP regeneration than stand-level abiotic factors such as climate variables, elevation or aspect. Fisichelli *et al.* (2013) hypothesized that mean climate may not explain regeneration variation well because more drastic, short term weather events (droughts, frost events, etc.) could be more important to establishing regeneration.

Our findings suggest that management may help maintain sustainable densities in areas of the Southwest with severe WPBR, but stands should be monitored for regeneration and WPBR incidence following treatments. We took opportunities to survey stands where recent (<20 years) management had occurred, but comparisons between pre- and post-treatments could not be made. However, differences in current conditions between treated and non-treated stands shed some light on the potential interactions between management, regeneration and disease. Stands where silviculture treatments had been applied in the past 20 years had lower densities of SWWP regeneration compared with stands not recently-managed, but non-managed stands in high severity areas were not sustainable, with 30% of regeneration infected. These infection rates would offset the benefits of higher densities if regeneration dies before reaching the next size class. WPBR negatively affects SWWP seedling counts most likely through rapid mortality of small trees but the disease can also reduce cone crops in heavily infected stands, thus severing functioning regeneration cycles (McKinney and Tomback, 2007; Schoettle and Sniezko, 2007).

The fungus that causes WPBR generally requires cool, humid conditions for spore development and germination, and relative humidity can be significantly reduced and temperatures increased following silviculture treatments (Ma *et al.*, 2010). Open conditions are not usually recommended in managing WPBR because it may stimulate *Ribes* species production (the secondary host required in the life cycle of WPBR and a source of inoculum for the fungus) and can increase fungal spore dispersal throughout the stand (Tomback *et al.*, 1995; Conklin *et al.*, 2009; Zeglen *et al.*, 2010). Site preparation and prescribed burning following silviculture treatments in high hazard sites may be needed to reduce *Ribes* densities and competing tree species (see Management recommendations Section). Areas where site preparation is needed (see Management recommendations Section) could be prioritized based on our current understanding of WPBR hazard in the Southwest. In the Sacramento Mountains of New Mexico (where WPBR has occurred the longest in southwestern forests), interacting site factors such as higher elevations, canyon bottoms or lower slope positions and presence/abundance of *Ribes* species are all are associated with higher WPBR hazard (relationships between site factors and WPBR have not been as well-defined in other parts of the Southwest) (Van Arsdel *et al.*, 1998; Geils *et al.*, 1999; Conklin, 2004; Looney *et al.*, 2015).

High WPBR infection levels across all diameter classes in non-managed stands indicates that these stands may eventually lose SWWP as a significant component, especially because the ratio between sapling-sized trees to the next size class was high in non-managed stands (Figure 5a). Avoiding drastic BA reduction through silviculture treatments that create open

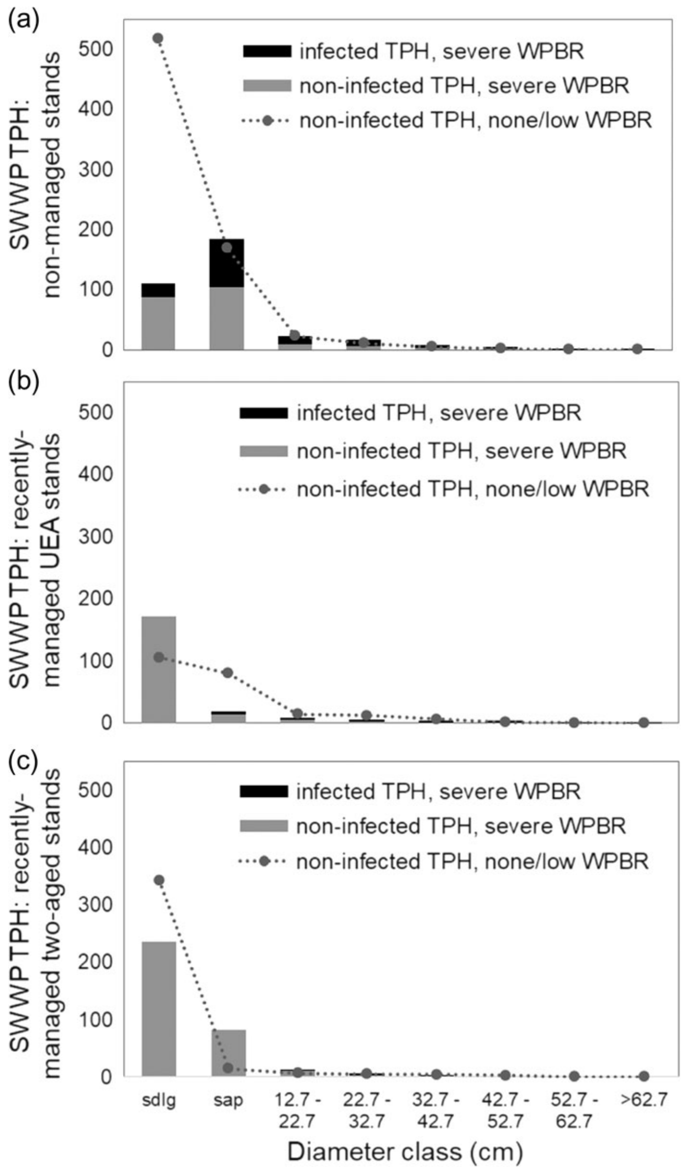

Figure 5 (a–c) Diameter distributions of non-infected and WPBR-infected SWWP per hectare (TPH) in (a) non-managed stands with none/low severity WPBR (n = 27 stands) and severe WPBR (n = 8 stands), (b) recently-managed UEA stands with none/low severity WPBR (n = 8 stands) and severe WPBR (n = 3 stands) and (c) recently-managed two-aged stands with none/low severity WPBR (n = 6 stands) and severe WPBR (n = 3 stands).

conditions for SWWP because *Ribes* abundance will increase should be weighed against the possibility of SWWP regeneration not progressing into the overstory because of closed conditions and WPBR infections. If potential WPBR hazard is considered too high on a specific site during pre-treatment surveys (i.e. low numbers of rust-free trees, many stem cankers, dead tops, high *Ribes* densities in the stand or in surrounding valley bottoms), planting genetically resistant seedlings could be considered instead of encouraging natural regeneration. Research on quantifying genetically resistant families and determining seed transfer models is ongoing (Waring *et al.*, 2016).

We lacked pre-treatment SWWP regeneration densities and WPBR information to compare to post-treatment data measured in this study. Because SWWP is a minor species component and often not the highest species preference (Conklin *et al.*, 2009), pre-treatment data were not available in our study area. The mean age of seedlings (measured by whorl count and adjusted with a regression equation modified by growth ring counts, Goodrich and Waring, 2017) illustrated seedlings were stimulated by treatments in most two-aged stands surveyed (Goodrich and Waring, 2017; Supplementary data Table S1). Mean and maximum seedling ages (i.e. advanced regeneration) were older than most treatment dates in recently-managed UEA structures and oldest in non-managed stands (Goodrich and Waring, 2017; Supplementary data Table S1). We acknowledge that saplings and some seedlings were likely retained during treatments and all SWWP densities were not solely the products of treatments. Seedling ages also limit inferences of WPBR infections in different stand structures, because disease takes time to develop. Seedlings in UEA and non-managed stands have been exposed to WPBR longer than seedlings in two-aged stands as they were older in general (Goodrich and Waring, 2017; Supplementary data Table S1).

We were not able to sample similar stand numbers within WPBR severity or silviculture treatment levels within each mountain range due to the geographic distribution of the disease and differences in forest management across land ownership, which led to an unbalanced design. The majority of EA regeneration treatments we sampled were in lower elevation areas where WPBR severity was low, although we did survey recently-managed, two-aged stands in high rust hazard areas, indicated by high rust severity in overstory trees and previous data from permanent plots (Conklin, 2004; Supplementary data Table S1). We attempted to sample across a wide geographic area within sites with disease and included enough stands with high WPBR severity for valid comparisons (at minimum, three stands per disease/management level) to be made. The random effects of site and stand within-site were quantified in ZINB models, and while stand to stand variation was high, estimates and standard deviations of the random effect of site were low (Table 4).

Management recommendations

Our surveys suggest that young SWWP were stimulated in treatments that created open structures, were more prolific in areas where PP seedlings and DF seedlings and saplings were successful, and were less prevalent where shade-tolerant overstory and saplings dominate. We recommend stimulating or planting SWWP in local areas where DF and PP successfully regenerate. Complementary research indicates that SWWP seedlings also grow fastest in these open areas without shade-tolerant understory species (Goodrich and Waring, 2017). WPBR has not yet spread to many forests throughout the Southwest (Fairweather and Geils, 2011; Looney *et al.*, 2015) and encouraging SWWP natural regeneration or outplanting genetically resistant seedlings follow proactive guidelines in place for other species (Schoettle, 2004; Schoettle and Sniezko, 2007; Conklin *et al.*, 2009). Increasing natural regeneration can increase the genetic, age and size class diversities of a stand and possibly increase resilience following the introduction of WPBR (Waring and

O'Hara, 2005; Schoettle and Sniekzo, 2007; Schwandt et al., 2010; Schoettle et al., 2012).

Results from predictive models could be helpful in locating or creating the best sites to outplant genetically resistant SWWP seedlings (Schoettle and Sniezko, 2007; Sniekzo et al., 2011), especially in areas where WPBR severity or potential hazard is high (e.g. areas of high elevation, canyon bottoms, prolific *Ribes* populations) (Van Arsdel et al., 1998; Conklin et al., 2009). We recommend ~300 SWWP seedlings ha^{-1} are planted (or stimulated in a successful treatment) to safeguard against potential WPBR mortality. Current work is in progress to collect seeds and quantify the frequency of genetic resistance to *C. ribicola* across the range of SWWP (Conklin et al., 2009; Sniezko et al., 2011; Waring et al., 2016; Goodrich et al., in press), but until these populations and families are identified, stimulating natural, local regeneration may help preserve genetic diversity and increase resilience at the stand level. We recommend managers anticipate that WPBR will eventually reach most mountain ranges in Arizona and New Mexico.

The open, two-aged stands in this study were created through establishment phase of shelterwood with reserve trees or patch clearcut with reserve tree regeneration systems. SWWP seedlings also grew fastest in these open stands (Goodrich and Waring, 2017). Eastern white pine, another shade mid-tolerant species, also grows well in stands with more light available if shade-intolerant understory regeneration is controlled, and shelterwood systems are applied to many eastern white pine-dominated stands (Fahey and Lorimer, 2013; Parker et al., 2013). High densities of shade-intolerant seedlings were measured in two-aged stands in this study, but densities of shade-intolerant saplings were low, indicating they were not reaching substantial sizes. A major concern regarding thinning or regeneration systems in areas with WPBR is that the extra light can increase the abundance of *Ribes* stems (Conklin et al., 2009; Zeglen et al., 2010). Although single-entry broadcast burning may stimulate seedbed *Ribes* germination and increase proliferation, repeated broadcast burning or another type of site preparation to kill *Ribes* stems may help limit densities and lower rust hazard. Prescribed burning and reintroducing surface fire also coincide with restoration goals to reintroduce fire back into southwestern mixed conifer forests, which historically had frequent fire regimes (Swetnam and Baisan, 1996; Brown et al., 2001; Huffman et al., 2015). It is possible that an increase in shade-intolerant species densities following treatments outcompeted the *Ribes* plants in two-aged stands we surveyed (e.g. sprouting species such as New Mexico locust and the abundance of oak species throughout the Southwest), and a lack of *Ribes* has been noted in intensively managed lower elevation areas of the Mescalero Apache Reservation in previous surveys (Van Arsdel et al., 1998). We recommend prioritizing silviculture treatments that drastically reduce BA in low hazard areas (stands with fewer current *Ribes* stems, lower elevations or non-canyon bottoms) (Van Arsdel et al., 1998; Geils et al., 1999; Conklin, 2004; Conklin et al., 2009) and evaluation and monitoring of SWWP regeneration in follow-up thinning treatments within open stands. Because the WPBR hazard of a site depends on time, an inoculum source and suitable environmental conditions for the fungus, it would be helpful to quantify whether shelterwood regeneration treatments across a range of elevations increase the WPBR hazard of a stand by monitoring *Ribes* densities, relative humidity and temperature data for several years pre- and post-treatments.

We recommend that open conditions to stimulate SWWP regeneration are created in areas where SWWP exists as an overstory species through either two-aged or UEA regeneration methods that reduce total BA to 9–20 m^2 ha^{-1} and retain high quality overstory SWWP without lethal WPBR infections (i.e. stem cankers). Modified single-tree selection treatments with target BA of 9–10 m^2 ha^{-1} with various size classes left in groups around larger openings may provide similar open conditions to the two-aged structures where disease-free SWWP regeneration occurred in this study and SWWP seedlings tend to grow the fastest (Goodrich and Waring, 2017). This range of residual BA could meet desired conditions for resilient forests as long as sustainable size classes and appropriate spatial structure are maintained (Reynolds et al., 2013). Site preparation and frequent surface fire to reduce *Ribes* seeds and stems may be necessary, but other pioneer shade-intolerant species, such as oaks, may outcompete *Ribes* in some southwestern mixed conifer stands. Stimulating natural SWWP regeneration in open conditions in low WPBR severity areas and/or planting genetically resistant SWWP seedlings in high WPBR severity stands with open conditions should lead to faster growth and recruitment of SWWP into the overstory compared with closed canopy stands under both scenarios (Goodrich and Waring, 2017). Precommercial thinning and timber stand improvement should remove SWWP with stem cankers but leave sapling-sized SWWP if they are free of WPBR stem infections. Current recommendations that include favouring seed-bearing SWWP, retaining trees with good form and vigour, and ranking SWWP higher in species preference should be maintained, as they increase the probability that SWWP will continue to occupy the site, provide a seed source and maintain genetic diversity (Conklin et al., 2009).

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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