

Initial tree mortality and insect and pathogen response to fire and thinning restoration treatments in an old-growth mixed-conifer forest of the Sierra Nevada, California

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Abstract: Fire and thinning restoration treatments in fire-suppressed forests often damage or stress leave trees, altering pathogen and insect affects. We compared types of insect- and pathogen-mediated mortality on mixed-conifer trees 3 years after treatment. The number of bark beetle attacked trees was greater in burn treatments compared with no-burn treatments, and in some cases, larger pine trees were preferentially attacked. Restoration treatments are not expected to change the trajectory of spread and intensification of dwarf mistletoe. Thinning treatments may have provided a sanitation effect in which large leave trees have lower levels of dwarf mistletoe. Although thinning treatments are known to exacerbate root disease, <12% of cut stumps were infected with root pathogens (*Armillaria gallica* and *Heterobasidion annosum*). Treatments increased *Ribes* (alternate host for white pine blister rust) frequency and abundance, which may have very localized impacts on white pine blister rust dynamics. In some instances, fire, insects, and pathogens appear to conflict with forest restoration goals by reducing the percentage of pine and producing proportionally higher rates of tree mortality in large-diameter size classes. To better understand the long-term effects of restoration treatments on pathogens and insects, continued monitoring over the course of varying climatic conditions will be needed.

Résumé : Le feu et l'éclaircie utilisés comme traitements de restauration dans les forêts protégées contre les incendies causent souvent des dommages ou des stress aux arbres qui restent, ce qui modifie l'effet des agents pathogènes et des insectes. Nous comparons les types de mortalité causée par les agents pathogènes et les insectes chez les arbres composés d'un mélange de conifères trois ans après un traitement. Un plus grand nombre de scolytes ont attaqué les arbres dans les traitements avec le feu que dans les traitements sans feu et, dans certains cas, les plus grosses tiges de pin ont été préférentiellement attaquées. On ne s'attend pas à ce que les traitements de restauration modifient le cours de la progression et de l'intensification du faux-gui. Les traitements d'éclaircie ont pu avoir un effet sanitaire en faisant en sorte que les gros arbres qui restent soient moins affectés par le faux-gui. Bien que les traitements d'éclaircie soient connus pour exacerber les maladies de racines, moins de 12% des souches ont été infectées par des agents pathogènes des racines (*Armillaria gallica*, *Heterobasidion annosum*). Les traitements ont augmenté la fréquence et l'abondance du *Ribes*, l'hôte alterne de la rouille vésiculeuse du pin blanc, qui peut avoir des impacts très localisés sur le développement de cette maladie. Dans certains cas, le feu, les insectes et les agents pathogènes semblent être en conflit avec les objectifs de la restauration de la forêt en réduisant le pourcentage de pin et en engendrant des taux de mortalité des arbres proportionnellement plus élevés dans les classes de grand diamètre. Pour mieux comprendre les effets à long terme des traitements de restauration sur les agents pathogènes et les insectes, il sera nécessaire d'effectuer un suivi continu dans différentes conditions climatiques.

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Introduction

Fire has long been considered the major ecosystem driver in Sierran mixed-conifer forests (McKelvey and Johnston 1992; Skinner and Chang 1996; North et al. 2007). Decades of fire suppression has significantly changed the structure and composition of the mixed-conifer forest type (SNEP

Science Team 1996), which constitutes 45% (by cover) of Sierra Nevada forests (Beardsley et al. 1999). These forest changes, in turn, can influence many host-pathogen and host-insect interactions. For example, overstocked forests can elevate drought stress leading to increased tree mortality owing to bark beetle attacks, root diseases, and other pathogens and pest complexes (Slaughter and Parmeter 1989; Fer-

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rell et al. 1994; Smith et al. 2005; Fettig et al. 2007). The role of pathogens and insects in fire-suppressed forests and their effect on forest dynamics after restoration treatments are applied, however, is not well understood.

Regional and national plans such as the Sierra Nevada Forest Plan Amendment (Sierra Nevada Forest Plan Amendment 2004) and the Healthy Forests Initiative (<http://www.healthyforests.gov>) have made forest restoration a priority. Restoration treatments often use mechanical thinning, prescribed fire, or both to reduce stem densities and fuel loads. Thinning may potentially mitigate pest problems by lowering stand and host densities and relieving the potential for drought- and competition-induced stress (Ferrell 1996; Fettig et al. 2007). However, such treatments also have the potential to increase pest incidence, as thinning often damages residual trees and can increase the buildup of root disease inoculum (e.g., *Heterobasidion annosum* and *Armillaria* spp.) owing to saprobic survival in stumps (Ferrell 1996). Prescribed fire can scorch trees, making them more susceptible to bark beetle attack (Ferrell 1996; Schwilk et al. 2006); these wounds can also provide infection courts for root pathogens such as *H. annosum*. It is unclear how insect and pathogen activity will affect the goal of many restoration treatments, which is to increase tree size and shift forest composition toward more fire-tolerant pine species. Because of the interaction between management practices and pathogens and insects, Ferrell (1996) recognized that certain levels of insect and pathogen activity might have to be tolerated as part of forest restoration treatments in the Sierra Nevada.

In this study, we examine pest and pathogen response to prescribed burning and mechanical thinning treatments in the Teakettle Experiment (established in 1998). We expect pest and pathogen response to change over time as leave trees adjust to altered stand conditions and treatment stress. In this study, we focus on the short-term response of four forest insects (bark beetles) and pathogens. Our objectives were to (i) assess posttreatment effects of fire and thinning prescriptions on tree mortality and bark beetle activity, (ii) project dwarf mistletoe spread for pre- and postburn and thinning treatments, (iii) determine levels of root diseases following thinning treatments, and (iv) determine the potential for restoration treatments to impact white pine blister rust (WPBR) spread and intensification.

Materials and methods

Study area

The Teakettle Experimental Forest is a 1300 ha old-growth forest located 80 km east of Fresno, California, in the drainage of the north fork of the Kings River. Elevation ranges from 1880 m along the eastern boundary to 2485 m at the top of Patterson Mountain along the western boundary. Annual precipitation averages 110 cm at 2100 m and falls mostly as snow between November and April (North et al. 2002). The Teakettle forest grades from mixed-conifer forest (white fir (*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.), sugar pine (*Pinus lambertiana* Dougl.), incense cedar (*Calocedrus decurrens* (Torr.) Florin), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and red fir (*Abies magnifica* A. Murr.) to *A. magnifica*, lodgepole pine (*Pinus contorta*

Dougl. ex Loud.), and western white pine (*Pinus monticola* Dougl. ex D. Don) at the higher elevations (North et al. 2002). Soils are dominated by Dystric and Lithic Xeropsamments of loamy sand and sandy loam textures derived from granitic rock, typical of the southwestern slopes of the Sierra Nevada (Anonymous 1993). Fire return intervals at Teakettle were estimated at 12–17 years prior to 1865, the year of the last widespread fire (North et al. 2005). No active logging had occurred at Teakettle prior to this experiment, except to remove trees for road construction and hazard tree reduction (North et al. 2002).

Treatments were applied to 18 permanent 4 ha plots, 200 m × 200 m, with a 50 m buffer between adjacent plots (see North et al. (2007) for plot layout and arrangement). Plots were replicated based on tree structure and composition (floristics) and environmental similarity employing variogram and cluster analysis (North et al. 2002). Forest regulations prevented one streamside plot from being mechanically treated, but otherwise, each of the remaining 17 plots was assigned randomly to one of six treatments in a full factorial design with two levels of burning treatments (burn and no burn) and three levels of thinning treatments (no thin, understory thin, and overstory thin). The six treatments were no burn – no thin, no burn – understory thin (defined below), no burn – overstory thin (defined below), burn – no thin, burn – understory thin, and burn – overstory thin. Following standard commercial thinning operations on the Sierra National Forest, trees were limbed where they fell and slash was left to dry for 1 year prior to burning. After thinning, slash and fuel loads were higher in more heavily thinned treatments (Innes et al. 2006), affecting fire intensity and extent in plots, which were subsequently prescribed burned. The understory thinning prescription followed the California spotted owl (CASPO) report (Verner et al. 1992), removing trees between 25 and 76 cm diameter at breast height (DBH) while retaining at least 40% canopy cover. Originally designed to minimize impact to spotted owl habitat, the CASPO guidelines are now widely used to also reduce fuels (SNFPA 2004). The overstory prescription removed trees >25 cm DBH, leaving only 22 regularly spaced large-diameter trees per hectare. Overstory thinning was widely practiced in Sierran forests before CASPO, and at Teakettle, it approximated a prescription of cutting trees up to 100 cm DBH. For future stand development, a significant shortcoming in the treatments was leaving all trees <25 cm DBH believing that logging operations and the prescribed burn would kill most of them (Mark Smith, Sierra National Forest silviculturist, personal communication). In many Sierra Nevada fuel treatments, this size class (<25 cm DBH) is either left on site or removed using expensive service contracts when funds are available. Many of these trees survived treatment, reducing fuel reduction effectiveness and leaving stand densities much higher than a Teakettle reconstruction of 1865 active-fire conditions (North et al. 2007). The burn prescription was designed to create a ground fire and avoid overstory ignition. The thinning treatments were applied in the fall of 2000 (thin and burn plots) and early spring of 2001 (thin only), and the prescribed fire was ignited in the fall of 2001 after fuels had dried. While the plots were not subject to sanitation thinning, unhealthy looking trees were often selected for cutting

Table 1. Posttreatment stand structure, composition, and mortality at Teakettle Experimental Forest.

Stand characteristics	No burn – no thin	No burn – understory thin	No burn – overstory thin	Burn – no thin	Burn – understory thin	Burn – overstory thin
Basal area (m ² /ha)	56.4	41.2	22.7	53.7	37.5	17.2
Total tree density (stems/ha)	469	239.5	150.3	353.8	143.4	93.6
Overall mortality (%)	3.1	9	12.7	18.5	43.5	56.1
% <i>A. concolor</i> dead (% FC)	4.3 (67)	9.6 (67)	14.0 (66)	18.8 (67)	46.8 (64)	58.8 (57)
Mean DBH	42.9	19.5	12.2	15.1	17.9	16.2
% <i>A. magnifica</i> dead (% FC)	4.8 (3)	1.4 (5)	3.4 (2)	0.0 (3)	0.0 (1)	0.0 (1)
Mean DBH	16.0	8.1	5.4			
% <i>C. decurrens</i> dead (% FC)	0.7 (3)	6.9 (12)	11.0 (10)	18.3 (16)	41.4 (20)	52.6 (22)
Mean DBH	12.4	11.9	14.2	15.7	14	16.2
% <i>P. jeffreyi</i> dead (% FC)	5.7 (7)	10.7 (4)	6.0 (8)	19.0 (4)	28.9 (7)	44.1 (7)
Mean DBH	53.9	23.3	13.1	29.5	22.4	24.8
% <i>P. lambertiana</i> dead (% FC)	4.4 (12)	7.8 (10)	10.6 (12)	22.0 (9)	43.3 (5)	45.7 (9)
Mean DBH	17.2	24.8	30.7	23.2	39.7	26.1

Note: Mortality by tree species was calculated as the number of dead for that species/number of dead for all trees. Percent FC is the species percentage of stand–forest composition based on stem numbers. Mean DBH is of dead stems for each species.

versus a healthy looking tree (M.P. North, personal observation).

Field sampling and data collection

Within the 18 plots, all trees were inventoried, permanently tagged, and mapped before and after treatments. Pretreatment assessments of disease and insects for all trees were conducted during 2000 and in 2002 for the control plots (Smith et al. 2005). The major insects and pathogens included *Scolytus ventralis* (associated with 34.8% of *A. concolor*), *Arceuthobium abietinum* f.sp. *concoloris* (associated with 24.8% of *A. concolor*), *Cronartium ribicola* (associated with 5% of *P. lambertiana*), and *H. annosum* (associated with 1.2% of *A. concolor*).

The pretreatment incidence of dwarf mistletoe on *A. concolor* was determined by the presence of cankers, swellings, or brooms and the presence of dwarf mistletoe shoots on infected branches or stems (Smith 2005). If mistletoe was present on a tree, the severity of infection was estimated using the rating method of Hawksworth (Hawksworth 1977; Hawksworth and Wiens 1996). This rating system (dwarf mistletoe rating (DMR)) is based on visual estimation of infection intensity of the crown. The tree crown is divided into thirds (top, middle, and lower) and each third is rated for dwarf mistletoe intensity: 0 = no infected branches, 1 = <50% of branches are infected, and 2 = >50% of branches are infected. Ratings for each third are added and a tree rating is obtained ranging from 1 (light infection) to 6 (heavy infection). The DMR is the average DMR (as stated above) for all *A. concolor* trees, infected and uninfected, whereas the dwarf mistletoe index is the average rating for all infected *A. concolor* trees (Kipfmüller and Baker 1998). For the pretreatment assessment of *A. abietinum* f.sp. *concoloris*, mean DMR was 0.701, while mean dwarf mistletoe index was 2.8.

During the summer months of 2004 and 2005, all living and dead trees and stumps ($N = 40\,563$) were recensused for the presence of bark beetles, root rot pathogens, dwarf mistletoe, and WPBR. Dead trees were closely examined to determine apparent mortality agent(s). Stems and branches were examined for evidence of bark beetle attack (e.g., bor-

ing dust, pitch tubes, frass) and bark was removed from dead trees to look for characteristic bark beetle galleries (Furniss and Carolin 2002; Woods et al. 2003). The presence of root rot pathogens was determined on cut stumps and dead trees by identifying fruiting bodies and characteristic decay patterns of *H. annosum* (Otrosina and Scharpf 1989; Scharpf 1993) and presence of mycelial fans, rhizomorphs, and (or) fruiting bodies of *Armillaria* spp. underneath the bark of trees and stumps (Scharpf 1993); root diseases were not assessed on live leave trees to avoid injury to the trees. Presence or absence of *C. ribicola* (WPBR) on the alternate host *Ribes* was recorded for each treatment plot, and blister rust incidence on *P. lambertiana* was recorded in the pretreatment survey (Smith 2005). Visible signs of fire damage (e.g., basal fire scar, bole scorch) were recorded on all living or standing dead trees.

Data analysis

A two-way analysis of variance (ANOVA) was used to determine differences in mortality, proportion of trees attacked by bark beetles, and DBH of bark beetle attacked trees in burn and thin treatments. For all analyses, burn and thin treatments were treated as fixed effects. Data were log transformed to meet the assumptions of an ANOVA, and where variances were unequal, a Welch ANOVA was used in which observations are weighted by the reciprocals of the estimated variances (SAS Institute Inc. 2005). Orthogonal contrasts were used to test for differences between treatments for the dependent variables. Spearman's Rho, non-parametric correlation analysis, was used to determine relationships between mean mortality and proportion of fire damage as well as mean DMR and mean proportion of fire damage. All statistical analyses were conducted with the software program JMP version 6.0 (SAS Institute Inc. 2005).

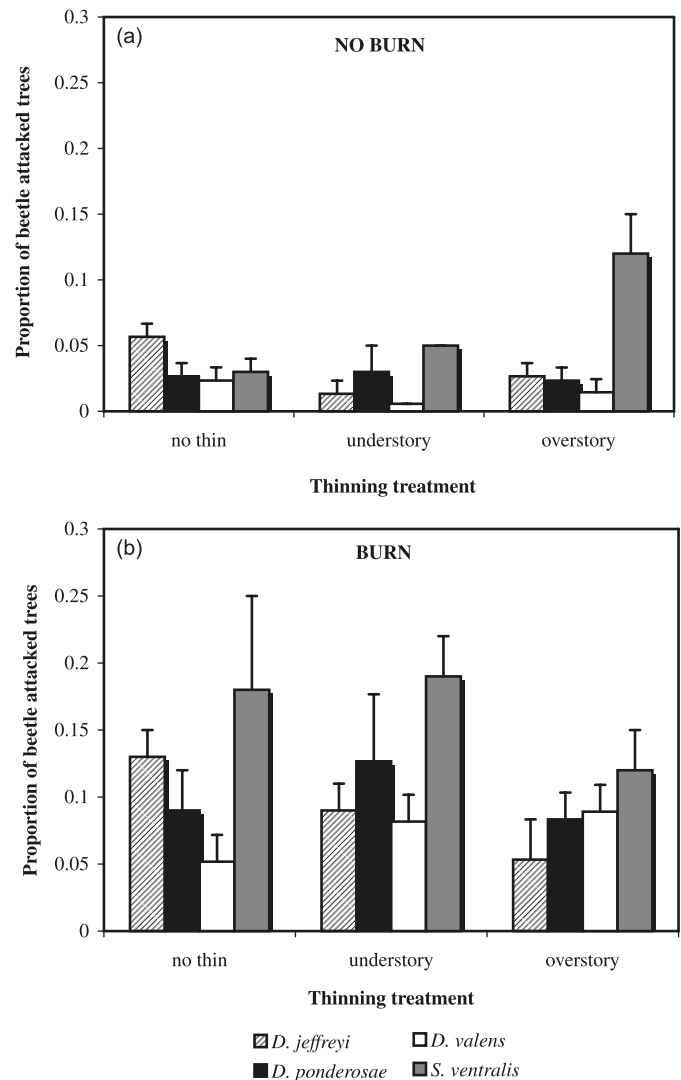
The forest vegetation simulator (FVS) was used to model spread of dwarf mistletoe (*Arceuthobium* spp.) through the Teakettle Experimental Forest. FVS is a collection of individual-tree and distance-independent models used by the USDA Forest Service to generate growth and yield information (Dixon 2002). The western Sierra Nevada (WESSIN) variant of the FVS model was used with pre- and posttreat-

ment data from Teakettle's plots to project dwarf mistletoe spread under the various management scenarios. Model dynamics are based on Hawksworth's (1977) six-class DMR system. Besides DMR (average DMR for all *A. concolor* trees, infected and uninfected), species, DBH, site conditions, stand density, regeneration, and height growth all contribute to projected changes in infection status (David 2005). Model output presented and analyzed in this study was DMR and DMR by 5.0 cm diameter classes for *A. concolor* for each 10 year interval over a 50 year projection.

Results

Assessments of tree mortality in 2004–2005 showed that posttreatment tree mortality differed significantly between the nine burned plots (mean = 38.8) and nine unburned plots (mean = 8.3) (Table 1) and was significantly correlated with fire damage, as measured by the presence of char and basal fire scars ($r = 0.74$, $P < 0.001$, $n = 18$). There were no statistical differences in mortality in the no-burn plots between the two thinning treatments and the no-thin treatment (orthogonal contrast: $F = 2.20$, $P = 0.16$) (Table 1). However, mortality was significantly greater in the burn–thinning treatments compared with the burn–no-thin treatments (orthogonal contrast: $F = 38.83$, $P < 0.001$) (Table 1). There were no significant differences in the percentage of dead among tree species but there was a significant burn effect on the overall percent dead ($F = 60.14$, $P < 0.001$) (Table 1). Mean DBH of dead trees did not differ significantly among burn and no-burn plots but differed significantly between species ($F = 2.6$, $P = 0.05$), with higher DBH found among the *Pinus* species (North et al. 2004) and smaller average DBH for dead trees among *A. concolor* and *C. decurrens* (orthogonal contrast: $F = 6.47$, $P = 0.01$) (Table 1). In the pretreatment assessment of mortality at Teakettle, Smith et al. (2005) found higher levels of mortality among large-diameter trees for most conifer species, except *P. jeffreyi*. The quadratic mean diameter for all trees averaged 19.6 cm DBH, but 67.6% of these stems were *A. concolor*. Pines had very low density at Teakettle pretreatment (23 stems/ha) but a quadratic mean diameter of 87.3 cm (see North et al. 2007; M. Hurteau and M.P. North, in review). In the no-burn treatment plots *A. concolor* makes up approximately 67% of the forest composition (by density) with an average of 9.3% mortality across thinning treatments, with mainly small-diameter trees dying (Table 1). Mortality of *P. lambertiana* and *P. jeffreyi* was slightly lower at 7.6% and 7.5%, respectively (Table 1). In burn treatment plots, *A. concolor* comprises about 62.6% of the forest composition; but fire-, pathogen-, and insect-related mortality is, on average, 41%. Fire-, pathogen-, and insect-related mortalities in burn treatments were high for *P. lambertiana* (mean = 37%) and *P. jeffreyi* (mean = 30.6%), given that they comprise 7.6% and 6% of the forest composition (Table 1). Bark beetle and fire-mediated mortalities were important contributing factors to *Pinus* mortality in these burn treatments. On average, 28% of dead *P. lambertiana* in burn treatments were attacked by *Dendroctonus ponderosae* (Fig. 1b) versus 13% in no-burn treatments (Fig. 1a). *Dendroctonus jeffreyi* was associated with 11% and 13% of dead *P. jeffreyi* trees from burn and no-burn treatments, respectively, *S. ventralis* was associated with

Fig. 1. Proportion of bark beetle attacked trees on their respective hosts in (a) no-burn and (b) burn treatments with no thinning, CASPO (understory), and shelterwood (overstory) silvicultural prescriptions.



29% and 31% of dead *A. concolor* in burn and no-burn treatments, respectively, and the red turpentine beetle *Dendroctonus valens* was associated with only 3% and 4% of dead *P. lambertiana* and *P. jeffreyi* in burn and no-burn treatments, respectively (Fig. 1).

The proportion of bark beetle attacked trees for each beetle species, *S. ventralis*, *D. jeffreyi*, *D. ponderosae*, and *D. valens*, was significantly different between burn and no-burn treatments (Table 2; Fig. 1). For all bark beetle species, except *D. jeffreyi*, there was no effect of thinning on the proportion of trees attacked and there was no significant interaction (burn $\times$ thin treatment) effect for all beetle species (Table 2). The proportion of *P. jeffreyi* trees attacked by *D. jeffreyi* was significantly greater on trees in the no-thin treatments (mean = 0.09) compared with *P. jeffreyi* in the understory (mean = 0.05) and overstory (mean = 0.04) treatments (orthogonal contrasts: $F = 8.55$, $P = 0.012$) (Fig. 1). The size (mean DBH) of trees attacked by bark beetles did not differ by either the burn or thin treatment for *P. jeffreyi*,

Table 2. Two-way ANOVA for proportion of trees attacked by bark beetle species at the Teakettle Experimental Forest.

Factor	<i>S. ventralis</i>			<i>D. jeffreyi</i>			<i>D. ponderosae</i>			<i>D. valens</i>		
	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>	df	<i>F</i>	<i>P</i>
Burn	1	14.19	<i>0.002</i>	1	14.78	<i>0.002</i>	1	10.57	<i>0.006</i>	1	22.34	<i><0.001</i>
Thin	2	0.48	0.628	2	4.46	<i>0.035</i>	2	0.45	0.642	2	0.52	0.607
Interaction	2,18	3.36	0.069	2,18	1.11	0.361	2,18	0.26	0.269	2,18	1.64	0.233

Note: Significant effects are in italics.

A. concolor, and *P. lambertiana* (Table 3; Figs. 2a, 2c, and 2d). However, the size of *P. lambertiana* (no-burn mean = 15.4 cm DBH, burn mean = 57.2 cm DBH) and *P. jeffreyi* (no-burn mean = 32.2 cm DBH, burn mean = 82.5 cm DBH) attacked by *D. ponderosae* and *D. valens*, respectively, did differ significantly between the burn and no-burn treatments (Table 3; Figs. 2b and 2d).

FVS was used to determine the effects of restoration treatments on dwarf mistletoe spread and intensification 50 years in the future for *A. concolor* in all plots (Figs. 3e and 3f). The model simulations found that within 50 years, without future thinning treatments, the DMR for larger *A. concolor* trees (>80 cm DBH) was significantly higher (mean = 4.4) compared with treatment plots (mean = 3.3) (orthogonal contrasts: $F = 37.03$, $P > 0.0001$) (Figs. 3a and 3b compared with Figs. 3c and 3d). The DMR of trees 40–80 cm DBH was significantly different and slightly higher in the treatment plots (orthogonal contrasts: $F = 17.81$, $P > 0.0007$) (Figs. 3c and 3d compared with Figs. 3a and 3b). Fifty year FVS projections showed DMR increasing to an average of 2.5 (Figs. 3e and 3f), regardless of silvicultural treatments. Treatments did not change the trajectory or rate of spread (Figs. 3e and 3f) of *A. abietinum* f.sp. *concoloris*. In the pre-treatment forest assessment, Smith et al. (2002) found that the average DMR for *A. concolor* was 0.70, which is fairly low. In addition, we found that in burn plots, dwarf mistletoe infected trees and fire damage were highly correlated ($r = 0.91$, $P < 0.001$, $n = 9$).

Root disease pathogens were observed mainly on cut stumps (50%–75%) in thinning treatments. Because only stumps and dead trees were assessed for root disease pathogens, we were unable to statistically analyze any spatial patterning. However, our observations combined with the previous survey (Smith 2005) suggest that the root diseases were widely dispersed throughout plots.

Mycelial fans of *Armillaria* were observed on 9.1% of the trees and stumps in the overstory and understory thinning treatments; it was found mainly on larger stumps and trees with an average diameter of 48.8 cm. The primary host was *A. concolor*, but *Armillaria* was also observed on *C. decurrens*, *P. jeffreyi*, and *P. lambertiana* (Fig. 4). On the treated plots, *Armillaria* appeared to be acting primarily as a saprobe or secondary pathogen. Although specific isolates of *Armillaria* were not identified to the species level in this study, based on a previous study in the Sierra Nevada, most stumps at Teakettle were likely colonized by *Armillaria gallica* (Baumgartner and Rizzo 2001). *Armillaria mellea* is common in Sierra Nevada mixed-conifer forests at elevations below 1500 m (Baumgartner and Rizzo 2001) but has not been found at the higher elevations found at the Teakettle Forest.

Signs and symptoms of *H. annosum* were observed on 2.1% of the stumps from cutover plots; the average diameter of colonized stumps and trees was 53.2 cm. The most commonly colonized host was *A. concolor* (Fig. 4). Only the fir type of *H. annosum* is found at Teakettle and on the west side of the Sierra Nevada in general (G. Slaughter, personal communication).

On average, 5% of *P. lambertiana* trees were infected with WPBR (Table 4), but incidence was quite variable, with 100% incidence in some locations and no rust in others (Maloney 2000). The incidence of WPBR did not change with burning and thinning treatments (Table 4). However, the frequency of the alternate host *Ribes* increased from 20% to 80% pre- to posttreatment, with very little change in percent cover (Table 4). In 2004, no *Ribes* was observed to be infected with *C. ribicola*, but in the summer of 2005, *Ribes* were infected in the control (no-burn–no-thin) plots.

Discussion

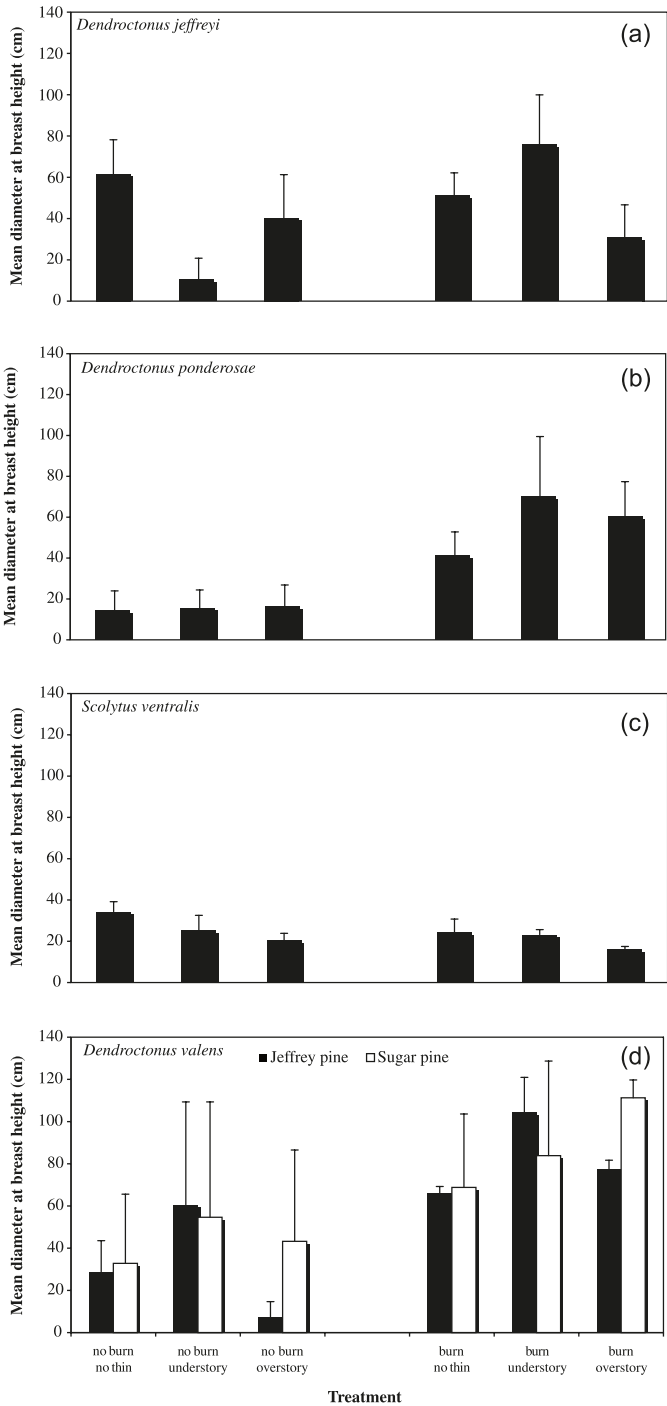
Forest treatments such as prescribed fire and (or) thinning in the Sierra Nevada are commonly used to reduce fuel loads and to restore historic (i.e., prefire suppression) stand conditions by increasing trees size and shifting composition toward more pine. Do insect-, pathogen-, and fire-mediated mortality help or hinder this restoration objective? We found that in the no-burn treatment plots (inclusive of thinning treatments), *A. concolor* maintains dominance within these stands with relatively low pathogen- and insect-mediated mortality. While mortality of *P. lambertiana* and *P. jeffreyi* is somewhat lower, the levels of pathogen- and insect-mediated mortality are relatively high, given the overall composition of these *Pinus* species. In burn treatment plots, *A. concolor* maintains its dominance, but by a lower relative amount. Fire-, pathogen-, and insect-associated mortality is much higher, thereby reducing *A. concolor* numbers, but the average postburn treatment of 62% is still substantially higher than the 34% suggested by a reconstruction of Teakettle's 1865 stand conditions (North et al. 2007). Fire-, pathogen-, and insect-related mortality in burn treatments was alarmingly high for *P. lambertiana* and *P. jeffreyi*, given that they comprise 7.6% and 6% of the forest composition. Fire- and bark beetle mediated mortalities were important contributing factors to *Pinus* mortality in these burn treatments, primarily killing larger diameter trees. No crown kill or bole scars were observed on pine trees owing to the low intensity of the prescription fire; thus, the contributing factor to most pine mortality was the interaction of basal fire damage and beetle invasion of fire-stressed trees. While there was beetle activity in no-burn (thinning and no-thin) treatments (Fig. 1a), it was not comparable with the levels observed in burn treatments (Fig. 1b). Fire-

Table 3. Two-way ANOVA for average DBH of bark beetle attacked trees for mixed-conifer species.

Factor	<i>A. concolor</i> – <i>S. ventralis</i>			<i>P. jeffreyi</i> – <i>D. jeffreyi</i>			<i>P. jeffreyi</i> – <i>D. valens</i>			<i>P. lambertiana</i> – <i>D. ponderosae</i>			<i>P. lambertiana</i> – <i>D. valens</i>		
	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P
Burn	1	1.98	0.184	1	1.16	0.301	1	7.70	0.016	1	10.00	0.008	1	1.92	0.190
Thin	2	2.61	0.114	2	0.74	0.495	2	1.93	0.186	2	0.45	0.647	2	0.23	0.790
Interaction	2,18	0.37	0.372	2,18	3.19	0.077	2,18	0.31	0.738	2,18	0.37	0.695	2,18	0.13	0.871

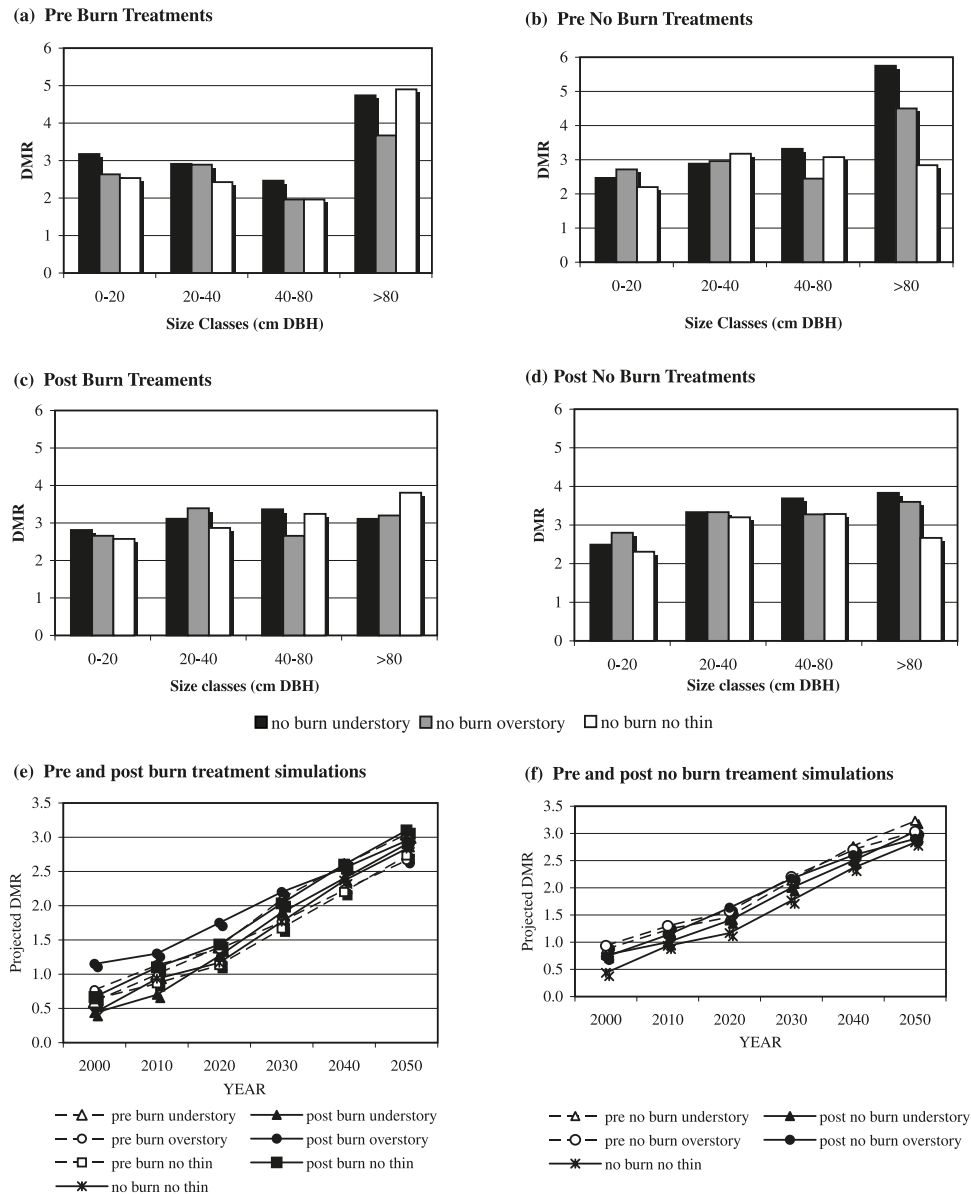
Note: Significant effects are in *italics*.

Fig. 2. Mean diameter at breast height for bark beetle attacked trees in burn and no-burn treatments with no thinning, understory, and overstory silvicultural treatments for (a) *D. jeffreyi* on *P. jeffreyi*, (b) *D. ponderosae* on *P. lambertiana*, (c) *S. ventralis* on *A. concolor*, and (d) *D. valens* on *P. jeffreyi* and *P. lambertiana*.



induced mortality and thinning treatments reduced stand densities but did not approach the low density (67 trees/ha) or species composition (50% pine) that stand reconstruction suggests existed before fire suppression (North et al. 2007). In the short term, fire and the presence of insects and pathogens appear to conflict with forest restoration goals by reducing the percentage of pine and produc-

Fig. 3. Fifty year DMR projections for *A. concolor* trees in four diameter size classes for (a and b) preburn and no-burn plots without silvicultural treatments and (c and d) postburn and no-burn treatment plots with respective silvicultural treatments and 50 year DMR projections for *A. abietinum* f.sp. *concoloris* on *A. concolor* for (e) pre- and postburn and thinning treatments and no burn – no thin and (f) pre- and post-no-burn and thinning treatments and no burn – no thin (Fig. 3f).



ing proportionally higher rates of tree mortality in the large-diameter size classes. More than one entry (of thinning and (or) burning) may be needed to achieve relative pre-fire-suppression and (or) desired forest conditions (Zald et al. 2008).

Overall, bark beetle activity was elevated in fire-treated stands, with most beetles preferentially attacking large-diameter individuals. Our findings agree with another Sierran study (Schwilk et al. 2006) that found that bark beetles respond immediately to fire restoration treatments, with elevated activity in burned stands. However, the level of beetle activity was somewhat lower at Teakettle compared with beetle activity in fire treatments at Sequoia and Kings Canyon National Park (Schwilk et al. 2006). Fire intensity at Sequoia and Kings Canyon National Park was somewhat

higher (in both early- and late-season burns; see Knapp and Keeley 2006) than at Teakettle, which had moderate levels of fire intensity in the late-season burn at this site (Innes et al. 2006).

One goal of forest restoration projects is the reduction of shade-tolerant species (i.e., *Abies* and *C. decurrens*), thereby increasing the relative proportion of *Pinus* species. Our results suggest that there may be a need to mitigate fire damage by removing litter and debris around large tree boles, clearing all small trees in a buffer zone around large leave trees, or apply a waiting period after thinning before fire treatments (Kolb et al. 2007). These actions may reduce fire damage to these reproductive and ecologically important pine trees and reduce their susceptibility to bark beetle attack. This is especially important for *P. lambertiana* in

Table 4. Posttreatment summary of white pine blister rust incidence on *Pinus lambertiana* (sugar pine) and abundance of the alternate host *Ribes roezlii*.

	Pretreatment	Posttreatment
Incidence of WPBR (%)	5.1	5.1
Frequency of <i>R. roezlii</i>	20	80
Abundance (sum of % cover) of <i>R. roezlii</i>	93.6	80.3

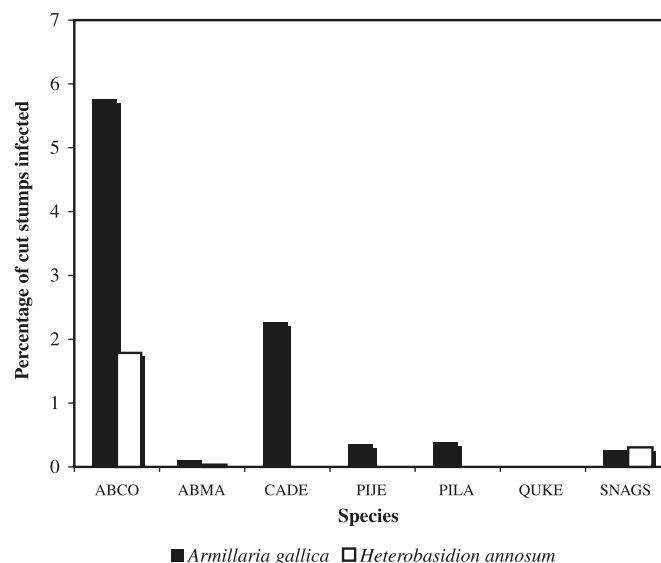
Note: *Ribes* frequency and abundance data from Wayman and North 2007.

WPBR-impacted forests. Large uninfected trees may potentially be rust resistant (Kinloch 1992) and preservation and conservation of these individuals is critical to the long-term survival and presence of *P. lambertiana* in mixed-conifer stands in the Sierra Nevada. Many large pines were lost that did not have significant bark char or duff mound reduction. The causes are unclear and subject to further research in the area of tree physiology (M.P. North and E.E. Knapp, unpublished work). Some researchers have found lower large tree mortality when litter and duff are raked away from the bole (Covington et al. 1997). This nested treatment, however, was not applied in the Teakettle Experiment's effort to mimic standard forest practices because labor costs limit its application to small, high-value areas such as campgrounds.

We expect the restoration treatments will not change the trajectory of spread and intensification of dwarf mistletoe. This may be largely due to the compositional dominance of *A. concolor* in these stands (even with treatments) as well as relatively low to moderate levels of dwarf mistletoe infection. In 50 years without restoration treatments, dwarf mistletoe infections increase in large trees as a result of within-tree intensification. Following restoration treatments, there appears to be a slight sanitation effect in which larger residual trees have lower levels of dwarf mistletoe infection. This will generally improve overall tree vigor of these individuals, making these larger trees more resilient when exposed to root diseases, beetles, and drought conditions. While the FVS is a probabilistic model rather than a spread model, it still provides important information on the potential of future spread and intensification.

Because Teakettle is an old-growth forest and not second growth, low to moderate levels of the root pathogens *Armillaria* and *H. annosum* were found on stumps and dead trees at Teakettle, mainly preexisting infections. Both of these native root diseases are common in forest communities and are most likely within the natural range of variability, with slightly elevated incidence given stand densification owing to fire suppression. Pretreatment observations of *Armillaria* fruiting bodies were made at Teakettle (D.M. Rizzo, T.F. Smith, and P.E. Maloney, personal observations), recognizing that the species was present in this old-growth forest but at undetectable levels. Thinning treatments, however, are known to exacerbate root disease conditions for both *Armillaria* and *H. annosum*, as these root pathogens can persist for decades occupying successive woody substrates as a result of parasitic and saprotrophic activity (Kile et al. 1991; Pronos 1996; Slaughter and Rizzo 1999). Because of this, consequences of management actions, such as tree removal or fire, may not be apparent for decades (Pronos 1996; Rizzo et al. 2000). It will be important to monitor root disease activity in the years following restoration activities, not

Fig. 4. Percentage of trees, stumps, and snags associated with the presence of *A. gallica* and *H. annosum* at Teakettle Experimental Forest. All host species are included. *Heterobasidion annosum* was found only on *Abies* spp.



only at Teakettle but also at other locations throughout the Sierra Nevada undergoing forest restoration treatments. Long-term monitoring, coupled with pre- and poststand condition information (density, structure, and composition), will be necessary to make adequate recommendations for restoration treatments based on trends and patterns observed across a broad array of forests and forest conditions. Both of these root diseases, particularly *H. annosum*, have much greater impacts on the true firs, which may have continued direct effects on fir mortality and reducing fir density over time.

Wildfires and forest restoration projects affect *Ribes* frequency and abundance, which may have very localized impacts on the dynamics of white pine blister on *P. lambertiana* in mixed-conifer forests. Infected *Ribes* were observed in no-thin-no-burn plots where there was an intact canopy, providing shaded and moist conditions that favor *Ribes* and *P. lambertiana* infection. Although cover remained the same, the significant increase in *Ribes* frequency, particularly in treated plots, suggests that resprouting and new seed establishment may dramatically increase *Ribes* presence (Wayman and North 2007). The increase in frequency of *Ribes* in these restoration treatments is epidemiologically important, as it may potentially increase *C. ribicola* inoculum on *Ribes*, from which the pathogen may disperse and infect *P. lambertiana*. However, there may be a lag period for conditions to be conducive for infections to occur on *Ribes* in treated stands. Restoration treatments and

subsequent stand opening dramatically changed microclimate, making the forest understory much drier and warmer during the summer (Ma 2003). These conditions do not favor WPBR infections and may explain why infected *Ribes* were not observed in 2005 in treated stands. Over several years, however, in-growth of trees and understory shrubs may provide suitable microclimatic conditions for WPBR infection. Long-term observations will be needed to evaluate these restoration treatments on the disease dynamics of the WPBR pathosystem in mixed-conifer ecosystems in the Sierra Nevada.

Forest pests can vary in their temporal response to forest restoration treatments, and our data only focused on immediate response to treatments. Within this short period, bark beetles are the most significant source of mortality, but we expect that root diseases, mistletoe, and blister rust will have an increasing impact with time. Certainly one desire of forest restoration is that treatment reductions in density and the reintroduction of fire might alter stand conditions enough that insects and pathogens would either kill trees in proportion to their posttreatment occurrence or increase selection and mortality of small-sized and shade-tolerant trees. Our findings suggest that this is not occurring, at least immediately after treatments. Large pines, particularly in burn treatments, have higher than expected beetle-mediated mortality. Although incidence of root disease on shade tolerants (i.e., *A. concolor* and *C. decurrens*) is high compared with that on pines, current mortality is proportionally lower in these species than their posttreatment frequency. Much of the *Abies* mortality is occurring among smaller diameter trees, whereas much of the *Pinus* mortality is occurring among larger diameter and reproductive individuals. For managers aiming to restore historic forest conditions, our results and those of others (Zald et al. 2008) suggest that one entry, be it thinning, fire, or their combination, may not be enough to achieve a target desired condition. A number of prescriptions and strategies may need to be applied so that loss of large-diameter *Pinus* spp. owing to fire- and beetle-mediated mortality is minimized, especially given that these are the species targeted for restoration and maintenance.

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