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Resiliency of an Interior Ponderosa Pine Forest to Bark Beetle Infestations Following Fuel-Reduction and Forest-Restoration Treatments

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Abstract: Mechanical thinning and the application of prescribed fire are commonly used to restore fire-adapted forest ecosystems in the Western United States. During a 10-year period, we monitored the effects of fuel-reduction and forest-restoration treatments on levels of tree mortality in an interior ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., forest in California. Twelve experimental plots, ranging in size from 77–144 ha, were established to create two distinct forest structural types: mid-seral stage (low structural diversity; LoD) and late-seral stage (high structural diversity; HiD). Following harvesting, half of each plot was treated with prescribed fire (B). A total of 16,473 trees (8.7% of all trees) died during the 10-year period. Mortality was primarily attributed to bark beetles (Coleoptera: Curculionidae, Scolytinae) (10,655 trees), specifically fir engraver, *Scolytus ventralis* LeConte, mountain pine beetle, *Dendroctonus ponderosae* Hopkins, western pine beetle, *D. brevicomis* LeConte, pine engraver, *Ips pini* (Say), and, to a much lesser extent, Jeffrey pine beetle, *D. jeffreyi* Hopkins. Trees of all ages and size classes were killed, but mortality was concentrated in the smaller-diameter classes (19–29.2 and 29.3–39.3 cm at 1.37 m in height). Most mortality occurred three to five years following prescribed burns. Higher levels of bark beetle-caused tree mortality were observed on LoD + B (8.7%) than LoD (4.2%). The application of these and other results to the

management of interior *P. ponderosa* forests are discussed, with an emphasis on the maintenance of large trees.

1. Introduction

Currently, >10 million hectares of forests are classified as having moderate- to high-fire hazards in the Western United States [1], and fuel-reduction treatments have been widely promoted to reduce the intensity and severity of future wildfires. Such conditions are most notable at lower elevations where short-interval, low- to moderate-intensity fire regimes predominate [2–10]. In general, these forests are characterized by the presence of ponderosa pine, *Pinus ponderosa* Dougl. ex Laws., an integral component of three forest cover types and a major component of >65% of all forests in the Western United States [11]. Prior to Euro-American settlement, many interior *P. ponderosa* forests in California, United States were dominated by open and park-like stands of widely-dispersed *P. ponderosa* and Jeffrey pines, *P. jeffreyi* Grev. & Balf. Frequent thinning of small-diameter (<19 cm diameter at breast height (dbh), 1.37 m) and fire-intolerant trees by low-intensity surface fires, and competitive exclusion of tree seedlings by understory grasses are believed to have maintained such conditions [12]. Today, many of these forests are denser, have more small trees and fewer large trees, and are dominated by more shade-tolerant and fire-intolerant tree species, such as white fir, *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. This is largely a result of fire exclusion and past harvesting practices [5,12].

When applied under prescription, both prescribed fire and mechanical thinning are generally effective in meeting short-term fuel reduction objectives as treated stands are more resilient to wildfire [13,14]. For example, their effectiveness for reducing the incidence of passive crown fire (*i.e.*, torching of small groups of trees) is well supported by modeling of predicted fire behaviors (e.g., [15]) and by empirical research (e.g., [16]). Ritchie *et al.* [16] studied the effects of fuel-reduction treatments at Blacks Mountain Experimental Forest, California on observed fire severity at the point of transition between treated (*see* Section 2) and untreated stands that were later impacted by a wildfire. Tree survival was highest in areas that were both thinned and prescribed burned. Survival in thinned-only areas was significantly greater than untreated areas, but less than areas that had received the combined treatment [16].

Following prescribed fire, tree mortality may be immediate due to consumption of living tissue and heating of critical plant tissues, or can be delayed occurring over the course of several years as a result of fire injuries to the crown, bole, or roots [17]. Levels of delayed tree mortality are difficult to predict, and depend on numerous factors including tree species, tree size, phenology, degree of fire-related injuries, initial and post-fire levels of tree vigor, the post-fire environment, and the frequency and severity of other predisposing, inciting, and contributing factors [13]. In specific, the propensity for bark beetles (Coleoptera: Curculionidae, Scolytinae) to attack fire-injured trees has led to questions regarding how the amount and distribution of bark beetle-caused tree mortality may negatively

impact efforts to restore fire-adapted forest ecosystems with prescribed fire [18]. Concerns also exist about the potential for bark beetle populations to increase in fire-injured trees and then colonize apparently-healthy trees in adjacent areas resulting in undesirable levels of tree mortality [13,14,18,19]. These trees may then serve as a source of beetles and attractive semiochemicals (*i.e.*, host volatiles and aggregation pheromones produced by many bark beetle species during host colonization) that attract other beetles into the vicinity resulting in additional levels of tree mortality over time. This is of particular importance in interior *P. ponderosa* forests, which are well recognized for the diversity of tree-killing bark beetle species inhabiting them, most notably western pine beetle, *Dendroctonus brevicomis* LeConte, mountain pine beetle, *D. ponderosae* Hopkins, Jeffrey pine beetle, *D. jeffreyi* Hopkins, pine engraver, *Ips pini* (Say), and fir engraver, *Scolytus ventralis* LeConte; and for which fuel reduction and forest restoration is a top priority [13,20].

Fuel-reduction treatments have functionally different effects on the fuel matrix, and, thus, on the structure and composition of residual forests as well as their resiliency to disturbances, such as bark beetle infestations [13,14,21,22]. For example, fuel-reduction treatments may affect the health and vigor of residual trees; the size, distribution and abundance of preferred hosts; and the physical environment within forests. Tree volatiles released during harvest operations and/or applications of prescribed fire are known to influence the physiology and behavior of bark beetles [23]; to increase bark beetle colonization rates on trees [24,25]; and to increase levels of tree mortality attributed to bark beetles [26] in *P. ponderosa* forests. Furthermore, associated reductions in tree density cause changes in microclimate that affect beetle fecundity and fitness, phenology and voltinism, as well as that of predators, parasites, and competitors [27]; or that may cause turbulences that disrupt pheromone plumes used for recruiting conspecifics during initial phases of host tree colonization [28], thus, negatively affecting host finding successes. Factors such as stand density, host density, average tree diameter, and average stand age are consistently identified as primary attributes associated with the severity of bark beetle infestations in the Western United States [21]. For example, Hayes *et al*. [29] showed that levels of *D. brevicomis*-caused tree mortality in *P. ponderosa* forests in California can be predicted (Adjusted $R^2 > 0.90$) at large spatial scales by simply measuring stand density, specifically the basal area of all tree species.

In the last decade, numerous studies have examined the effects of fuel-reduction and forest-restoration treatments on the amount, distribution and causes of tree mortality in *P. ponderosa* (e.g., [24,25,30–41]). Most were conducted on small experimental plots for a relatively short period of time. Our work is part of a long-term ecological research project (Blacks Mountain Ecological Research Project) managed by the Pacific Southwest Research Station (USDA Forest Service), and conducted at large spatial scales that represent reasonable management scenarios in interior *P. ponderosa*. The primary objectives of the Blacks Mountain Ecological Research Project are to enhance understanding of the effects of forest structural complexity on the health and vigor of interior *P. ponderosa* forests; to quantify resilience to natural and human-caused disturbances; and to determine how these forests can be managed for sustained resource values [12]. In other work, we described the effects of structural diversity and the application of prescribed fire on levels and causes of tree mortality two ([36], sample period 1) and five years ([37], sample period 2) following prescribed burns. The objective of this study was to further our understanding of these relationships during the initial 10 years (sample period 3) following prescribed burns. Our goal is to address the

following questions: (1) What are the effects of structural diversity and the application of prescribed fire on levels of tree mortality? (2) What are the primary causes of tree mortality and how might these vary temporally? (3) How do levels of tree mortality attributed to bark beetles vary by bark beetle species, host species, and tree size; (4) What are the potential implications to the management of interior *P. ponderosa* forests?

2. Experimental Section

This study was conducted at Blacks Mountain Experimental Forest (Blacks Mountain; 40°40′ N, 121°10′ W; 1700–2100 m elevation) located on the Lassen National Forest, California. Blacks Mountain was established in 1934 as a research facility for the study of forest management in interior *P. ponderosa*, and has produced a rich history of research concerning the effects of silvicultural treatments on forest insects. For example, Salman and Bongberg [42] developed their famous risk-rating system at Blacks Mountain. The climate is characterized by hot, dry summers and cold, moist winters. Mean daily temperatures range from −9 °C to 29 °C. Annual precipitation averages 50.8 cm, with most coming as snow between October and May. Prior to treatment, stands within the study area were dominated by two age cohorts consisting of 300–500 year-old *Pinus* (*P. ponderosa* and *P. jeffreyi*) and incense cedar, *Calocedrus decurrens* (Torr.) Flori, with a dense understory and mid-story of 50–100 year-old *Pinus*, *A. concolor*, and *C. decurrens* [12]. There were 32.4 ± 1.5 (mean ± SEM) m^2/ha of basal area and 871 ± 58 trees/ha [43].

Twelve experimental plots, ranging in size from 77–144 ha (mean = 111 ha), were established to create two distinct forest structural types: mid-seral stage (low structural diversity; LoD) and late-seral stage (high structural diversity; HiD). Each structure was randomly assigned to two plots within each of three blocks. Blocking allowed for allocating variation to differences in tree species composition associated with elevational gradients (as *A. concolor* and *C. decurrens* become increasingly abundant with elevation) and year of treatment. LoD was created by removing larger overstory trees and small understory trees leaving only trees of intermediate size, while HiD was attained by thinning smaller trees and retaining larger trees. Following harvesting, half of each plot was treated with prescribed fire in fall (B) (Table 1). For a comprehensive description of treatments and a depiction of their placement on the landscape, *see* Oliver [12]. Earlier, we described climatic conditions, fuel moistures, and other parameters associated with prescribed burns [36]. In short, burns were implemented using head, backing and spot fires. Hourly fuel moistures averaged from 10.5% for 6–25 mm fuels (Block 1) to 39.2% for duff (<20 mm) (Block 1 and 2). Following treatments, LoD and HiD averaged 10 and 25 m^2/ha of basal area and 282 and 513 trees/ha, respectively. Species composition ranged from 49% *Pinus* and 42% *A. concolor* (HiD + B) to 61% *Pinus* and 29% *A. concolor* (LoD + B) [43].

A 100% cruise (census) was conducted on each plot to locate dead and dying *Pinus* and *Abies* by presence of crown fade, an irreversible symptom of tree mortality. While both *C. decurrens* and western juniper, *Juniperus occidentalis* Hook., are minor components of Blacks Mountain (*i.e.*, representing <7.7% and <0.1% of trees, respectively) [12,43], these species generally are not attacked and killed by bark beetles and were ignored. Due to the large spatial scale of this study, treatment implementation and our evaluations were staggered across multiple years (Table 1). All recently-killed *Pinus* and *Abies* >19 cm dbh were identified, tallied, and causal agent of mortality

identified. Tree species, dbh, crown color, colonizing bark beetle species, presence of wood borers (Coleoptera: Cerambycidae, Buprestidae), and ranking of burn severity (1–4, based on external measures of bole char and bark consumption) [36,37] were recorded. A section of bark ~625 cm^2 was removed on each recently-killed tree with a hatchet at ~2 m in height on at least two aspects to determine if any bark beetle galleries were present in the phloem or cambium. The shape, distribution and orientation of galleries are commonly used to distinguish among bark beetle species [44]. Bark removal also served as a means of separating mortality tallied during each of three sample periods.

Table 1. Treatment and evaluation dates, Blacks Mountain Experimental Forest, California.

Plot	Stand Structure [1]	Prescribed Burn	Sample Period 1 [2]		Sample Period 2	Sample Period 3 [3]
			Unburned	Burned	All	All
38	HiD	October 1997	September 1998	August 1999	September 2002	June 2008
39	LoD	October 1997	September 1998	September 1999	September 2002	June 2008
40	LoD	October 2000	August 2002	July 2002	August 2005	May 2012
41	HiD	October 1997	August 1998	August 1999	September 2002	June 2008
42	HiD	November 1999	September 2001	August 2001	September 2004	October 2009
43	LoD	October 1997	August 1998	August 1999	October 2002	June 2008
44	LoD	November 1999	July 2001	August 2001	August 2004	August 2009
45	LoD	November 1999	October 2001	October 2001	October 2004	October 2009
46	LoD	October 2000	June 2002	June 2002	[4]	[4]
47	HiD	November 1999	July 2002	July 2002	August 2004	August 2009
48	HiD	October 2000	July 2002	July 2002	August 2005	May 2012
49	HiD	October 2000	August 2002	August 2002	October 2005	May 2012

[1] HiD = high structural diversity, LoD = low structural diversity [12]; [2] Burned-split plots were initially evaluated the second field season following prescribed burns; [3] Plots burned in 1999 were evaluated the tenth field season. Plots burned in 1997 were evaluated in early 2008 prior to bark beetle flight. Plots burned in 2000 were evaluated in 2012 prior to bark beetle flight, but only trees killed in 2010 (based on crown fade) were tallied; [4] Plot damaged by wildfire and excluded from study in 2002.

In September 2002, a wildfire (Cone Fire) ignited adjacent to Blacks Mountain and burned portions of three of the 12 plots with variable intensities [16]. One plot (plot 46) suffered low- to moderate-severity wildfire throughout much of the plot, and therefore was excluded from our study (Table 1). The two other plots were partially burned. Only the burned split was impacted in plot 41 and the affected portion (*i.e.*, as noted by the presence of bole char and/or crown scorch on trees) amounted to 8.7% (of 55.6 ha). About 27% (of 51.6 ha) of the burned split, and 28.2% (of 64.5 ha) of the unburned split, were affected in plot 43 [37]. The affected areas were subtracted from the original area and data were adjusted accordingly.

The primary variables of interest were the mean percentage of trees killed by (1) all causes; (2) all bark beetle species across all tree species; (3) individual bark beetle and host tree species; and (4) individual bark beetle species by host tree species within diameter class (19–29.2, 29.3–39.3, 39.4–49.5, 49.6–59.7, >59.7 cm dbh). In general, the precise role of each bark beetle species in contributing to tree mortality is unknown. Furthermore, fire-injured *P. ponderosa* are susceptible to colonization by several species of bark beetles at Blacks Mountain. In some cases, trees must have

green phloem for successful colonization and brood production to occur. Such is commonly the case for *D. brevicomis* [45]. In other species, such as *I. pini*, colonization and successful brood production can occur in dead and dying trees [46]. We attributed tree mortality to *D. brevicomis*, *D. ponderosae*, *D. jeffreyi*, and *S. ventralis* if evidence of colonization was found despite the potential presence of other bark beetle species. On occasion, we found *D. brevicomis* and *D. ponderosae* infesting the same *P. ponderosa* and in these rare situations we attributed tree mortality to *D. brevicomis* [36,37]. Tree mortality was attributed to *Ips* spp. only when evidence of *D. brevicomis*, *D. ponderosae*, and *D. jeffreyi* was absent. Mortality was only attributed to bark beetles when burn severity rankings on individual trees were ≤3 (*i.e.*, we estimated that prescribed fire did not directly kill the tree based on external measures of fire severity; [36,37]).

Data presented here were analyzed cumulatively over the 10-year period. The experimental design was a randomized complete block with split plots with three blocks, two treatments (HiD and LoD), and two replicates per treatment (*N* = 12) [12]. Blacks Mountain is included in cattle grazing allotments and therefore six of 12 plots were fenced in an attempt to permit analyses of the effects of grazing on several variables of interest to the interdisciplinary team. However, we viewed grazing as having little or no influence on bark beetle responses [36,37], and therefore this variable was ignored. Due to the imbalance in the number of plots as a result of the Cone Fire, the Satterthwaite approximation method was used to estimate the appropriate degrees of freedom. We performed an analysis of variance on each response variable at α = 0.05 (SAS Institute Inc., Cary, NC, USA). If a significant treatment effect was detected, Tukey's multiple comparison test (Tukey's HSD) was used for separation of treatment means.

3. Results and Discussion

A total of 188,793 *Pinus* and *Abies* were monitored for mortality during the 10-year period. Of these 106,314 were *P. ponderosa*, 63,636 were *A. concolor*, and 18,843 were *P. jeffreyi*. Numbers of trees varied widely among diameter classes and treatments, and therefore statistical analyses are based on percentages. For a comprehensive account of treatment effects on stand structure and composition, *see* Zhang *et al*. [43]. Fettig *et al*. ([36], page 1, Figure 1) provide data on numbers of trees monitored by diameter class and treatment during our study.

3.1. Tree Mortality

A total of 16,473 trees (8.7% of all trees) died during the 10-year period, of which 42.1%, 5.2%, and 52.7% were *P. ponderosa*, *P. jeffreyi*, and *A. concolor*, respectively. This represents mortality from all sources (*i.e.*, prescribed fire, bark beetles, pathogens, mechanical damage, and unidentified sources, and their many interactions), the majority (64.7%) of which was attributed to bark beetles (*see* Section 3.2). The highest levels of tree mortality were observed during the initial sample period (1–2 years, [36]) followed by the second (3–5 years, [37]) and third (6–10 years) sample periods. This was expected as fire-susceptible trees (e.g., small-diameter *A. concolor*) are often directly killed by the immediate effects of prescribed fire [13]. Overall, tree mortality was concentrated (10,320 trees) in the smallest-diameter class (24.1 cm), while the 54.7-cm diameter class had the lowest levels of tree mortality (252 trees). Tree size is well known to influence the probability of tree mortality following

prescribed fire [47], which in most cases is attributed to variation in bark thickness. For example, Regelbrugge and Conard [48] showed that tree diameter and height were positively correlated with postfire survival of *P. ponderosa* in the Central Sierra Nevada, California. McHugh and Kolb [32] sampled 1367 trees in *P. ponderosa* forests impacted by wildfires and prescribed fire in Northern Arizona, United States. They reported mortality ranged from 13.9% (Bridger-Knoll wildfire) to 32.4% (Side wildfire) during the three-year period following fire. Most of the tree mortality (>95% for the prescribed fire) occurred during the first two years. In their study, mortality was greatest for trees with the smallest diameters (<20 cm dbh) and then decreased as diameter increased, as would be expected due to increasing bark thickness. However, mortality increased as diameter increased among the largest trees (>50 cm dbh) [32]. Others have reported similar results described as a "U-shaped" distribution of tree mortality by tree diameter [49], which agrees with our observations at Blacks Mountain.

Figure 1. Mean percentage of trees killed by all sources by diameter class (mid-point of 10-cm diameter classes) and treatment (LoD, low structural diversity; HiD, high structural diversity) 10 years following prescribed burns, Blacks Mountain Experimental Forest, California. Means (+ SEM, standard error of the mean) followed by the same letter within groups are not significantly different (Tukey's HSD; *p* > 0.05).
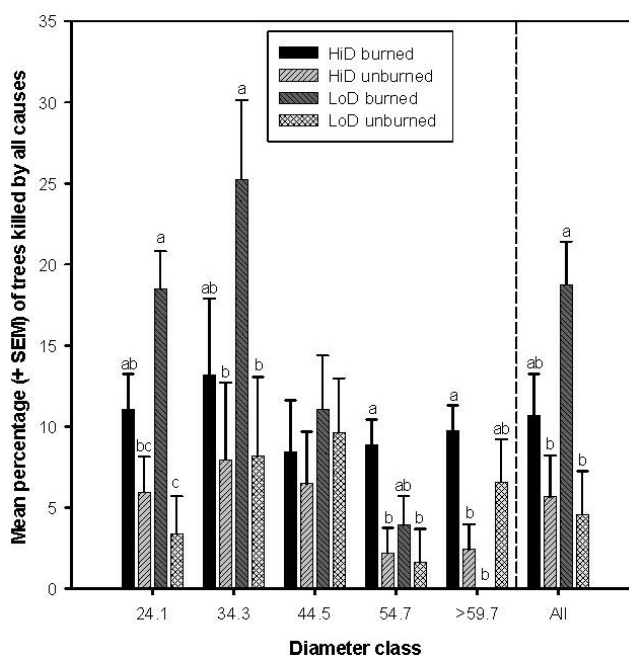
Kolb *et al*. [50] suggested that growth of large *P. ponderosa* can be accelerated by thinning, but warned that prescribed fire may predispose trees to increased levels of delayed mortality, often by bark beetles. In recent work at Blacks Mountain, Ritchie *et al*. [51] reported tree vigor increased in thinned stands, but that an increase in the mortality of large trees occurred when thinning was followed by prescribed fire. The authors suggested that this is likely a one-time phenomenon occurring shortly after the application of prescribed fire [51]. Higher levels of tree mortality occurred on LoD + B (18.8%) compared to HiD (5.7%) and LoD (4.6%) (*p* = 0.017; Figure 1, all trees). Higher levels of tree mortality were also observed on LoD + B in the two smallest-diameter classes (*p* < 0.02, Figure 1, 24.1 and 34.3), but in the two largest-diameter classes higher levels were observed in HiD + B

($p < 0.05$; Figure 1, 54.7 and >59.7). Presumably the latter is influenced by the few large-diameter trees occurring on LoD plots, as related to mortality attributed to bark beetles, as many species tend to concentrate searching in patches of high preferred host density (*see* Section 3.2.1) [21]. For example, only 565 trees occurred in the two largest diameter classes on LoD compared to 17,593 on HiD. Of these 1.4% and 3.4% were killed by bark beetles, respectively (Table 2). Interestingly, no significant treatment effect was observed for the 44.5-cm diameter classes ($p = 0.90$; Figure 1). Fettig *et al*. [39] examined the effects prescribed fire season (spring, fall, and none) on levels of tree mortality in *P. ponderosa* and *P. jeffreyi* forests in the Central Sierra Nevada, and also reported few significant treatment effects in the intermediate-diameter classes. These trees are likely large enough to be resistant to prescribed fire [47], but may be less susceptible to bark beetle colonization due to their size (e.g., from *D. brevicomis*) [21]. Both LoD and HiD structures contained large numbers of intermediate-sized trees [36,43].

Table 2. Numbers of trees killed by bark beetles, Blacks Mountain Experimental Forest, California.

Treatment	Dbh Class	*Dendroctonus brevicomis* [1]	*Dendroctonus ponderosae*	*Dendroctonus jeffreyi*	*Ips* spp.	*Scolytus ventralis*	Total
HiD + B	24.1	190	448	7	129	1354	2,128
	34.3	198	227	11	28	537	1,001
	44.5	102	59	2	1	157	321
	54.7	66	10	2	2	27	107
	>59.7	250	28	2	1	14	295
	All	806	772	24	161	2089	3,852
HiD	24.1	119	450	1	2	1071	1,643
	34.3	89	175	1	0	626	891
	44.5	33	37	2	0	200	272
	54.7	27	10	0	0	29	66
	>59.7	100	13	0	0	17	130
	All	368	685	4	2	1943	3,002
LoD + B	24.1	65	221	5	252	1151	1,694
	34.3	86	104	3	60	549	802
	44.5	18	13	1	2	66	100
	54.7	0	4	0	0	*	4
	>59.7	*	*	0	*	0	0
	All	169	342	9	314	1766	2,600
LoD	24.1	12	68	4	6	586	676
	34.3	27	30	1	1	381	440
	44.5	11	3	0	0	67	81
	54.7	1	0	0	0	*	1
	>59.7	0	2	0	0	1	3
	All	51	103	5	7	1035	1,201
Total		1394	1902	42	484	6833	10,655

* No hosts were present.

The rates of tree mortality observed in our study (*i.e.*, ranging from 4.6% to 18.8% for LoD and LoD + B, respectively) are somewhat higher than reported elsewhere for *P. ponderosa* forests following fuel-reduction and forest-restoration treatments. For example, Fettig *et al*. [39] found 14% and 16.7% of trees (>10.2 cm dbh) were killed during a three-year period following spring and fall burns in the Central Sierra Nevada. In the Southern Cascades, 9.2% of trees (>19.5 cm) were killed by bark beetles (total tree mortality was not reported, which would have been higher than the value reported for bark beetles) during a four-year period following prescribed burns [38]. In Northern Arizona, Breece *et al*. [35] reported 7.6% of trees (>13 cm dbh) died during a three-year period following prescribed burns. In these cases stands were not recently thinned prior to the application of prescribed fire, and therefore higher levels of tree mortality would have been expected compared to our study. For example, Fettig *et al*. [38] reported that only 3.3% of trees were killed by bark beetles when thinning occurred prior to burning. It is important to note that slash (activity fuels) was removed prior to the application of prescribed fire at Blacks Mountain, and therefore was not a significant factor influencing fire severity. The level of tree mortality observed in LoD + B (18.8%) is surprising given the minimum threshold diameter of trees (>19 cm dbh) monitored in our study (i.e., many small trees were killed that were ignored during our evaluations). However, treatments at Blacks Mountain included a restoration objective of promoting *Pinus* over *A. concolor* [12], and much of this mortality occurred in *A. concolor* and was attributed to *S. ventralis* (*see* Section 3.2.5). It is important to stress that our data represent mortality occurring during a 10-year period following fuel-reduction and forest-restoration treatments, and, therefore, do not allow for direct comparisons with most similar studies, which were of shorter duration.

3.2. Tree Mortality Attributed to Bark Beetles

As indicated, the majority of tree mortality was attributed to bark beetles. *Dendroctonus brevicomis* and *D. ponderosae* were observed colonizing *P. ponderosa*; *D. jeffreyi* was observed colonizing *P. jeffreyi*; and *S. ventralis* was observed colonizing *A. concolor*. We also found *I. pini* and, to a much lesser extent, emarginate ips, *I. emarginatus* (LeConte) and *I. latidens* (=*Orthotomicus)* (LeConte) colonizing *P. ponderosa* and *P. jeffreyi*. *Hylastes* spp., primarily *H.* macer LeConte, *Hylurgops* spp., primarily *Hy. subcostulatus* (Mannerheim), and *Pseudohylesinus* spp. were occasionally observed, but are not considered important sources of tree mortality [44]. Red turpentine beetle, *D. valens* LeConte, a common species found throughout much of North America, was found colonizing many *Pinus* on burned-split plots (e.g., 72.7% of dead *Pinus* during sample period 1), but their activity was largely limited to the initial sample period. Attacks by *D. valens* are usually confined to basal portions of stressed, weakened, or dead and dying *Pinus* [44], and are typically not considered a significant threat to tree health. For a comprehensive account of treatment effects on *D. valens*, *see* Fettig *et al*. [36]. The California fivespined ips, *Ips paraconfusus* Lanier, a common species along the western slope of the Sierra Nevada, was not observed colonizing *Pinus* at Blacks Mountain and likely is not indigenous to the area [44].

A total of 10,655 trees (5.6% of all trees) were killed by bark beetles (all bark beetle species combined) during the 10-year period (Table 2). The highest levels of bark beetle-caused tree mortality were observed during the second sample period (4193 trees) followed by the first (2684 trees) and

third (3778) sample periods when adjusted for temporal scale (*i.e.*, annualized) (Table 3). Overall, bark beetle-caused tree mortality was concentrated (6141 trees) in the smallest-diameter class (24.1 cm, Table 2), while the 54.7-cm diameter class had the lowest levels (178 trees) (Table 2). Higher levels of bark beetle-caused tree mortality were observed on LoD + B than LoD in the 34.3-cm diameter class (15.4% and 7.3%, respectively) and for all trees (8.7% and 4.2%, respectively) ($p < 0.05$; Figure 2). HiD + B (6.4%) exhibited higher levels of bark beetle-caused tree mortality than HiD (1.7%) in the 54.7-cm diameter class ($p < 0.05$; Figure 2). HiD + B (6.6%) also exhibited higher levels of bark beetle-caused tree mortality than LoD + B (0%) in the >59.7-cm diameter class ($p = 0.02$; Figure 2). No other significant differences were observed. These findings differ from those observed during the first five years following prescribed burns when higher levels of bark beetle-caused tree mortality were observed on LoD + B (5.3%) and HiD + B (4.8%) than LoD (1.1%) [36]. Approximately 60.5% of all bark beetle-caused tree mortality occurred on burned-split plots.

Table 3. Cumulative numbers of trees killed by bark beetles by sample period, Blacks Mountain Experimental Forest, California.

Sample Period	Interval [1]	*Dendroctonus brevicomis*	*Dendroctonus ponderosae*	*Dendroctonus jeffreyi*	*Ips* spp.	*Scolytus ventralis*	Total
1	1–2	442	468	18	456 [2]	1300	2,684
2	3–5	747	947	17	15	2467	4,193
3	6–10	205	487	7	13	3066	3,778
Total		1394	1902	42	484	6833	10,655

[1] Years following prescribed burns; [2] Fettig *et al.* [36] reported this value as 494, which is in error.

Figure 2. Mean percentage of trees killed by bark beetles (all species) by diameter class (mid-point of 10-cm diameter classes) and treatment (LoD, low structural diversity; HiD, high structural diversity) 10 years following prescribed burns, Blacks Mountain Experimental Forest, California. Means (+ SEM, standard error of the mean) followed by the same letter within groups are not significantly different (Tukey's HSD; $p > 0.05$).
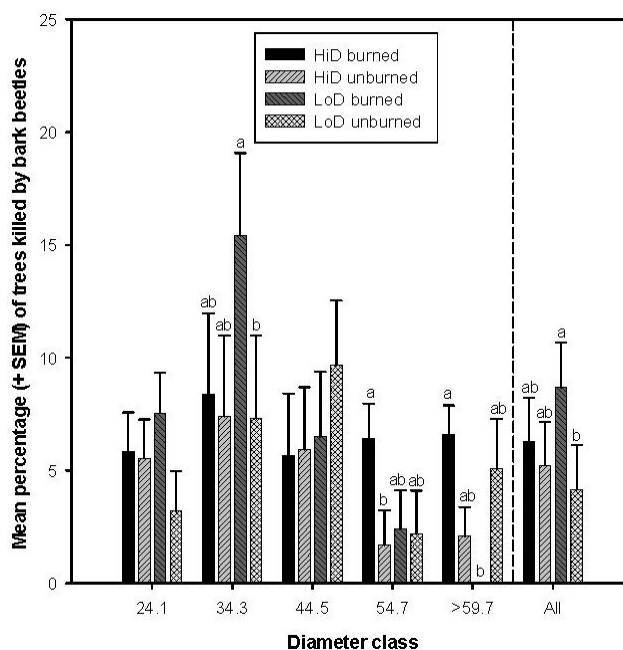
Some authors have expressed concerns about the potential for bark beetle populations to increase in fire-injured trees and subsequently colonize apparently-healthy trees. Large numbers of stressed trees provide abundant host material and once this resource is exhausted bark beetles may attack and kill trees that might otherwise have survived. However, in their synthesis on the effects of fuel-reduction treatments in the United States, Stephens *et al*. [13] concluded that while bark beetles often colonize fire-injured trees responses tend to be relatively short-lived and concentrated in the smaller-diameter classes, which generally agrees with our observations at Blacks Mountain. In the longer-term, the additional reduction in stand density achieved as a result of prescribed burns over mechanical thinning alone likely influenced stand susceptibility to bark beetle attack on burned-split plots. Fettig *et al*. [21] reviewed tree, stand, and landscape factors associated with bark beetle infestations, and analyzed the effectiveness of silvicultural treatments for mitigating undesirable levels of tree mortality attributed to bark beetles. They reported that reductions in stand density impact tree vigor, inter-tree spacing, and pheromone plumes, among other factors, which reduce stand susceptibility to bark beetle infestation [21]. To that end, earlier we reported that the amount of bark beetle-caused tree mortality increased considerably on unburned-split plots compared to burned-split plots three to five years after prescribed burns at Blacks Mountain [37]. For example, a 500% increase in the amount of bark beetle-caused tree mortality was observed on unburned-split plots as compared to a 50% increase on burned-split plots in HiD. This trend continued 6–10 years after prescribed burns, most notably a 251% increase in the amount of bark beetle-caused tree mortality was observed on unburned-split plots compared to a 70% increase on burned-split plots in LoD. Most of this mortality (94.3%) was attributed to *S. ventralis* (*see* Section 3.2.5).

3.2.1. Tree Mortality Attributed to *Dendroctonus brevicomis*

Dendroctonus brevicomis is a major cause of *P. ponderosa* mortality in much of Western North America. Unlike many other bark beetles, *D. brevicomis* is unique in that it has a very narrow host range. The only other common host is Coulter pine, *P. coulteri* D. Don [52], a species primarily indigenous to the mountains of Southern California and Northern Baja California, Mexico [11]. Preferred hosts are larger-diameter trees. For example, an outbreak in Southern California in the early 2000s, that was associated with a severe drought, resulted in the mortality of >73% of *P. ponderosa* >43.2 cm dbh over an extensive area [53]. However, trees of all ages and size classes may be colonized and killed [52].

A total of 1394 *P. ponderosa* (0.7% of all trees) were killed *D. brevicomis* during the 10-year period (Table 2). The highest levels of *D. brevicomis*-caused tree mortality were observed during the second sample period (747 *P. ponderosa*) followed by the first (442 *P. ponderosa*) and third (205 *P. ponderosa*) sample periods (Table 3). Overall, *D. brevicomis*-caused tree mortality was concentrated (400 *P. ponderosa*) in the 34.3-cm diameter class (Table 2), while the 54.7-cm diameter class had the lowest levels of tree mortality (96 *P. ponderosa*) (Table 2). Higher levels of *D. brevicomis*-caused tree mortality were observed on HiD + B (3%) compared to HiD (1.1%) and LoD (0.5%) ($p = 0.016$; Figure 3, all trees). HiD + B (4.5%) exhibited higher levels of tree mortality compared to LoD + B (0%) in the 54.7-cm diameter class ($p = 0.013$; Figure 3). No other significant differences were observed. There were no *P. ponderosa* within the >59.7-cm diameter class on LoD + B,

and therefore statistical analyses were not conducted for this diameter class. Approximately 70% of all *D. brevicomis*-caused tree mortality occurred on burned-split plots, specifically on HiD + B (Table 2).

Figure 3. Mean percentage of trees killed by *Dendroctonus brevicomis* by diameter class (mid-point of 10-cm diameter classes) and treatment (LoD, low structural diversity; HiD, high structural diversity) 10 years following prescribed burns, Blacks Mountain Experimental Forest, California. Means (+ SEM, standard error of the mean) followed by the same letter within groups are not significantly different (Tukey's HSD; *p* > 0.05). * Denotes analysis was not performed due to absence of host trees in one or more treatments within diameter class.
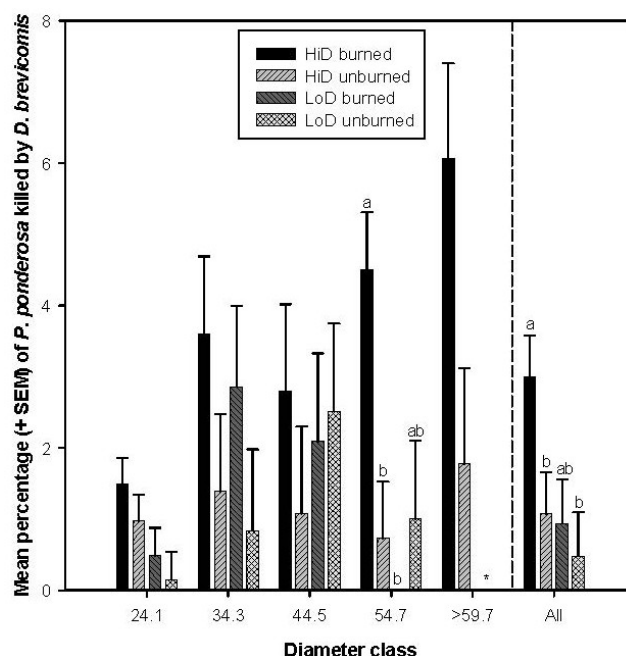
McHugh *et al*. [33] reported that *D. brevicomis* colonized only three of 222 trees following a prescribed fire in Northern Arizona. Similarly, Sánchez-Martínez and Wagner [54] detected no significant difference in the amount of *D. brevicomis*-caused tree mortality between managed (including prescribed fire) and unmanaged stands in Northern Arizona, but others have established a link between fire-injury and the increased susceptibility of *P. ponderosa* to *D. brevicomis* attack [45]. While the overall impact of *D. brevicomis* seems to be rather limited in fire-injured trees at Blacks Mountain, levels of *D. brevicomis*-caused tree mortality in the largest-diameter class (>59.7 cm) may be of concern on HiD + B (Table 2). Most of this mortality occurred during the first five years following prescribed burns. During this time, growth (net change in basal area) was positive for all treatments except HiD + B [43]. There are tools available to protect individual *P. ponderosa* from mortality attributed to *D. brevicomis* [55,56] that could be considered for protecting large-diameter *P. ponderosa* (*see* Section 4).

3.2.2. Tree Mortality Attributed to *Dendroctonus ponderosae*

Dendroctonus ponderosae is a major disturbance in coniferous forests of western North America where it colonizes several tree species, most notably, lodgepole pine, *P. contorta* Dougl. ex Loud.,

P. ponderosa, sugar pine, *P. lambertiana* Dougl., limber pine, *P. flexilis* E. James, western white pine, *P. monticola* Dougl. ex D. Don, and whitebark pine, *P. albicaulis* Engelm. [57]. *Dendroctonus ponderosae* was only found colonizing *P. ponderosa* at Blacks Mountain as other hosts (e.g., *P. lambertiana*) are rare. The extent of tree mortality resulting from *D. ponderosae* may be limited to small spatial scales (e.g., small groups of trees) or impact entire landscapes [57].

A total of 1902 trees (1.0% of all trees) were killed *D. ponderosae* during the 10-year period (Table 2). As with *D. brevicomis*, the highest levels of *D. ponderosae*-caused tree mortality were observed during the second sample period (947 *P. ponderosa*) followed by the first (468 *P. ponderosa*) and third (487 *P. ponderosa*) sample periods when adjusted for temporal scale (*i.e.*, annualized) (Table 3). Overall, *D. ponderosae*-caused tree mortality was concentrated (1187 *P. ponderosa*) in the smallest-diameter class (24.1 cm, Table 2), while the 54.7-cm diameter class had the lowest levels (24 *P. ponderosa*) (Table 2). In California, *D. ponderosae* infestations are typically confined to smaller (<31.8 cm dbh) *P. ponderosa* with single trees or small groups of trees being killed, and its role is often secondary to that of *D. brevicomis* in larger-diameter *P. ponderosa* [44]. This is supported by our results (Table 2).

Overall, no significant treatment effect was observed ($p = 0.73$; Figure 4, all trees). However, in the 54.7-cm diameter class significantly higher levels of *D. ponderosae*-caused tree mortality were observed on LoD + B (2.3%) compared to HiD (0.3%) and LoD (0.02%) ($p = 0.03$, Figure 4). No other significant differences were observed. There were no *P. ponderosa* within the >59.7-cm diameter class on LoD + B, and, therefore, statistical analyses were not conducted for this diameter class. Approximately 59% of all *D. ponderosae*-caused tree mortality occurred on burned-split plots, primarily HiD + B. Earlier, we reported that the application of prescribed fire resulted in significant increases in *D. ponderosae*-caused tree mortality in all but the two largest-diameter classes at Blacks Mountain [36]. During the second sample period, significantly higher levels of *D. ponderosae*-caused tree mortality occurred on HiD + B (2.1%) and LoD + B (1.8%) compared to LoD (0.5%) [37].

Jenkins *et al.* [58] recently reviewed, among other factors, the literature concerning *D. ponderosae* responses to prescribed fire and mixed-severity wildfire. Early research suggested that *D. ponderosae* contributed little to delayed tree mortality, but some of this work was conducted in *P. contorta* forests. Davis *et al.* [25] reported that levels of fire injury in *P. ponderosa* that were suitable for colonization by *D. ponderosae* differed from those of *P. contorta*. *Pinus contorta* has thinner bark than *P. ponderosa*, and as a result trees are often more likely to be directly killed by fire. To that end, stressed trees with phloem resources suitable for successful colonization by *D. ponderosae* are presumably more ephemeral in *P. contorta* than in *P. ponderosa* following prescribed burns of similar intensity. Interestingly, Stark *et al.* [41] examined the effects of prescribed fire and thinning (alone and in combination) on the responses of bark beetles in a mixed-conifer forest in the Central Sierra Nevada, and reported *D. ponderosae* did not colonize any fire-injured *P. ponderosa*, but attacks were observed on fire-injured *P. lambertiana*.

Figure 4. Mean percentage of trees killed by *Dendroctonus ponderosae* by diameter class (mid-point of 10-cm diameter classes) and treatment (LoD, low structural diversity; HiD, high structural diversity) 10 years following prescribed burns, Blacks Mountain Experimental Forest, California. Means (+ SEM, standard error of the mean) followed by the same letter within groups are not significantly different (Tukey's HSD; *p* > 0.05). * Denotes analysis was not performed due to absence of host trees in one or more treatments within diameter class.
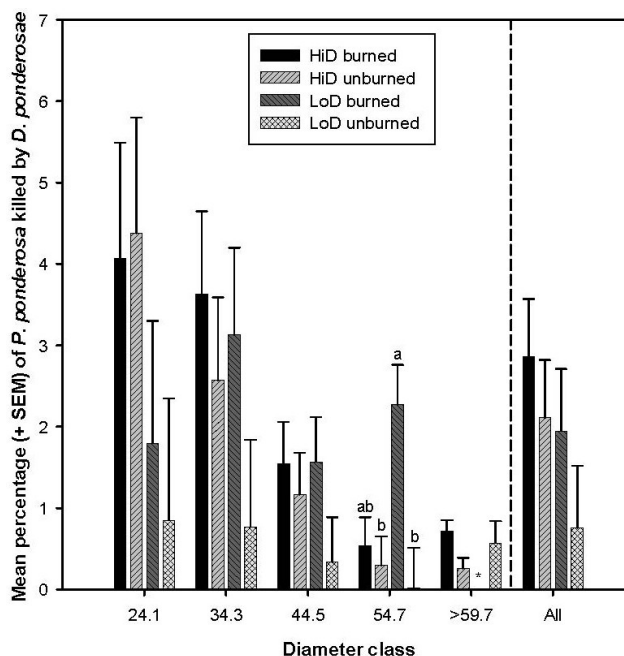
3.2.3. Tree Mortality Attributed to *Dendroctonus jeffreyi*

Dendroctonus jeffreyi only colonizes *P. jeffreyi* a tree species that ranges from the Klamath Mountains in Southwestern Oregon, United States throughout much of the Sierra Nevada to the Transverse and Peninsular Ranges of Southern California, and the Sierra San Pedro Mártir of Baja California, Mexico [11]. Under endemic conditions attacks by *D. jeffreyi* are usually confined to individual mature trees, however during epidemics group kills of 20–30 trees are common [59]. A total of 42 *P. jeffreyi* (0.2% of all *P. jeffreyi*) were killed by *D. jeffreyi* during the 10-year period (Table 2), and therefore statistical analyses were not conducted. Much of this mortality (38%) was confined to a single split plot (HiD + B). While minimal research has occurred, the response of *D. jeffreyi* to fire-injured trees appears limited [30,39].
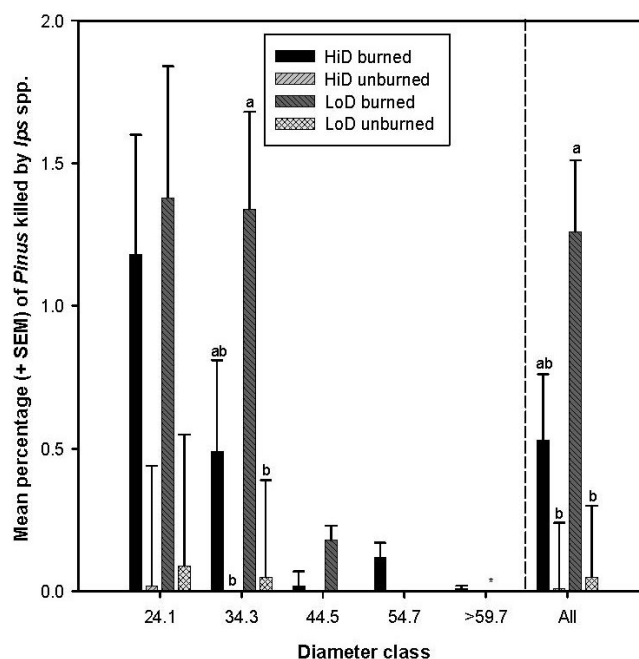
3.2.4. Tree Mortality Attributed to *Ips* spp.

Ips spp. generally colonize slash, saplings, and weakened trees. Outbreaks are often short-lived, but increase in duration and extent when suitable host material is plentiful and populations grow sufficiently to colonize apparently-healthy trees [46]. A total of 484 *Pinus* (0.3% of all trees) were killed by *Ips* spp. during the 10-year period (Table 2), primarily (456 *Pinus*) during the first sample period (Table 3). Most of this mortality (475 *Pinus*) occurred on burned-split plots within the two smallest-diameter classes (Table 2). *Ips pini* most frequently colonizes trees 5–20 cm dbh [46],

and attack rates are negatively correlated with tree diameter in *P. ponderosa* [60]. It is, therefore, likely that our minimum threshold diameter (19 cm dbh) resulted in a conservative estimate of *Ips*-caused tree mortality. While concerns regarding *Ips* populations increasing in logging residuals and subsequently colonizing leave trees are important [26], harvest criteria at Blacks Mountain required utilization (*i.e.*, biomass or chips) and removal of slash from the site [12]. In some locations, top killing of *Pinus* by *Ips* spp. is a concern [46], but was not common in our study.

Higher levels of *Ips*-caused tree mortality were observed on LoD + B as compared to LoD and HiD in the 34.3-cm diameter class (1.3%, 0.05% and 0%, respectively) and for all trees (1.3%, 0.05% and 0.01%, respectively) ($p < 0.05$; Figure 5). No other significant differences were observed. There were no *P. ponderosa* within the >59.7-cm diameter class on LoD + B, and therefore statistical analyses were not conducted for this diameter class. Fettig *et al*. [39] reported significantly higher levels of tree mortality were attributed to *Ips* spp. following late season burns compared to the untreated control in the Central Sierra Nevada. As in our study, most of this mortality occurred in the smallest-diameter class. The response by *Ips* spp. to fire-injured *Pinus* at Blacks Mountain appears limited, short-lived and concentrated in smaller-diameter trees, and therefore does not appear to interfere with management objectives.

Figure 5. Mean percentage of trees killed by *Ips* spp. by diameter class (mid-point of 10-cm diameter classes) and treatment (LoD, low structural diversity; HiD, high structural diversity) 10 years following prescribed burns, Blacks Mountain Experimental Forest, California. Means (+ SEM, standard error of the mean) followed by the same letter within groups are not significantly different (Tukey's HSD; $p > 0.05$). ***** Denotes analysis was not performed due to absence of host trees in one or more treatments within diameter class.

3.2.5. Tree Mortality Attributed to *Scolytus ventralis*

Scolytus ventralis colonizes *Abies*, particularly *A. concolor*, throughout much of the Western United States. Trees of all ages and size classes may be attacked and killed. Outbreaks are typically associated with drought, defoliation or other factors [44]. A total of 6833 *A. concolor* (3.6% of all trees) were killed by *S. ventralis* during the 10-year period (Table 2). Most this mortality occurred during the first five years, however substantial levels were observed during the third sample period (Table 3). This differs from other bark beetles species monitored during this study whose activity declined substantially during the third sample period (Table 3). Overall, *S. ventralis*-caused tree mortality was concentrated (4162 *A. concolor*) in the smallest-diameter class (24.1 cm, Table 2), while the largest-diameter class had the lowest levels of tree mortality (32 *A. concolor*) (>59.7 cm, Table 2). Higher levels of *S. ventralis*-caused tree mortality were observed on LoD + B (20%) than any other treatment (*p* = 0.003; Figure 6). A similar effect was observed in the smallest-diameter class (24.1 cm, *p* = 0.006, Figure 6). No other significant differences were observed. There were no *A. concolor* within the 54.7-cm diameter class on LoD and LoD + B, and therefore statistical analyses were not conducted for this diameter class. As indicated earlier, treatments at Blacks Mountain included a restoration objective of promoting *Pinus* over *A. concolor* [12], and therefore while substantial numbers of *A. concolor* were killed by *S. ventralis* this may be of limited concern.

Figure 6. Mean percentage of trees killed by *Scolytus ventralis* by diameter class (mid-point of 10-cm diameter classes) and treatment (LoD, low structural diversity; HiD, high structural diversity) 10 years following prescribed burns, Blacks Mountain Experimental Forest, California. Means (+ SEM, standard error of the mean) followed by the same letter within groups are not significantly different (Tukey's HSD; *p* > 0.05). * Denotes analysis was not performed due to absence of host trees in one or more treatments within diameter class.
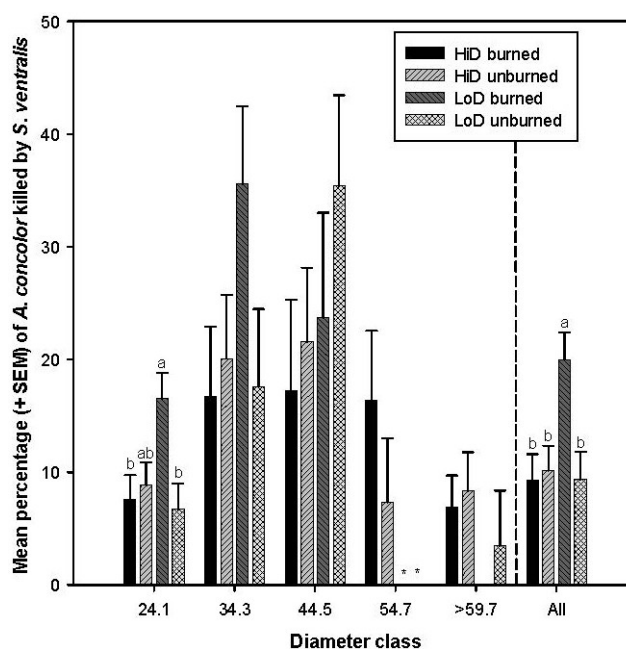
Few studies have analyzed responses of *S. ventralis* to fire-injured trees. Schwilk *et al.* [34] found attacks and associated levels of tree mortality were greater for smaller-diameter *Abies* following prescribed fire in the Central Sierra Nevada. Fettig *et al.* [38] reported significantly higher levels of tree mortality were attributed to *S. ventralis* on plots that were thinned and burned compared to thinned only. Stark *et al.* [41] found no significant differences in levels of tree mortality attributed to bark beetles among fuel-reduction treatments, except for *S. ventralis* in small- (11.5–25.2 cm dbh) and medium-sized (25.3–45.5 cm dbh) *A. concolor*. In their study, significantly higher levels (percentage) of tree mortality were attributed to *S. ventralis* in treatments including prescribed fire [41].

3.3. Tree Mortality Attributed to Wood Borers

During the first sample period, we reported that it appeared wood borers were directly contributing to tree mortality in fire-injured trees at Blacks Mountain, and that this mortality would likely not have occurred in the absence of such attacks (*i.e.*, these trees were alive the summer following prescribed burns) [36]. Wood borers are attracted to fire-injured trees [18,19,33], but their contribution to tree mortality, while thought to be rare [18], is unclear and difficult to decipher given numerous confounding factors. Several species are regarded as forest pests and known to cause tree mortality in California, particularly during extended periods of drought [44]. If such an effect occurred at Blacks Mountain, it was limited to the first two years following prescribed burns.

3.4. Tree Mortality and Stand Density

Levels of bark beetle-caused tree mortality observed during this study occurred during a period of elevated bark beetle activity in the region, but as previously mentioned there is a strong positive relationship between stand density and susceptibility to bark beetle infestation in *P. ponderosa* [21]. In our study, stand densities averaged 25.2, 24.2, 9.8, and 9.1 m^2/ha of basal area for HiD + B, HiD, LoD + B, and LoD, respectively, immediately following treatments [43]. Fiddler *et al.* [61] showed that thinning significantly reduced the amount of *P. ponderosa* mortality attributed to *D. ponderosae* in a study conducted near Blacks Mountain. No tree mortality occurred in stands of <9 m^2/ha of basal area, which agrees with the optimal stocking level of 11 m^2/ha described by Oliver [62,63]. Furthermore, Oliver [63] reported maximum stand density index (SDI) for even-aged *P. ponderosa* stands in northern California was regulated by bark beetle infestations. A SDI value of 230 defined a threshold for a zone of imminent bark beetle-caused tree mortality within which endemic populations kill a few trees but net growth is positive. Maximum SDI was defined at 365. While the SDI relationships described by Oliver [63] are a tenuous fit for HiD, which does not represent an even-aged structure, it is quite appropriate for LoD. LoD plots averaged SDI values of 118 and 124 for the unburned and burned-split plots, respectively [36]. These values are much less than the threshold SDI value of 230 [63]. Higher levels of bark beetle-caused tree mortality should be expected following similar treatments that retain higher residual stand densities, independent of the confounding effects of prescribed fire.

4. Conclusions

A primary objective of the Blacks Mountain Ecological Research Project was to create stand conditions that serve as a model of "resiliency" to allogenic (e.g., wildfire) and autogenic (e.g., bark beetle infestations) disturbances in interior *P. ponderosa* [12]. While numerous definitions of resiliency exist, here we define resiliency as the capacity of a system to return to its more-or-less pre-disturbance state, focusing on variability in levels of tree mortality. Some have defined ecological resiliency as the amount of disturbance that an ecosystem can withstand while maintaining certain ecological goods and services and without changing functional states [64]. While changes in functional state have been observed as a result of severe bark beetle outbreaks (e.g., conversion from forest to shrub land), examples are very rare and of limited scale.

During the 10-year period, 8.7% of all trees died, most of which was attributed to bark beetles (64.7%), primarily *S. ventralis*, *D. ponderosae*, and *D. brevicomis* (Table 2). Trees of all ages and size classes were killed, but mortality was generally concentrated: (1) on HiD structures (64.3%); (2) on burned-split plots (60.5%); (3) within the two smallest-diameter classes (87%); and (4) during the second sample period (*i.e.*, three to five years after prescribed burns) (Tables 2 and 3). These observations were consistent for all bark beetle species with few notable exceptions: (1) the response of *Ips* spp. was limited to the first sample period (one to two years following prescribed burns); and (2) substantial numbers of *P. ponderosa* were killed by *D. brevicomis* in the largest-diameter class. Our observation concerning bark beetle-caused tree mortality being concentrated three to five years after prescribed burns differs from many other studies in *P. ponderosa* that reported mortality was concentrated during the first year or two (e.g., [25,35]). However, many of those studies were of limited duration compared to ours. To that end, it is important to note that the treatment effects observed in our study varied by sample period [36,37], further emphasizing the importance of long-term studies in forest management.

No significant differences were observed between HiD and LoD for any of the variables analyzed within any diameter class (Figures 1–6); suggesting that over the 10-year period these structures were of similar resilience to bark beetle infestations and other disturbances. Overall, higher levels of tree mortality occurred on LoD + B (18.8%) compared to HiD (5.7%) and LoD (4.6%) (Figure 1), and higher levels of bark beetle-caused tree mortality occurred on LoD + B (8.7%) compared to LoD (4.2%) (Figure 2). This is presumably due to the increased proportion of smaller-diameter trees on LoD [43], which tend to be of increased susceptibility to injury and mortality following prescribed fire [47,48,50]. To that end, no significant differences were observed between HiD and HiD + B, except for trees in the 54.7-cm diameter class for mortality attributed to all causes (Figure 1), bark beetles (Figure 2), and *D. brevicomis* (Figure 3).

Concerns about maintaining large-diameter trees, particularly *Pinus* on HiD + B, have been expressed by members of the interdisciplinary research team at Blacks Mountain and others [37,51]. We found the majority (77.9%) of mortality in the largest-diameter class occurred during the first five years following prescribed burns. During this time, significantly higher levels of tree mortality were observed on HiD + B (8.4%) compared to HiD (1.2%) [36], however, during the second five years, no significant difference was observed between these treatments (1.5% and 1.3%, respectively). During the latter period (6–10 years), most of this tree mortality was attributed to bark beetles (95.3%),

while during the first five years only 66.3% was attributed to bark beetles. There are insecticide- and semiochemical-based tools available that could be selectively used to protect individual trees from colonization by bark beetles [55,56]. Insecticides are typically applied with ground-based sprayers at high pressures to the tree bole, and depending on the active ingredient, among other factors, may provide adequate levels of tree protection for up to two years [56]. However, bole sprays require transporting large equipment typically into remote areas, which can be problematic. A semiochemical-based tool for protecting *P. ponderosa* from *D. brevicomis* is not yet available, but the recent development of an effective semiochemical blend is promising and commercialization is ongoing [55]. Semiochemical-based tools are available for protecting *P. ponderosa* from *D. ponderosae* [65], but efficacy is somewhat limited. No semiochemical-based tool is available for protecting *A. concolor* from *S. ventralis*. Semiochemical-based tools are easily carried and applied by hand, but their effectiveness and longevity is less than that of insecticides.

Perrakis *et al.* [66] suggested, based on research executed in *P. ponderosa* forests in Oregon, that fuel-reduction treatments should be implemented gradually to improve the vigor of individual trees prior to all but the least intense prescribed burns. Furthermore, methods such as raking of litter and duff a short distance from the base of large-diameter *P. ponderosa* have been shown effective for reducing fire severity and subsequent levels of tree mortality when applied prior to burning [67]. Such techniques might be considered in the future. Continued monitoring of the effects of structural diversity and the application of prescribed fire on causes and levels of tree mortality at Blacks Mountain will facilitate better management of interior *P. ponderosa* forests in the future.

Acknowledgments

Conflicts of Interest

The authors declare no conflict of interest.

References

1. Stephens, S.L.; Ruth, L.W. Federal forest-fire policy in the United States. *Ecol. Appl.* **2005**, *15*, 532–542.

2. Arno, S.F. Forest fire history of the northern Rockies. *J. For.* **1980**, *78*, 460–465.

3. Swetnam, T.W. Fire History and Climate in the Southwestern United States. In *Effects of Fire Management on Southwestern Natural Resources. Proceedings of the Symposium*; Krammes, J.S., Ed.; US Department of Agriculture, Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 1990; pp. 6–17.

4. Agee, J.K. Fire history along an elevational gradient in the Siskiyou Mountains, Oregon. *Northwest Sci.* **1993**, *65*, 188–199.

5. Covington, W.W.; Moore, M. Southwestern ponderosa pine forest structure: Changes since Euro-American settlement. *J. For.* **1994**, *92*, 39–47.

6. Skinner, C.N.; Chang, C. Fire Regimes, Past and Present. In *Sierra Nevada Ecosystem Project: Final Report to Congress. Volume II: Assessments and Scientific Basis for Management Options*; Water Resources Center Report No. 37; University of California: Davis, CA, USA, 1996; pp. 1041–1069.

7. Taylor, A.H. Fire regimes and forest changes along a montane forest gradient, Lassen Volcanic National Park, southern Cascade Mountains, USA. *J. Biogeogr.* **2000**, *27*, 87–104.

8. Taylor, A.H.; Skinner, C.N. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *For. Ecol. Manag.* **1998**, *111*, 285–301.

9. Swetnam, T.W.; Baisan, C.H. Tree-Ring Reconstructions of Fire and Climate History in the Sierra Nevada and Southwestern United States. In *Fire and Climatic Change in Temperate Ecosystems of the Western Americas*; Veblen, T.T., Baker, W., Montenegro, G., Swetnam, T.W., Eds.; Springer-Verlag: New York, NY, USA, 2002; pp. 154–191.

10. Stephens, S.L.; Skinner, C.N.; Gill, S.J. Dendrochronology-based fire history of Jeffrey pine-mixed conifer forests in the Sierra San Pedro Martir, Mexico. *Can. J. For. Res.* **2003**, *33*, 1090–1101.

11. Burns, R.M.; Honkala, B.H. *Silvics of North. America. Vol. I. Conifers*; US Department of Agriculture, Forest Service: Washington, DC, USA, 1990; p. 675.

12. Oliver, W.W. *Ecological Research at the Blacks Mountain Experimental Forest in Northeastern California*; US Department of Agriculture, Forest Service, Pacific Southwest Research Station: Albany, CA, USA, 2000; p. 66.

13. Stephens, S.L.; McIver, J.D.; Boerner, R.E.J.; Fettig, C.J.; Fontaine, J.B.; Hartsough, B.R.; Kennedy, P.L.; Schwilk, D.W. The effects of forest fuel-reduction treatments in the United States. *Bioscience* **2012**, *62*, 549–560.

14. McIver, J.D.; Stephens, S.L.; Agee, J.K.; Barbour, J.; Boerner, R.E.J.; Edminster, C.B.; Erickson, K.L.; Farris, K.L.; Fettig, C.J.; Fiedler, C.E.; *et al*. Ecological effects of alternative fuel reduction treatments: Highlights of the national Fire and Fire Surrogate study (FFS). *Int. J. Wildland Fire* **2013**, *22*, 63–82.

15. Stephens, S.L.; Moghaddas, J.J.; Edminster, C.; Fiedler, C.E.; Haase, S.; Harrington, M.; Keeley, J.E.; Knapp, E.E.; McIver, J.D.; Metlen, K.; *et al*. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. *Ecol. Appl.* **2009**, *19*, 305–320.

16. Ritchie, M.W.; Skinner, C.N.; Hamilton, T.A. Probability of tree survival after wildfire in an interior pine forest of northern California: Effects of thinning and prescribed fire. *For. Ecol. Manag.* **2007**, *247*, 200–208.

17. Hood, S.M.; Smith, S.L.; Cluck, D.R. Delayed Conifer Tree Mortality Following Fire in California. In *Restoring Fire-Adapted Ecosystems: Proceedings of the 2005 National Silviculture Workshop*; Powers, R.F., Ed.; U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station: Albany, CA, USA, 2007; pp. 261–283.

18. Parker, T.J.; Clancy, K.M.; Mathiasen, R.L. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. *Agric. For. Entomol.* **2006**, *8*, 167–189.

19. Rasmussen, L.A.; Amman, G.D.; Vandygriff, J.C.; Oakes, R.D.; Munson, A.S.; Gibson, K.E. *Bark Beetle and Wood Borer Infestations in the Greater Yellowstone Area During Four Postfire Years*; US Department of Agriculture, Forest Service, Intermountain Research Station: Ogden, UT, USA, 2000; p. 66.

20. Aronson, G.; Kulakowski, D. Bark beetle outbreaks, wildfires and defensible space: How much area do we need to treat to protect homes and communities? *Int. J. Wildland Fire* **2012**, *22*, 256–265.

21. Fettig, C.J.; Klepzig, K.D.; Billings, R.F.; Munson, A.S.; Nebeker, T.E.; Negrón, J.F.; Nowak, J.T. The effectiveness of vegetation management practices for prevention and control of bark beetle outbreaks in coniferous forests of the western and southern United States. *For. Ecol. Manag.* **2007**, *238*, 24–53.

22. Schwilk, D.W.; Keeley, J.E.; Knapp, E.E.; McIver, J.; Bailey, J.D.; Fettig, C.J.; Fielder, C.E.; Harrod, R.J.; Moghaddas, J.J.; Outcalt, K.W.; *et al*. The National Fire and Fire Surrogate Study: Effects of alternative fuel reduction methods on forest structure. *Ecol. Appl.* **2009**, *19*, 285–304.

23. Seybold, S.J.; Huber, D.P.W.; Lee, J.C.; Graves, A.D.; Bohlmann, J. Pine monoterpenes and pine bark beetles: A marriage of convenience for defense and chemical communication. *Phytochem. Rev.* **2006**, *5*, 143–178.

24. Fettig, C.J.; McMillin, J.D.; Anhold, J.A.; Hamud, S.M.; Borys, R.R.; Dabney, C.P.; Seybold, S.J. The effects of mechanical fuel reduction treatments on the activity of bark beetles (Coleoptera: Scolytidae) infesting ponderosa pine. *For. Ecol. Manag.* **2006**, *230*, 55–68.

25. Davis, R.S.; Hood, S.; Bentz, B.J. Fire-injured ponderosa pine provide a pulsed resource for bark beetles. *Can. J. For. Res.* **2012**, *42*, 2022–2036.

26. DeGomez, T.; Fettig, C.J.; McMillin, J.D.; Anhold, J.A.; Hayes, C.J. *Managing Slash to Minimize Colonization of Residual Leave Trees by* Ips *and Other Bark Beetle Species Following Thinning in Southwestern Ponderosa Pine*; University of Arizona: Tucson, AZ, USA, 2008; p. 12.

27. Bartos, D.L.; Amman, G.D. *Microclimate: An Alternative to Tree Vigor as a Basis for Mountain Pine Beetle Infestations*; U.S. Department of Agriculture, Forest Service, Intermountain Research Station: Ogden, UT, USA, 1989; p. 10.

28. Thistle, H.W.; Peterson, H.; Allwine, G.; Lamb, B.K.; Strand, T.; Holsten, E.H.; Shea, P.J. Surrogate pheromone plumes in three forest trunk spaces: Composite statistics and case studies. *For. Sci.* **2004**, *50*, 610–625.

29. Hayes, C.J.; Fettig, C.J.; Merrill, L.D. Evaluation of multiple funnel traps and stand characteristics for estimating western pine beetle-caused tree mortality. *J. Econ. Entomol.* **2009**, *102*, 2170–2182.

30. Bradley, T.; Tueller, P. Effects of fire on bark beetle presence on Jeffrey pine in the Lake Tahoe Basin. *For. Ecol. Manag.* **2001**, *142*, 205–214.

31. Ganz, D.J.; Dahlsten, D.L.; Shea, P.J. The Post-Burning Responses of Bark Beetles to Prescribed Burning Treatments. In *Fire, Fuel Treatments, and Ecological Restoration: Conference Proceedings*; Omi, P.N., Joyce, L.A., Eds.; US Department of Agriculture, Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 2003; pp. 143–158.

32. McHugh, C.W.; Kolb, T.E. Ponderosa pine mortality following fire in northern Arizona. *Int. J. Wildland Fire* **2003**, *12*, 7–22.

33. McHugh, C.W.; Kolb, T.E.; Wilson, J.L. Bark beetle attacks on ponderosa pine following fire in northern Arizona. *Environ. Entomol.* **2003**, *32*, 510–522.

34. Schwilk, D.W.; Knapp, E.E.; Ferrenberg, S.M.; Keeley, J.E.; Caprio, A.C. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. *For. Ecol. Manag.* **2006**, *232*, 36–45.

35. Breece, C.R.; Kolb, T.E.; Dickson, B.G.; McMillin, J.D.; Clancy, K.M. Prescribed fire effects on bark beetle activity and tree mortality in southwestern ponderosa pine forests. *For. Ecol. Manag.* **2008**, *255*, 119–128.

36. Fettig, C.J.; Borys, R.R.; McKelvey, S.R.; Dabney, C.P. Blacks Mountain Experimental Forest: Bark beetle responses to differences in forest structure and the application of prescribed fire in interior ponderosa pine. *Can. J. For. Res.* **2008**, *38*, 924–935.

37. Fettig, C.J.; McKelvey, S.R. Bark beetle responses to stand structure and prescribed fire at Blacks Mountain Experimental Forest, California, USA: 5-year data. *Fire Ecol.* **2010**, *6*, 26–42.

38. Fettig, C.J.; Borys, R.R.; Dabney, C.P. Effects of fire and fire surrogate treatments on bark beetle-caused tree mortality in the Southern Cascades, California. *For. Sci.* **2010**, *56*, 60–73.

39. Fettig, C.J.; McKelvey, S.R.; Cluck, D.R.; Smith, S.L.; Otrosina, W.J. Effects of prescribed fire and season of burn on direct and indirect levels of tree mortality in ponderosa and Jeffrey pine forests in California, USA. *For. Ecol. Manag.* **2010**, *260*, 207–218.

40. Maloney, P.E.; Smith, T.F.; Jensen, C.E.; Innes, J.; Rizzo, D.M.; North, M.P. 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. *Can. J. For. Res.* **2008**, *38*, 3011–3020.

41. Stark, D.T.; Wood, D.L.; Storer, A.J.; Stephens, S.L. Prescribed fire and mechanical thinning effects on bark beetle caused tree mortality in a mid-elevation Sierran mixed-conifer forest. *For. Ecol. Manag.* **2013**, *306*, 61–67.

42. Salman, K.A.; Bongberg, J.W. Logging high-risk trees to control insects in the pines stands of northeastern California. *J. For.* **1942**, *40*, 533–539.

43. Zhang, J.; Ritchie, M.W.; Oliver, W.W. Vegetation responses to stand structure and prescribed fire in an interior ponderosa pine ecosystem. *Can. J. For. Res.* **2008**, *38*, 909–918.

44. Furniss, R.L.; Carolin, V.M. *Western Forest Insects*; US Department of Agriculture, Forest Service: Washington, DC, USA; p. 654.

45. Fischer, W.C. Prescribed fire and bark beetle attack in ponderosa pine forests. *Fire Manag. Notes* **1980**, *41*, 10–12.

46. Kegley, S.J.; Livingston, R.L.; Gibson, K.E. *Pine Engraver,* Ips pini *(Say), in the United States*; US Department of Agriculture, Forest Service: Portland, OR, USA, 1997; p. 8.

47. Agee, J.K.; Skinner, C.N. Basic principles of forest fuel reduction treatments. *For. Ecol. Manag.* **2005**, *211*, 83–96.

48. Regelbrugge, J.C.; Conard, S.G. Modeling tree mortality following wildfire in *Pinus ponderosa* forests in the central Sierra Nevada of California. *Int. J. Wildland Fire* **1993**, *3*, 139–148.

49. Fulé, P.Z.; Covington, W.W.; Smith, H.B.; Springer, J.D.; Heinlein, T.A.; Huisinga, K.D.; Moore, M.M. Comparing ecological restoration alternatives: Grand Canyon, Arizona. *For. Ecol. Manag.* **2002**, *170*, 19–41.

50. Kolb, T.E.; Agee, J.K.; Fulé, P.Z.; McDowell, N.G.; Pearson, K.; Sala, A.; Waring, R.H. Perpetuating old growth ponderosa pine. *For. Ecol. Manag.* **2007**, *249*, 141–157.

51. Ritchie, M.W.; Wing, B.M.; Hamilton, T.A. Stability of the large tree component in treated and untreated late-seral interior ponderosa pine stands. *Can. J. For. Res.* **2008**, *38*, 919–923.

52. DeMars, C.J.; Roettgering, B.H. *Western Pine Beetle*; US Department of Agriculture, Forest Service: Portland, OR, USA, 1982; p. 8.

53. Walker, R.; Rosenberg, M.; Warbington, R.; Schwind, B.; Beardsley, D.; Ramirez, C.; Fischer, L.; Frerichs, B. Inventory of Tree Mortality in Southern California Mountains (2001–2004) due to Bark Beetle Impacts. Available online: http://www.frap.fire.ca.gov/projects/mast/reports.html (accessed on 11 November 2013).

54. Sánchez-Martínez, G.; Wagner, M.R. Bark beetle community structure under four ponderosa pine forest stand conditions in northern Arizona. *For. Ecol. Manag.* **2002**, *170*, 145–160.

55. Fettig, C.J.; McKelvey, S.R.; Dabney, C.P.; Huber, D.P.W.; Lait, C.G.; Fowler, D.L.; Borden, J.H. Efficacy of "Verbenone Plus" for protecting ponderosa pine trees and stands from *Dendroctonus brevicomis* (Coleoptera: Curculionidae) attack in British Columbia and California. *J. Econ. Entomol.* **2012**, *105*, 1668–1680.

56. Fettig, C.J.; Grosman, D.M.; Munson, A.S. Advances in Insecticide Tools and Tactics for Protecting Conifers from Bark Beetle Attack in the Western United States. In *Insecticides—Development of Safer and More Effective Technologies*; Trdan, S., Ed.; InTech: Rijeka, Croatia, 2013; pp. 472–492.

57. Gibson, K.; Kegley, S.; Bentz, B. *Mountain Pine Beetle*; US Department of Agriculture, Forest Service: Portland, OR, USA, 2009; p. 12.

58. Jenkins, M.J.; Runyon, J.B.; Fettig, C.J.; Page, W.G.; Bentz, B.J. Interactions among the mountain pine beetle, fires, and fuels. *For. Sci.* **2014**, doi:10.5849/forsci.13-017.

59. Smith, S.L.; Borys, R.R.; Shea, P.J. *Jeffrey Pine Beetle*; US Department of Agriculture, Forest Service: Portland, OR, USA, 2009; p. 8.

60. Kolb, T.E.; Guerard, N.; Hofstetter, R.W.; Wagner, M.R. Attack preference of *Ips pini* on *Pinus ponderosa* in northern Arizona: Tree size and bole position. *Agric. For. Entomol.* **2006**, *8*, 295–303.

61. Fiddler, G.O.; Hart, D.R.; Fiddler, T.A.; McDonald, P.M. *Thinning Decreases Mortality and Increases Growth of Ponderosa Pine in Northeastern California*; US Department of Agriculture, Forest Service, Pacific Southwest Research Station: Albany, CA, USA, 1989; p. 12.

62. Oliver, W.W. *Fifteen-Year Growth Patterns after Thinning a Ponderosa Pine-Jeffrey Pine Plantation in Northeastern California*; US Department of Agriculture, Forest Service, Pacific Southwest Research Station: Albany, CA, USA, 1979; p. 10.

63. Oliver, W.W. Is Self-Thinning in Ponderosa Pine Ruled by *Dendroctonus* Bark Beetles? In *Forest Health Through Silviculture: Proceedings of the 1995 National Silviculture Workshop*; Eskew, L.G., Ed.; US Department of Agriculture, Forest Service, Rocky Mountain Research Station: Fort Collins, CO, USA, 1995, pp. 213–218.

64. Holling, C.S. Resilience and stability of ecosystems. *Annu. Rev. Ecol. Syst.* **1973**, *4*, 1–23.

65. Progar, R.A.; Gillette, N.; Fettig, C.J.; Hrinkevich, K. Applied chemical ecology of the mountain pine beetle. *For. Sci.* **2014**, doi:10.5849/forsci.13-010.

66. Perrakis, D.B.; Agee, J.K.; Eglitis, A. Effects of prescribed burning on mortality and resin defenses in old growth ponderosa pine (Crater Lake, Oregon): Four years of post-fire monitoring. *Nat. Areas J.* **2011**, *31*, 14–25.

67. Fowler, J.F.; Sieg, C.H.; Wadleigh, L.L. Effectiveness of litter removal to prevent cambial kill-caused mortality in northern Arizona ponderosa pine. *For. Sci.* **2010**, *56*, 166–171.