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Species composition influences management outcomes following mountain pine beetle in lodgepole pine-dominated forests

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ABSTRACT

Mountain pine beetle outbreaks have killed lodgepole pine on more than one million hectares of Colorado and southern Wyoming forest during the last decade and have prompted harvest operations throughout the region. In northern Colorado, lodgepole pine commonly occurs in mixed stands with subalpine fir, Engelmann spruce, and aspen. Variation in tree species composition will influence structure, fuel profiles and fire hazard as forests recover from bark beetle outbreaks, and this diversity has implications for design and implementation of fuel reduction treatments. We used stand inventory data to predict forest structure and fuel loads starting after needle fall through one century after bark beetle infestation for three lodgepole pine-dominated forest types (pine, pine with aspen, pine with fir and spruce), and compared simulated effects of no-action and fuel reduction treatments (thinning, broadcast burning). In pine stands mixed with significant density of fir and spruce, the high canopy bulk density and low canopy base height increases passive and active crown fire hazards compared to stands with few shade tolerant trees. In contrast, stands of pine mixed with aspen had lower canopy bulk density and active crown fire hazard. All three forest types had high snag and coarse woody debris loads. Thinning and broadcast burning reduced canopy fuels in all forest types for several decades, but had the largest effect in forests with abundant fir. Burning temporarily reduced fine woody fuel, and caused a longer-term reduction in coarse wood and duff. Overall, these simulations indicate that management aimed at reducing canopy fuels in beetle-killed lodgepole pine forests should prioritize stands with high densities of overstory and understory fir and spruce. Forest growth following treatment requires frequent stand manipulation (as often as every 20 years) to maintain reduced fuel loads, and since such treatments are expensive and likely not analogous to natural disturbances these activities are most appropriate where resource and infrastructure protection and human safety concerns are high.

1. Introduction

Mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins) has killed trees on over one million hectares of lodgepole pine-dominated (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm. ex S. Wats.) forests in Colorado and southern Wyoming since the late 1990s (U.S.D.A. Forest Service, 2010). The severity of tree mortality elevated concerns about crown fire hazard (U.S.D.A. Forest Service, 2011; Hicke et al., 2012; Page et al., 2013). Low foliar moisture content increases flammability of fine fuels during the 'red needle phase' (Jolly et al., 2012; Page et al., 2012), though this contributor to crown fire hazard is thought to decline with needle fall, typically 3–5 years after beetle infestation (Simard et al., 2011; Page et al., 2013). The fire hazard implications of the 'red stage' have been widely discussed, but we focus on forest fuels after needles have fallen (the 'grey-stage' of post-beetle development) since most forests affected by the recent outbreak are in this condition. The abundance of snags and subsequent accumulation of coarse woody debris generated by overstory mortality represent a longer-term fire hazard (Gray, 2013; Page et al., 2013). Loss of the relatively uniform lodgepole pine overstory (even age, single strata) has also been shown to increase dominance of shade-tolerant conifers in some stands and create more vertically continuous fuel profiles, increasing crown fire hazard starting 1–2 decades after beetle infestation (e.g., Lynch et al., 2006; Page and Jenkins, 2007a,b; Collins et al., 2012; Hicke et al., 2012; Pelz and Smith, 2012; Gray, 2013; Page et al., 2013). These longer-term contributors to fire hazard have prompted planning of fuels reduction treatments on nearly 100,000 hectares throughout Colorado and

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southern Wyoming (U.S.D.A. Forest Service, 2011; Colorado State Forest Service, unpublished data).

Post-outbreak changes in forest structure and fuel profiles depend on the size and species composition of the remaining live trees in addition to MPB-caused mortality severity and killed tree biomass. Non-host tree species are unaffected and small diameter lodgepole are less susceptible to MPB attack (Cole and Amman, 1969; Klutsch et al., 2009; Diskin et al., 2011). Even the nearly pure lodgepole stands selected for post-outbreak treatments are well stocked with live pine and non-host advance regeneration (Collins et al., 2012). Lodgepole pine-dominated forests of the Southern Rockies are commonly mixed with Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) or quaking aspen (*Populus tremuloides* Michx.) (Peet, 1981; Diskin et al., 2011; Kayes and Tinker, 2012). Where present, these co-occurring species will play an important role in future forest conditions.

Fire hazard will likely vary with species composition in beetle-killed lodgepole pine forests (Klutsch et al., 2011; Hicke et al., 2012; Pelz and Smith, 2012). Lodgepole forests mixed with subalpine fir or Engelmann spruce typically have lower canopy base height (CBH) and higher canopy bulk density (CBD) than pure lodgepole stands (Muir, 1993; Scott and Reinhardt, 2001; Gray, 2013). Vertical continuity of branches and foliage from the forest floor to the overstory canopy create ladder fuels that permit surface fires to burn into the canopy and become active crown fires (Alexander et al., 2004). In these mixed pine, fir and spruce stands, the combination of ladder, canopy and coarse fuels, from the release of understory conifers and windthrow of beetle-killed overstory, may lead to torching and high intensity surface fires with long residence time and increased potential for spotting (Hvenegaard, 2012; Albini et al., 2012; Page et al., 2013). In contrast, crown fire probability is expected to be lower where pine is mixed with abundant aspen due to the high CBH and greater foliage moisture of this forest type compared to pure lodgepole (Turner and Romme, 1994; Cumming, 2000). Simulated fire in lodgepole forests recently attacked by MPB showed crown fire was unlikely in stands with aspen, but much more likely when fir and spruce were present (Klutsch et al., 2011).

Clearcut harvests are the most widely applied prescription in beetle-affected lodgepole pine forests, but we need to evaluate potential alternatives for future management. We need to know how varying amounts of spruce, fir, and aspen affect fuels reduction treatment effectiveness, and how treatments complement or conflict with other management objectives. For example, the increase in coarse wood and fir and spruce abundance will enhance Canada lynx (*Lynx canadensis*) habitat following MPB (Chan-McLeod, 2006), and protection of forest structure beneficial to lynx will conflict with fuel reduction priorities. Here we simulated forest structure and fuel dynamics in three lodgepole-dominated forest types common to the Southern Rockies and examined changes following two potential fuel reduction treatments (thinning, broadcast burning) during the century after bark beetle infestation. In the absence of replicated thinning and prescribed burning trials, these simulations provide a first approximation to help assess the consequences of these treatments on forest structures and fuel profiles in multiple forest types.

2. Methods

2.1. Study area and data collection

We used stand inventory and fuels data collected in uncut stands within four bark beetle management areas in northern Colorado (105°51′ to 106°38′W and 39°53′ to 40°36′N; Collins et al., 2012) to initiate simulations of post-bark beetle stand development and to inform treatment comparisons. Significant beetle activity began in this area between 1998 and 2002 (U.S.D.A. Forest Service, 2010), peaked around 2008, and killed 60–92% of total basal area (Collins et al., 2011; Chapman et al., 2012; Meddens and Hicke, 2014). Forest and fuels were inventoried in 2008 after the majority of pine needles had fallen. Diameter, species, and condition (live or dead) were recorded along 100 × 5 m belt transects for trees ⩾2.5 cm diameter at breast height (1.37 m high, dbh). We tallied regeneration (trees <2.5 cm dbh and ⩾0.15 m tall) by species in two, 3.6-m radius plots per transect. Surface fuel loads were measured along two, 15-m transects (Brown et al., 1982) per belt transect. Fuels ⩾7.62 cm in diameter (coarse woody debris, CWD) were classified as rotten or sound, and litter and duff depths were measured at three points along each fuel transect (see Collins et al., 2012, for more details).

We partitioned the inventoried stands into: (1) lodgepole pine (LP) (⩾90% of pre-outbreak basal area in lodgepole and <1% basal are in aspen or spruce/fir, with fir-dominated regeneration); (2) lodgepole pine with aspen (LP-AS) (5–30% of pre-outbreak basal area in aspen, <1% basal area in spruce and fir, with aspen-dominated regeneration) and, (3) lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) (10–30% of pre-outbreak basal area in spruce and fir, <5% of basal area in aspen, with fir-dominated regeneration) (Table 1).

2.2. Simulations of forest and fuel dynamics

We used the Central Rockies variant of the Forest Vegetation Simulator (FVS) (Dixon, 2002, 2008) and its Fire and Fuels Extension (FFE) (Rebain, 2012) to project forest and fuel changes for 100 years after mountain pine beetle outbreak. FVS is a density-dependent growth and yield model that projects forest structure and fuels based on initial forest and fuel data and site index. Self-thinning began when stands reached 60% relative density. Regional maximum heights, basal areas, and densities were used to adjust the model's default levels of aspen growth (Shepperd, 1990; Shepperd, unpublished data; Smith et al., 2011). We used Regeneration Imputation Extractor (REPUTE) to add seedling cohorts based on inventory data from beetle-affected forests in Colorado and southern Wyoming (Vandendriesche, 2010).

FFE-FVS generates surface fuel loads and canopy characteristics based on initial fuels measurements and simulated stand development. It accounts for litter and woody fuel inputs, and biomass decomposition through time (Reinhardt and Crookston, 2003; Rebain, 2012). Canopy bulk density (CBD; kg dry foliage + branch [<6 mm diameter] biomass m^{-3}) is estimated by averaging within 0.3 m-thick horizontal layers (Scott and Reinhardt, 2001). Needles and branches from live trees are included in this calculation. Stand CBD is defined as the maximum value of a 4.5 m-running mean from the 0.3-m layers. Stand canopy base height (CBH) is the height at which stand CBD first exceeds 0.01 kg m^{-3}.

2.3. Treatment design and effectiveness criteria

Simulated fuel reduction treatments were scheduled to coincide with formation of dense ladder fuel strata, commencing 10 years after the outbreak (Gray, 2013; Page et al., 2013). At this time in all forest types, about half of the dead pine snags had fallen and half were still standing. A thin-from-below treatment was designed to reduce canopy fuels in the short and long term. This treatment removed 95% of subalpine fir and Engelmann spruce trees <15.2 cm dbh and immediately eliminated canopy biomass from the ladder fuel stratum. It also aimed to delay subsequent development of ladder fuels by removing small fir and spruce trees and to promote lodgepole pine and aspen. Resulting biomass from

Table 1
Species composition, basal area, and tree density in lodgepole pine [LP], lodgepole pine with aspen [LP-AS], and lodgepole pine with subalpine fir and Engelmann spruce [LP-SF] forest types. Data from 2008 inventory of untreated stands in four mountain pine beetle management areas in north-central Colorado. All forest types occurred in each management area.

		LP ($n = 11$)		LP-AS ($n = 8$)		LP-SF ($n = 12$)	
		Mean	(SE)	Mean	(SE)	Mean	(SE)
Pre-MPB proportion of total live basal area	Lodgepole	1.00	(<0.01)	0.93	(<0.01)	0.82	(0.01)
	Aspen	<0.01	(<0.01)	0.07	(0.01)	0.03	(0.01)
	Fir	<0.01	(<0.01)	<0.01	(<0.01)	0.11	(0.02)
	Spruce	<0.01	(<0.01)	0.00	(0.00)	0.05	(0.02)
				m^2 ha^{-1}			
Total live basal area	Pre-MPB	29.64	(3.14)	44.44	(5.21)	33.55	(2.62)
	Post-MPB	5.10	(0.96)	5.59	(0.50)	12.93	(0.86)
Post-MPB live basal area	Lodgepole	4.99	(0.93)	2.80	(0.44)	6.73	(0.83)
	Aspen	0.02	(<0.01)	2.79	(0.15)	0.93	(0.32)
	Fir	0.06	(0.03)	<0.01	(<0.01)	3.31	(0.47)
	Spruce	0.03	(0.03)	0.00	(0.00)	1.96	(0.81)
				stems ha^{-1}			
Post-MPB live density	Lodgepole	1184	(540)	262	(117)	74	(24)
	Aspen	124	(87)	849	(372)	408	(165)
	Fir	797	(335)	62	(23)	1970	(718)
	Spruce	39	(22)	0	(0)	142	(68)

the thinning treatment was left on-site due to the high cost of removing sub-merchantable material. The second treatment, a broadcast burn, was modeled after a planned U.S. Forest Service project in beetle-killed forests of southern Wyoming. It was designed to reduce ladder fuels by killing small fir, to promote future lodgepole pine and aspen dominance, to encourage beetle-killed snag fall, and to consume heavy surface fuels (M. Hood, U.S.D.A. Forest Service, 2012, *personal communication*). Fall season burning was simulated using the following moderate weather conditions: 13 km h windspeed at 6.1 m above ground, 19.5 °C air temperature, and 7%, 8%, and 9% moisture in 1-, 10-, and 100-h time lag fuel classes (See Rebain, 2012 for FVS fire modeling details).

We selected regionally-established forest structure, fuel and habitat criteria to evaluate the treatment alternatives (Table 2). We chose CBH and CBD levels for which FVS-FFE would predict low likelihood of passive or active crown fire initiation with 1-min wind gusts typical of 97 percentile weather conditions and 2-m surface fire flame lengths (Rebain, 2012). We used the following CWD levels stipulated by local fuels reduction projects (U.S.D.A. Forest Service, 2009b, 2012): >22 Mg ha^{-1} to provide sufficient structure for wildlife habitat (Brown et al., 2003) and <67 Mg ha^{-1} to allow firefighter access and reduce smoldering fires and spotting. Biomass of MPB-killed snags was added to CWD loads to account for all coarse fuels that would eventually be contributed by MPB-caused mortality.

2.4. Statistical analysis

We compared differences in forest composition and structure among the three forest types and the effects of treatments using a repeated-measures, generalized mixed linear model, with forest type and treatment as fixed effects and site as a random effect (GLIMMIX, SAS 9.3, SAS Institute Inc., Cary, NC). We used a model with the form y = forest type + year + type $*$ year to examine the difference among untreated stands of the three forest types (LP, LP-AS, and LP-SF). We examined the effect of treatments within each forest type separately with the model y = treatment + year + treatment $*$ year.

Residual plots were used to select the appropriate response distributions for each variable. Basal area, surface litter, and surface duff were normally distributed; woody surface fuels, CBH, and CBD were lognormal. We used logistic regression to compare the proportion of total basal areas contributed by each species. We report significant differences at the $\alpha = 0.05$ level plus a Bonferroni adjustment when comparing forest types or treatments at specific times.

3. Results

3.1. Forest and fuel dynamics in untreated stands

Species composition, basal area, and canopy fuels changed over the century-long simulation, but the three forest types remained distinct. In both the LP and LP-SF types, fir became an increasing proportion of total basal area with time and pine decreased (Fig. 1). Aspen was consistently about 40% of total basal area in the LP-AS type and <10% of basal area in the others. Mountain pine beetle killed a similar percent of basal area in the LP and LP-AS types (83% and 87%, respectively) but a lower percentage in the LP-SF type (62%) (Table 1). Live basal area differed among forest types at the end of the outbreak, but these differences receded

Table 2
Canopy and surface fuel criteria based on fuels reduction objectives for mountain pine beetle management in the U.S. Forest Service, Rocky Mountain Region (R2).

Attribute	Criteria	Rationale
Canopy fuels	Canopy base height (CBH) > 3.5 m	At CBH > 3.5 m, passive crown fire initiation ("torching") likelihood is low at <97 percentile windspeeds, 110% live fuel moisture, and 2 m surface fire flame lengths (Van Wagner, 1977)
	Canopy bulk density (CBD) < 0.086 kg m^{-3}	At CBD < 0.086 kg m^{-3}, active crown fire spread likelihood is low at < 97 percentile windspeeds, constant slope, 0.05 kg m^{-2} critical horizontal mass flow rate (Scott and Reinhardt, 2001; after Van Wagner, 1977)
Coarse woody debris	Coarse woody debris (CWD) 22 to 67 Mg ha^{-1}	CWD is limited to reduce smoldering, improve fire fighter mobility and reduce wildfire resistance to control while leaving woody biomass for wildlife (U.S.D.A. Forest Service, 2009a; Brown et al., 2003; Page et al., 2013). Biomass from MPB-killed snags was added to surface CWD loads to account for all coarse fuels contributed by the MPB outbreak

through time (Fig. 2). Basal area of the LP-SF type was 8–12 m^2 ha^{-1} greater than the other types during the first half of the simulation. Average CBH extended to within 1 m of the forest floor in the LP-SF type for more than 50 years after the outbreak (Fig. 3a). In contrast, in the LP and LP-AS forest types CBH exceeded 6 m for two decades after the outbreak, before CBH lowered with the increase in understory tree density and became similar to the LP-SF type. CBD was low after the outbreak in all forest types and increased steadily with time (Fig. 3b). The LP-AS and LP-SF types consistently had the lowest and highest CBD throughout the simulation.

Simulated treefall removed 50% and 90% of snags within 10 and 20 years of the outbreak, respectively, in all forest types. Consequently, coarse wood loads increased rapidly and peaked after 20 years. The LP-AS type had nearly 2 times more snag mass initially and subsequently 0.5–2 times more CWD than the other types during the first 50 years (Table 3). By the end of the simulation, CWD loads were similar among types. Fine woody debris (FWD), litter, and duff were also similar among forest types. Litter declined during the first decade, and then along with FWD doubled over the 100 year simulation.

3.2. Treatment effects

3.2.1. Species composition and stand basal area

The treatments altered the species composition of the LP and LP-SF, but had little effect in the LP-AS type. Thinning and burning both reduced the proportion of fir in the LP and LP-SF types, but

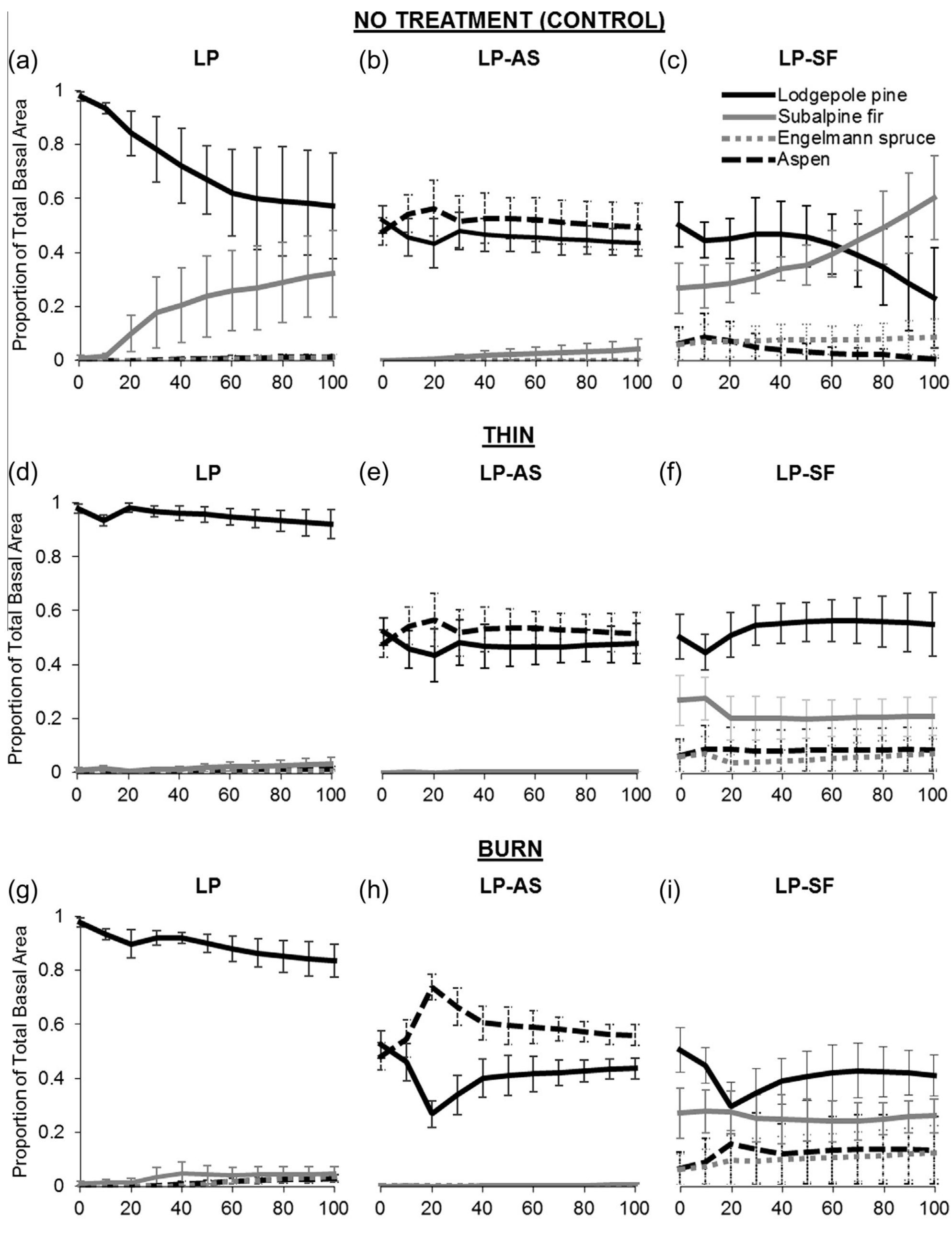

Fig. 1. Species composition in lodgepole pine (LP), lodgepole pine with aspen (LP-AS) and the lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) stands after MPB infestation and simulated Thin, Burn and Control treatments. Data are median proportion of total basal area type (±absolute deviation) by species and forest type. Simulated treatments were implemented 10 years after the outbreak.

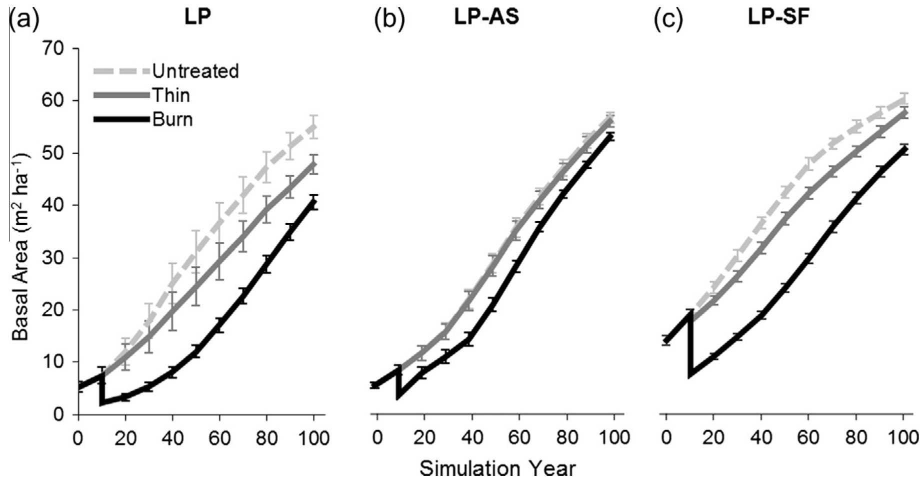

Fig. 2. Live basal area (Mean ± SE) after MPB in lodgepole pine (LP), lodgepole pine with aspen (LP-AS), and lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) forest types after Thin, Burn and Control treatments. Simulated treatments were implemented 10 years after the outbreak.

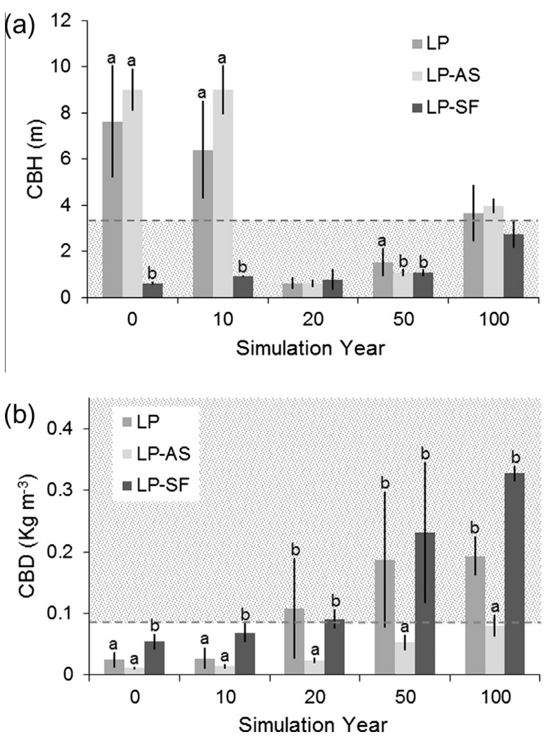

Fig. 3. Canopy base height (CBH) and canopy bulk density (CBD) for lodgepole pine (LP), lodgepole pine with aspen (LP-AS) and lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) forest types 0, 10, 20, 50 and 100 years after MPB (medians ± absolute deviations). Shaded areas denote where CBH and CBD violated hazardous fuel criteria. Letters indicate significant differences among forest types within a time period ($\alpha = 0.05$; Bonferroni adjusted).

had no effect on proportion of fir in the pine – aspen mix (Fig. 1). Both treatments increased the proportion of aspen in LP-SF stands; aspen represented 8% and 13% in Thin and Burn stands, respectively, by year 100, compared to the untreated stands where it comprised <0.1% of basal area (Fig. 1). In the LP-AS mix, burning increased aspen by 7–17% relative to untreated stands.

The Thin and Burn treatments reduced live basal area by varying degrees in the three forest types (Fig. 2). Thinning removed 1532 fir and 78 spruce ha^{-1} from the LP type, 117 fir and 0 spruce ha^{-1} from the LP-AS type, and 3951 fir and 410 spruce ha^{-1} from the LP-SF type. Although the thinning removed <10% of stand basal area in all types, basal area reductions persisted through much of the simulation in the LP-SF and LP types. Thinning had no effect on LP-AS basal area due to the scarcity of understory spruce and fir. The Burn treatment lowered average basal area 55–60% initially in all forest types, and the reductions remained significant until year 100. At that time, burning had eliminated 14, 5, and 11 m^2 ha^{-1} of basal area (26%, 6% and 16%) from the LP, LP-AS and LP-SF types relative to untreated stands.

3.2.2. Canopy and surface fuels

The Thin treatment elevated CBH from years 20 through 30 in the LP and LP-AS forest types relative to untreated stands. Burning raised CBH in all three forest types, and similar to thinning, the effects were relatively short-lived and diminished by year 40 (Fig. 4a–c). Thinning reduced CBD in the LP and LP-SF types; burning reduced it in all forest types (Fig. 4d–f). The effect of thinning on CBD became evident in year 20 in the LP and LP-SF types and continued until the end of the simulation; the reduction from burning persisted throughout the simulation for these forest types. For the LP-AS type, the effect of burning on CBD was only evident during the first half of the simulation (Fig. 4e).

Thinning did not increase surface fuels in any forest type, but rather reduced them in the LP and LP-SF types over the long term (Table 3). The only effect of the treatment on snag or CWD loads was a 26% reduction measured in year 100 in the LP-SF type relative to the Control. Thinning reduced FWD by 32% and 27% in the LP-SF and LP types in latter periods of the simulation, respectively. Thinning also reduced litter mass in the LP-SF type in year 20 and in later years for the LP and LP-SF types, respectively.

Burning reduced duff mass by roughly 50% in all forest types throughout the simulation, but its effects on other surface fuel loads varied through time and with forest type (Table 3). In all forest types, burning reduced standing snag mass by nearly 90% the year of treatment, but had little effect on snags in subsequent years. Burning decreased CWD loads throughout the simulation in the LP and LP-AS types; maximum CWD loads were reduced 27% relative to untreated stands. In the LP-SF type, burning reduced CWD by 45% the year of treatment, and by 42% at the end of the simulation, but not during the interim. Burning reduced FWD loads 43–72% in all the forest types initially, but responses differed among types later in the simulation. For example, in the second half of the simulation, FWD loads were lower in burned

Table 3
Surface fuel and snag loads (Mg ha^{-1}) with and without fuels reduction treatments for lodgepole pine (LP), lodgepole pine with aspen (LP-AS) and lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) forest types. For Untreated stands the $^{+}$ symbol indicates loads were significantly different among forest types within a time period. Subscript letters indicate significant differences among forest types within a time period (α = 0.05; Bonferroni adjusted). Simulated treatments were implemented 10 years after the outbreak.

Simulation year		0	10 (Treatment year)			20			50			100		
Var.	Trt / Type	Untreated	Untreated	Thin	Burn	Untreated	Thin	Burn	Untreated	Thin	Burn	Untreated	Thin	Burn
Snag*	LP	22.4 (5.8)	11.1 (3.0)^{a}	11.1 (3.0)^{a}	0.7 (0.5)^{b}	0.9 (0.4)	0.7 (0.5)	0.7 (0.5)	0.22 (0.19)	0.13 (0.09)	0.04 (0.03)	3.8 (2.3)^{a}	1.7 (0.5)^{b}	0.8 (0.6)^{c}
	LP-AS	39.3 (6.3)$^{+}$	19.9 (2.8)$^{+,a}$	19.9 (2.8)^{a}	2.7 (1.1)^{b}	2.8 (1.1)$^{+}$	2.8 (1.1)	2.7 (1.1)	0.19 (0.11)	0.17 (0.11)	0.05 (0.02)	1.6 (0.2)$^{+,a}$	1.6 (0.2)^{a}	1.3 (0.2)^{b}
	LP-SF	22.7 (7.8)	11.0 (5.3)^{a}	11.0 (5.3)^{a}	1.2 (0.9)^{b}	0.9 (0.5)	0.5 (0.3)	1.1 (0.9)	2.05 (0.79)$^{+}$	0.25 (0.09)	0.13 (0.05)	5.9 (2.6)^{a}	2.4 (0.7)^{b}	1.3 (0.4)^{b}
CWD*	LP	10.5 (3.7)	41.5 (12.4)^{a}	41.5 (12.4)^{a}	19.1 (5.8)^{b}	55.7 (12.7)^{a}	55.7 (12.7)^{a}	37.9 (11.4)^{b}	46.8 (10.4)^{a}	46.8 (11.1)^{a}	32.7 (9.5)^{b}	47.7 (8.5)^{a}	44.2 (10.8)^{a}	24.9 (6.2)^{b}
	LP-AS	24.9 (6.1)$^{+}$	69.3 (10.1)$^{+,a}$	69.3 (10.1)^{a}	35.0 (7.8)^{b}	98.6 (20.6)$^{+,a}$	98.6 (12.6)^{a}	69.5 (14.0)^{b}	86.1 (18.4)$^{+,a}$	86.1 (18.3)^{a}	60.8 (11.4)^{b}	69.3 (11.3)^{a}	69.2 (11.5)^{a}	48.1 (6.5)^{b}
	LP-SF	14.7 (3.6)	35.5 (11.4)^{a}	35.5 (11.4)^{a}	19.5 (6.5)^{b}	52.4 (20.5)	52.4 (20.5)	44.6 (16.1)	44.9 (16.9)	44.7 (18.1)	38.7 (14.2)	52.5 (14.9)^{a}	38.6 (9.3)^{b}	30.6 (8.1)^{b}
FWD*	LP	6.4 (3.3)	6.1 (2.0)^{a}	6.2 (2.0)^{a}	3.5 (0.6)^{b}	6.7 (1.3)	6.8 (1.4)	6.9 (2.2)	6.8 (2.8)^{a}	4.7 (1.2)^{a}	2.8 (1.2)^{b}	13.0 (4.0)^{a}	9.5 (1.4)^{b}	6.6 (0.7)^{c}
	LP-AS	5.9 (2.2)	8.2 (0.3)^{a}	8.2 (0.3)^{a}	2.3 (0.2)^{b}	8.4 (1.3)	8.4 (1.3)	9.2 (1.9)	6.8 (2.1)^{a}	6.7 (2.1)^{a}	8.5 (2.2)^{b}	18.7 (0.9)^{a}	18.6 (0.7)^{a}	21.6 (0.2)^{a}
	LP-SF	8.1 (4.4)	8.9 (4.2)^{a}	9.9 (4.2)^{a}	3.9 (0.4)^{b}	9.8 (3.4)^{a}	10.0 (3.5)^{ab}	11.9 (1.5)^{b}	10.5 (2.7)^{a}	7.7 (0.4)^{b}	7.1 (1.4)^{b}	21.2 (6.5)^{a}	12.8 (0.9)^{b}	11.6 (1.8)^{b}
Litter**	LP	6.4 (2.8)	2.6 (1.5)^{a}	2.8 (1.7)^{a}	1.1 (0.8)^{b}	3.6 (2.4)^{a}	3.0 (2.3)^{a}	0.9 (0.5)^{b}	9.4 (4.7)^{a}	7.2 (3.9)^{b}	3.5 (1.0)^{c}	15.6 (3.7)^{a}	12.5 (1.5)^{b}	11.3 (1.1)^{b}
	LP-AS	7.1 (1.8)	3.2 (0.8)^{a}	3.2 (0.8)^{a}	1.2 (0.2)^{b}	4.0 (1.4)^{a}	3.9 (1.4)^{a}	2.2 (0.7)^{b}	9.9 (1.7)^{a}	9.8 (1.8)^{a}	7.8 (1.4)^{b}	19.5 (1.5)	19.5 (1.5)	19.5 (1.1)
	LP-SF	9.0 (3.3)	5.9 (1.1)^{a}	6.5 (1.2)^{a}	2.5 (0.7)^{b}	7.6 (1.3)^{a}	6.1 (1.0)^{b}	2.9 (0.4)^{c}	13.3 (2.6)^{a}	9.6 (1.2)^{b}	7.0 (0.7)^{c}	18.1 (2.3)^{a}	14.3 (1.7)^{b}	14.3 (1.5)^{b}
Duff**	LP	20.7 (9.3)	20.8 (9.3)a	20.8 (9.3)^{a}	9.1 (4.1)^{b}	20.9 (9.2)^{a}	20.9 (9.2)^{a}	9.2 (4.0)^{b}	21.6 (9.0)^{a}	21.4 (9.0)^{a}	9.5 (4.0)^{b}	24.3 (8.8)^{a}	23.4 (8.6)^{a}	11.2 (4.0)^{b}
	LP-AS	26.2 (11.8)	26.3 (11.7)^{a}	26.3 (11.7)^{a}	11.5 (5.1)^{b}	26.4 (11.6)^{a}	26.4 (11.6)^{a}	11.6 (5.1)^{b}	27.1 (11.2)^{a}	27.1 (11.2)^{a}	12.5 (4.9)^{b}	30.5 (10.7)^{a}	30.5 (10.7)^{a}	16.2 (4.8)^{b}
	LP-SF	27.4 (9.9)	27.6 (9.8)^{a}	27.6 (9.8)^{a}	12.1 (4.3)^{b}	27.8 (9.8)^{a}	27.8 (9.8)^{a}	12.3 (4.3)^{b}	29.0 (9.7)^{a}	28.6 (9.6)^{a}	13.0 (4.2)^{b}	32.4 (9.7)^{a}	30.9 (9.3)^{a}	15.6 (4.0)^{b}

* Medians (median absolute deviation) shown for coarse woody debris (CWD), snag, and fine woody debris (FWD) loads, which were analyzed with a lognormal distribution.
** Means (standard error) shown for litter and duff loads, which were analyzed with a normal distribution.

LP and LP-SF stands compared to untreated stands, but the treatment increased FWD loads in the LP-AS type.

4. Discussion

Approximately 75% of Colorado's lodgepole pine-dominated forests occur in mixed species stands (Woudenberg et al., 2010). In spite of different stand structure and species composition, the three forest types found within our study areas are typically treated with a prescription based on the dominant lodgepole pine overstory. However, we found that responses to the fuel reduction treatment alternatives differ between our forest types. Our simulations of the post-outbreak dynamics in canopy structure, fuel conditions and fire hazard also indicated that stands of all three forest types will fail to meet fuel criteria without management intervention. The failure is most severe in the LP and LP-SF forests where fir understory density increases following outbreak (Table 4). Forests similar to our LP-SF and LP forest types should therefore be priorities for fuel reduction treatment.

In each of our forest types, growth of advanced regeneration and seedling recruits following MPB outbreaks will create fuel profiles that will require active management to meet desired fuels thresholds (Table 4). As has been widely suggested (Klutsch et al., 2011; Collins et al., 2012; Gray, 2013) and documented (Page and Jenkins, 2007a,b; Pelz and Smith, 2012), we project that subalpine fir will become a dominant component in stands such as our LP and LP-SF forest types that contained fir prior to the beetle outbreak. Development of post-outbreak fir creates vertical fuel continuity that promotes torching and a dense overstory canopy that favors active crown fire. All our LP-SF stands had sufficient ladder fuels to violate our CBH criteria during most of the simulation; similarly, growth of abundant ladder fuels lowered the CBH in all LP stands within two decades of the outbreak (Table 4). Forest structure that develops in these LP and LP-SF stands also contains adequate canopy bulk density to create active crown fire hazards in most stands, as was shown in forest of comparable composition in the decades following outbreak in Utah (Page and Jenkins, 2007b). Similar regeneration and growth processes contribute ladder fuels in LP-AS stands and make torching likely by year 20, though self-pruning subsequently lifts the canopy base height above the critical threshold in almost all LP-AS stands. The higher fire hazard in the LP and LP-SF than the LP-AS stands is supported by evidence showing crown fire is more likely in MPB-affected forests with high fir densities than in forest where aspen were present (Page and Jenkins, 2007b; Klutsch et al., 2011).

Snag fall peaked within two decades of the outbreak, as has been observed following mountain pine beetle in lodgepole pine forests elsewhere (Mitchell and Preisler, 1998; Lewis and Thompson, 2011). This overstory loss generated surface CWD loads in excess of our criteria for many stands of all forest types (Table 4). More than half our LP and LP-SF stands exceeded the maximum CWD load initially, and nearly all LP-AS stands were above the threshold during the first half of the simulation. Regardless, the decomposition of surface woody debris steadily increased the portion of forest with desired CWD during the second half of the simulation.

4.1. Treatment effectiveness

The effectiveness of the Thin and Burn treatments at reducing fuel hazards varied among forest types in these recovering forests. Thinning increased the proportion of LP and LP-SF stands that met canopy fuels criteria, but there were few understory

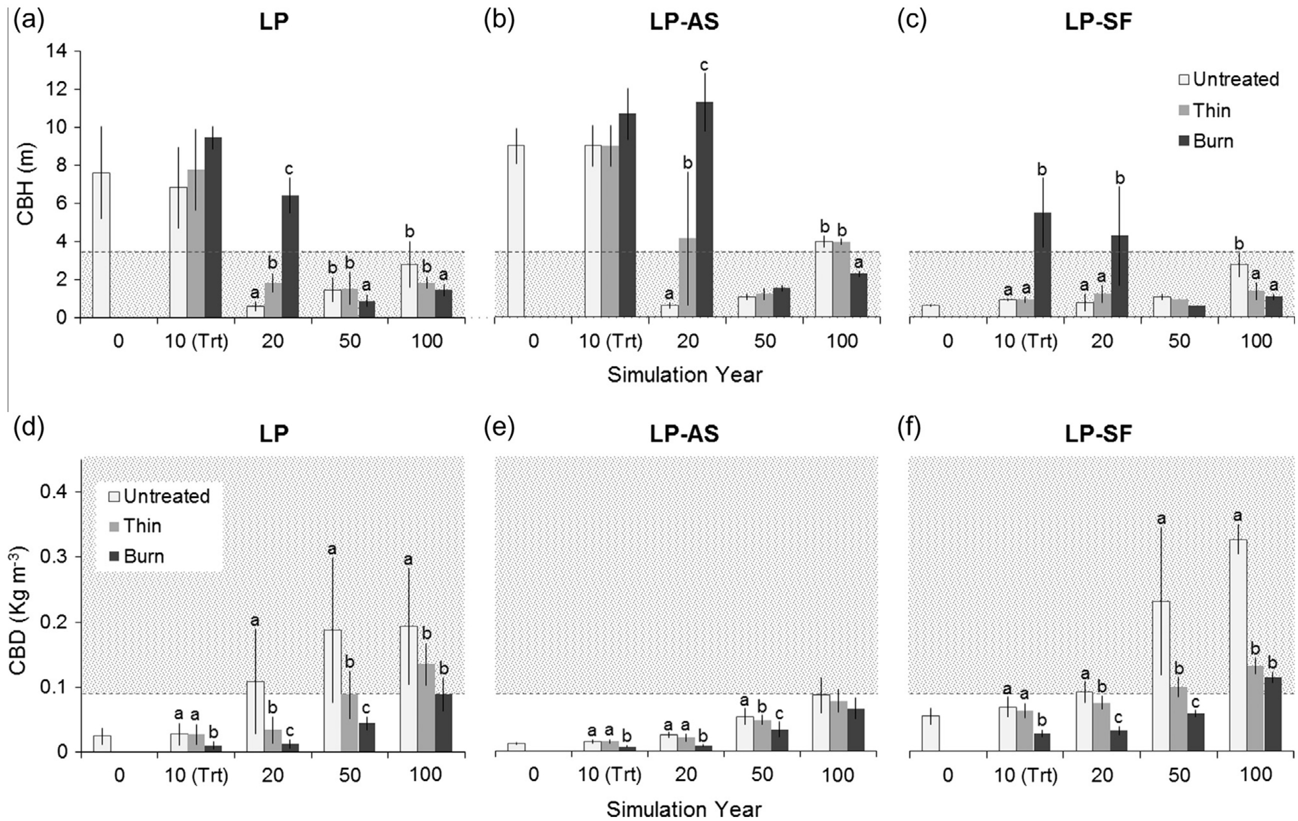

Fig. 4. Canopy base height (CBH) and canopy bulk density (CBD) for lodgepole pine (LP), lodgepole pine with aspen (LP-AS) and lodgepole pine with subalpine fir and Engelmann spruce (LP-SF) forest types after simulated Thin, Burn and Control treatments (medians ± absolute deviations). Shaded areas denote where CBH and CBD violated hazardous fuel criteria. Letters indicate significant differences among forest types within a time period ($\alpha = 0.05$; Bonferroni adjusted). Simulated treatments were implemented 10 years after the outbreak.

spruce and fir trees to remove in our LP-AS stands so thinning had little effect (Table 4). Thinning in LP stands, for example, resulted in a 40% increase in stands that met the canopy fuels criteria in the decade after the treatment. Thinning also increased the proportion of LP-SF stands with CBD values below the maximum hazard threshold. However, the Thin treatment did not remove sufficient large fir and spruce in our LP-SF type to be effective at increasing compliance with the CBH criteria.

One concern with using thinning to reduce canopy fuels is a likely increase in surface fuels (Agee and Skinner, 2005; Reinhardt et al., 2008). However, our simulated Thin treatment did not significantly add to surface fuels owing to the very small size of the trees removed. This demonstrates an advantage of conducting treatments shortly after the outbreak, before understory trees have grown in response to overstory mortality. Further, the thinning lowered stand density and actually reduced long-term surface fuel additions in the LP and LP-SF types and increased the proportion of stands that met the CWD criteria.

In general, the simulated Burn was more effective than the Thin at reducing fuel hazards (Table 4). Burning scorched spruce and fir branches, killed many overstory trees, and increased the CBH immediately in many LP-SF stands. It limited the number of small trees that developed into ladder fuels resulting in a delayed, positive effect on CBH, and increased the number of stands that met the CWD criteria in all types due to its consumption of fuels. The greater effect of burning is not surprising since burning is often more effective at reducing fuels and fire hazard than thinning alone (e.g., Stephens and Moghaddas, 2005; Agee and Skinner, 2005; Reinhardt et al., 2008).

4.2. Implications for management of recovering bark beetle forests

Our results highlight the need to explicitly consider even slight species composition variation when designing fuels reduction treatments following bark beetle-caused mortality. Site-specific prescriptions that account for the species composition and fuel profiles of individual stands will clearly be more effective than these generic Thin or Burn treatments. For example, treatments which combine thinning and burning may prove more effective than either alone (Agee and Skinner, 2005; Reinhardt et al., 2008). Raising the diameter limit of spruce and fir removed in our LP-SF stands would both elevate CBH and increase revenue generated by thinning. Similarly, removal of standing live or dead biomass could enhance both the fuel reduction aims and provide economic rewards if small-diameter forest products become more profitable. Pruning to directly increase CBH may be appropriate in specific, sensitive areas. However, modifications could also reduce the effectiveness of treatments so should be considered carefully. For example, fire prescribed for higher fuel moisture may be seen as less risky but may not reduce surface fuels as much as expected (e.g., Stephens and Moghaddas, 2005; Knapp et al., 2005; Battaglia et al., 2008).

Like numerous other studies, our simulations showed that ladder fuel and residual overstory growth decreases fuels reduction treatment effectiveness within a few decades (Battaglia et al., 2008; Reinhardt et al., 2010; Collins et al., 2012; Stephens and Collins, 2012; Stephens et al., 2012; Chiono et al., 2012). We found that re-entry will be required every 20 years to maintain desired CBH, regardless of forest or treatment type. Further, additional

Table 4
Percent of post-MPB stands that met canopy base height (CBH), canopy bulk density (CBD), and coarse woody debris (CWD) hazardous fuel criteria (see Table 2) with and without fuels reduction treatments (Unshaded = 75–100%; Light Grey = 50–75%; Dark Grey = <50% of stands met criteria). Percents are underlined when Thin or Burn treatment changed the proportion of stands to meet the hazardous fuel criteria.

		Simulation Year														
		0			10 (Trt year)			20			50			100		
	Criteria:	*CBH*	*CBD*	*CWD*	*CBH*	*CBD*	*CWD*	*CBH*	*CBD*	*CWD*	*CBH*	*CBD*	*CWD*	*CBH*	*CBD*	*CWD*
Trt	*Type*	%														
Untreated (Control)	LP	64	100	45	100	100	55	0	45	64	0	36	82	55	0	82
	LP-AS	100	100	0	100	100	0	38	100	13	0	100	25	88	50	38
	LP-SF	0	100	40	0	80	50	0	30	60	0	0	70	10	0	60
Thin	LP	-	-	-	100	100	55	**36**	**82**	64	0	**45**	82	**27**	**18**	**91**
	LP-AS	-	-	-	100	100	0	**50**	100	13	0	100	25	88	**63**	38
	LP-SF	-	-	-	0	**100**	50	0	**80**	**50**	0	**30**	70	**20**	0	**100**
Burn	LP	-	-	-	100	100	**82**	**82**	**100**	**91**	0	**91**	**91**	**0**	**45**	**73***
	LP-AS	-	-	-	100	100	**25**	**100**	100	**38**	**13**	100	**75**	**25**	**75**	**87**
	LP-SF	-	-	-	**90**	**100**	**60**	**60**	**100**	**80**	**10**	**100**	**90**	10	**10**	**100**

[a] In the LP stands in year 100, criteria was not met in 100% of stands only because fuel loads were too low (below 22 Mg ha^{-1}).

manipulations are needed in year 20 and 40 to maintain CBD target levels after thinning in LP-SF and LP forest types, respectively. This treatment schedule is likely neither realistic, nor desirable, except for in high-value locations in the wildland urban interface.

Our results indicate that forests like our LP and LP-SF types, characterized by dense fir and spruce advance regeneration, should be top priorities for fuel reduction treatments given regional fuel reduction criteria. However, intervention to remove ladder fuels, increase CBH, and reduce torching conflicts with requirements to maintain or enhance habitat of the federally-listed, threatened Canada lynx (U.S.D.A. Forest Service, 2009a). Treatments conducted in forests like our LP-AS and pure LP stands may avoid the conflicting management objectives but result in treating lower priority, lower hazard areas. Though simulations and field experimentation are needed, treatments that create or expand within-stand and landscape variation may help achieve a balance between fuels reduction and lynx habitat needs.

These projections of forest dynamics should be interpreted with appropriate care. Our previous modeled predictions of general structural and compositional change following MPB derived from plot measurements (Collins et al., 2011, 2012) have been corroborated by resurvey of historical MPB outbreaks (Pelz and Smith, 2012). Nevertheless, the ability of current models to accurately predict tree regeneration and long-term forest change following MPB and associated management is uncertain. The FVS-FFE model, for example, generally underestimates CBD and canopy fuel hazard in conifer forests (Keyser and Smith, 2010). Further, our simulation does not account for factors that could alter future tree growth and mortality, such as extreme weather events and climate change, insect, disease, and animal damage (Worrall et al., 2013). Well-replicated, long-term measurement of forest development in distinct forest types and management treatments is the best way to make certain estimates of post MPB forest recovery. In the absence of appropriate operational trials, our simulations demonstrate important relative differences among forest types and treatments.

5. Conclusion

Differences in species composition can help prioritize fuels reduction treatments following mountain pine beetle. Post-outbreak canopy structure poses a relatively high fire hazard immediately after outbreak in pine-dominated stands mixed with fir and spruce in the overstory and understory (our LP-SF type). Within two decades of the outbreak, lodgepole stands containing fir and spruce advance regeneration (our LP type) develop low canopy base heights and high canopy bulk densities that create similarly high hazards. In contrast, in lodgepole forest mixed with aspen (our LP-AS type), the hazard of active crown fire is relatively low for many decades after outbreak. Fuel reduction treatments are therefore likely to have the greatest effect on canopy fire hazard in forests where subalpine fir is abundant. Burning, and to a lesser extent thinning, have potential to reduce canopy fire hazard and resistance to control, though there is a need for repeated interventions to account for growth and formation of the ladder fuel strata. Decade-scale treatment intervals are not consistent with the century-scale return interval of natural disturbances in high elevation forests (e.g., Romme and Despain, 1989; Kipfmueller and Baker, 2000; Schoennagel et al., 2004), but intensive hazardous fuel management may be justified in the wildland urban interface and other high-value areas due to increasing wildfire suppression costs and wildfire occurrence with climate change (U.S.D.A. Office of Inspector General, 2006; Aronson and Kulakowski, 2012; Gorte, 2013; Westerling et al., 2011).

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