

# Comparison of riparian and upland forest stand structure and fuel loads in beetle infested watersheds, southern Rocky Mountains



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## ABSTRACT

Extensive outbreaks of mountain pine beetle (MPB), spruce beetle (SB), and other insects are altering forest stand structure throughout western North America, and thereby contributing to the heterogeneity of fuel distribution. In forested watersheds, conifer-dominated riparian forests frequently occur as narrow linear features in the landscape mosaic and contribute to the spatial complexity of forest stands and fuel complexes. These streamside forests are valued for providing aquatic and terrestrial habitat, serving as sources of instream and floodplain large wood, and maintenance of streamside microclimates and stream water quality. Despite the ecological importance of riparian forests, few data exist on riparian stand attributes and fuel complexes in watersheds affected by recent beetle outbreaks. To address this need, we measured stand characteristics and fuel loads in riparian areas and adjacent uplands. Within beetle-infested watersheds in northern Colorado and southeastern Wyoming, we sampled 30 pairs of riparian and upland plots (0.05 ha). Our goal was to identify bark beetle induced differences in forest structure and fuel profiles between riparian and upland stands. Specific objectives were: (1) to quantify and compare riparian and upland forest characteristics, specifically structure, extent of insect-caused canopy mortality and understory regeneration; (2) to characterize and compare riparian and upland fuel profiles. Basal area did not differ significantly for live, dead, or total (live + dead) overstory trees ( $\geq 10$  cm diameter at breast height (DBH)) between upland and riparian stands, although variability was high between plot types and among plots. Although riparian and upland plots were both dominated by lodgepole pine, Engelmann spruce, and subalpine fir, they differed in relative proportions of lodgepole pine (higher in uplands) and Engelmann spruce (higher in riparian areas). For these two species, bark beetles caused greater than 80% mortality in diameter classes larger than 20 cm DBH across all plots. For subalpine fir, which is not directly affected by MBP or SB, live overstory basal area and stem densities were roughly similar in riparian and upland plots. The combination of MPB-and-SB-caused canopy mortality has diminished differences in overstory basal area composition of riparian and upland stands, making them more structurally similar than prior to the beetle outbreaks. Total understory stem densities of poles, saplings and seedlings were largely comparable across plot types. However, understory live subalpine fir densities were significantly higher in both riparian and upland plots compared to lodgepole pine and Engelmann spruce, suggesting that fir will play an increasingly important role in future forest development across the landscape. With the exception of 1-h fuels and herbaceous plant cover (higher in riparian plots), fuel complexes were also similar in riparian and upland plots, with total woody fuel loads of approximately  $45 \text{ Mg ha}^{-1}$ . Although current basal area, understory characteristics and surface fuel distribution are largely similar in riparian areas and uplands, fuel distribution and corresponding fire risk will likely change as the SB infestation progresses, stands respond to overstory mortality, and dead trees fall.

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## 1. Introduction

Throughout much of the western USA and Canada, conifer forests are undergoing bark beetle epidemics of unprecedented

extent and severity (Raffa et al., 2008). Outbreaks of mountain pine beetle (MPB; *Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae), spruce beetle (SB; *Dendroctonus rufipennis* Kirby, Coleoptera: Curculionidae), and other insects have affected millions of acres, altering forest stand composition and structure, the distribution, quality and quantity of fuels, and ecosystem processes (Raffa et al., 2008; Jenkins et al., 2008, 2012). The effects of MPB

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outbreaks on stand structure, notably basal area, species composition, and size class distribution, are reasonably well documented in the Rocky Mountain region in ponderosa (*Pinus ponderosa* C. Lawson) and lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) dominated forests (Romme et al., 1986; Axelson et al., 2009). In some mixed-aged stands, MPB has caused nearly 70% tree mortality, while nearly 90% mortality has been observed in large trees (Cole and Amman, 1980; Romme et al., 1986; Collins et al., 2011; Pelz and Smith, 2012). Similarly, effects of SB on subalpine forests dominated by Engelmann spruce (*Picea engelmannii* (Parry) Engelm.) in the Intermountain West (Jenkins et al., 2008; Jorgensen and Jenkins, 2011; DeRose and Long, 2012a,b) and Colorado (Veblen et al., 1991; Eisenhart and Veblen, 2000) have been described for previous and current large-scale epidemics. Research on the recent beetle outbreaks has increased understanding of the spatial variation in canopy mortality, trajectories of forest recovery (Collins et al., 2011), and the influence on distribution of fuels and potential fire behaviour (Page and Jenkins, 2007; Hicke et al., 2012).

Riparian forests occupy only a small proportion of area within the landscape mosaic, generally occurring as narrow linear streamside features. In the Rocky Mountains, conifer-dominated riparian vegetation is frequently similar to surrounding uplands in overstory species composition, although it can have higher basal area, stem densities, plant diversity, and rates of production in the understory (Carsey et al., 2003; Romme and Knight, 1981). Streamside forests provide valued aquatic and terrestrial habitat, maintain riparian microclimates and stream water quality, and serve as sources of in-stream and floodplain large wood (NRC, 2002). Because of their ecological importance, riparian areas are afforded additional protection; they are administratively designated zones adjacent to stream channels with specific management objectives and regulations aimed at maintaining or improving valued ecosystem services, especially water quality (USDA Forest Service, 2012). Despite the valued functions of riparian ecosystems, few data exist on streamside forest stand attributes and fuel characteristics in watersheds affected by recent beetle outbreaks. Assessment and monitoring of forest condition, both plot-based and remotely sensed, have emphasized impacts on upland forests (Collins et al., 2012; Colorado State Forest Service, 2012). Comparable information on forest stand structure, extent of canopy mortality, composition of the residual overstory, and distribution of fuel loads in riparian areas is lacking. This limited knowledge, combined with administrative regulations for riparian management, presents additional challenges to resource specialists planning fuel treatment projects and other management actions in beetle infested watersheds.

To address this need, we measured stand characteristics and fuel loads in streamside and adjacent upland stands within selected beetle-infested watersheds in northern Colorado and southeastern Wyoming. Our objective was to compare bark beetle effects in riparian and upland forests with respect to species composition, structure, extent of insect-caused mortality, regeneration, and fuel profiles. Our broader objective is to provide basic ecological information about the condition of riparian forests in beetle-infested watersheds that could be useful for designing current and future conservation and management strategies.

## 2. Methods

### 2.1. Study area

The study was conducted in subalpine forests between 2500 and 3200 m in elevation in the Medicine Bow, Routt, Arapaho, and Roosevelt National Forests (Fig. 1), in southeastern Wyoming's

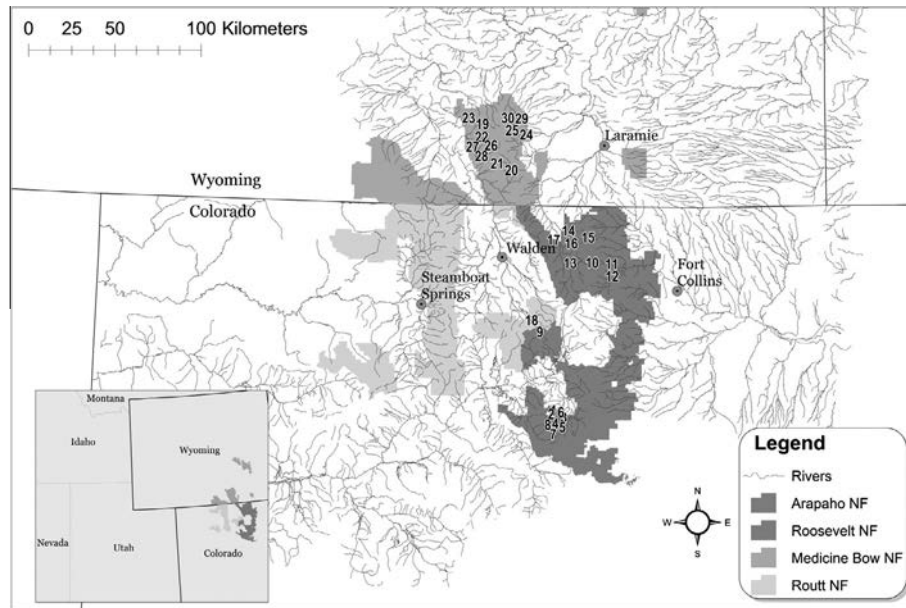
Medicine Bow Mountains, and Colorado's Front Range (39°50'22"N, 105°55'3"W to 41°50'22"N, 106°12'14"W; Table 1). This elevation band was selected to sample effects of both MPB and SB. Within this elevation band, lodgepole pine generally comprises 45–55% of the tree cover, and Engelmann spruce and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) each contributes approximately 25–35% cover (Dillon et al., 2005; Alexander et al., 1986). Lodgepole pine usually dominates lower elevations and drier sites, whereas Engelmann spruce and subalpine fir tend to dominate at higher elevations, on north-facing slopes, and along riparian corridors, though lodgepole pine is frequently present. The study area has a temperate, continental climate with long, cold winters and short, cool summers (Kittel et al., 2002). Mean annual precipitation ranges from 450 mm to 660 mm across the study area (Fig. 1), with approximately 65% falling as snow between October and May. Air temperature ranges from an average low of  $-10^{\circ}\text{C}$  in January to an average high of  $22.1^{\circ}\text{C}$  in July (PRISM Climate Group, 2012). The stream flow regime throughout the area is snowmelt dominated, and peak flow usually occurs in June (Jarrett, 1990).

The primary agents of natural disturbance in these subalpine forests are fire (Sherriff et al., 2001; Sibold and Veblen, 2006; Sibold et al., 2006), wind (Romme and Knight, 1981; Aplet et al., 1988), and bark beetle infestations (Kulakowski et al., 2003; Sibold et al., 2007; Jenkins et al., 2014). In the study area, mean fire intervals have been estimated based on age-class sampling, fire scars, historical records, and evaluation of stand structure and fuel accumulation. Estimated mean fire intervals for a given stand of subalpine forest range from 50 to 700 years, with most estimates between 200 and 500 years (Romme and Knight, 1981; Kipfmüller and Baker, 2000; Sibold and Veblen, 2006; Sibold et al., 2006). This large variation has been attributed to differences in site characteristics and species composition, with the longest fire-free intervals associated with mesic sites occurring on north-facing slopes, at high elevations or along streams (Dillon et al., 2005). Fire suppression was the dominant management policy from about 1920 until the early 1990s (Dillon et al., 2005; Sibold et al., 2006; Sibold and Veblen, 2006), and effectively managed wildfires during that period.

Throughout the study area, extensive lodgepole pine mortality from MPB became increasingly evident between 1998 and 2002, and the annual acreage affected peaked in 2008 (Colorado State Forest Service, 2010, 2012). The SB outbreak in north-central Colorado and southern Wyoming has been underway since 2005, and continues to spread. In 2012, the acreage impacted by SB surpassed that of MPB in Colorado for the first time since the MPB epidemic began in the late 1990s (Colorado State Forest Service, 2012).

### 2.2. Site selection

Potential study watersheds, i.e. those with >50% MPB beetle infestation, were selected using aerial detection survey maps of MPB beetle infestation compiled by US Forest Service Forest Health Monitoring program (USDA, 2011). Watersheds with previous clear-cuts were avoided. Potential riparian study locations were identified through examination of topographic maps, digital elevation models, forest vegetation maps for the selected watersheds, and suggestions from local land managers. Criteria were conifer-dominated riparian areas along gentle-to-moderate stream gradients, moderately confined stream segments with narrow floodplains, within the elevation range 2500–3200 m. Upland plots were located 200–400 m upslope from each riparian plot, on a randomly selected (coin-toss) side of the adjacent stream. Riparian study locations were selected first, followed by selection of a paired upland plot location. In cases where a road was present on one side of the channel, the upland plots were located on the non-roaded side.



**Fig. 1.** Map of study area showing plot locations on four National Forests in northern Colorado and southern Wyoming. Site numbers correspond to paired plot locations presented in Table 1.

**Table 1**  
National forest, stream, site location, and riparian plot characteristics. Each riparian plot was paired with an adjacent upland plot. Site numbers correspond to paired-plot locations shown in Fig. 1.

National Forest	Stream	Site No	Latitude (deg)	Longitude (deg)	Elevation (m)	Aspect	Stream Order	Drainage Area (km <sup>2</sup> )
Arapaho NF	Dead Horse Creek	1	39°54'01"	105°54'15"	2890	SE	1	3.61
Colorado	Dead Horse Creek	2	39°54'01"	105°54'13"	2975	SE	1	3.60
	East St. Louis Creek	3	39°53'21"	105°52'27"	2930	NE	1	9.84
	Fool Creek	4	39°53'04"	105°52'28"	2929	N	1	3.97
	Fool Creek	5	39°52'35"	105°52'15"	3047	NE	1	3.95
	St. Louis Creek	6	39°53'28"	105°53'34"	2844	NW	2	55.75
	St. Louis Creek	7	39°50'22"	105°55'03"	2932	NE	2	36.84
	West St. Louis Creek	8	39°53'04"	105°55'31"	2945	E	1	7.81
	Unnamed	9	40°18'34"	106°02'14"	2770	NW	1	4.17
Roosevelt NF	Bennett Creek	10	40°40'24"	105°36'24"	2696	N	1	9.56
Colorado	Bennett Creek	11	40°40'04"	105°34'15"	2511	N	2	21.23
	E. Fork Sheep Creek	12	40°37'14"	105°42'29"	3154	W	1	6.44
	Laramie River	13	40°40'14"	105°51'30"	2626	N	2	26.16
	Lone Tree Creek	14	40°50'23"	105°51'22"	2975	NW	1	0.67
	No. Fork Cache la Poudre River	15	40°48'17"	105°44'15"	2940	NW	2	13.46
	Sand Creek	16	40°50'16"	105°48'28"	3072	W	1	2.60
	Stub Creek	17	40°47'30"	105°54'18"	2560	SW	2	15.03
Routt NF CO	Parkview Creek	18	40°22'13"	106°07'05"	2843	NE	1	7.89
Medicine Bow NF	Cortez Creek	19	41°23'30"	106°28'32"	2652	N	1	17.41
Wyoming	Flume Creek	20	41°09'09"	106°16'12"	2690	N	1	3.85
	Horse Creek	21	41°11'15"	106°16'36"	2842	W	1	7.84
	Lincoln Creek	22	41°21'16"	106°29'13"	2589	N	1	8.33
	Middle Cedar Creek	23	41°25'18"	106°31'34"	2650	S	2	12.04
	Mill Creek	24	41°20'16"	106°29'24"	2596	SW	2	6.92
	No Fork Little Laramie River	25	41°22'22"	106°10'15"	2839	W	2	30.23
	No. French Creek	26	41°19'30"	106°25'16"	2684	SE	2	28.71
	No. French Creek	27	41°18'17"	106°26'35"	2820	W	2	39.43
	Middle French Creek	28	41°17'15"	106°27'29"	2638	SW	2	19.84
	So. Fork Rock Creek	29	41°25'22"	106°12'14"	3076	NE	2	8.88
	Trail Creek	30	41°25'31"	106°12'27"	3013	W	2	12.37

All upland stands have been previously managed, mostly through selective thinning within the last 50–60 years (Alexander, 1975; Dillon et al., 2005). Recently, numerous salvage logging treatments have been conducted in upland areas in response to high levels of MPB mortality (Colorado State Forest Service, 2010, 2012). None of the upland plots were located in or near recently treated stands, although three were scheduled for treatment in the near future. Management history

of riparian forests is more difficult to determine, but old growth was avoided and the selected riparian sites appeared to have been previously managed, based on presence of stumps and other indications of prior logging activity. Along roads running parallel to streams, MPB mortality has resulted in removal of hazard trees, thus influencing some riparian areas. However, none of the riparian plots were located along recently treated transportation corridors.

### 2.3. Forest overstory and understory characteristics

All data were collected in summer 2012, approximately two years post-outbreak for MPB and during the SB outbreak. Riparian and upland forest stand characteristics were sampled in 0.05-ha circular plots. The approximate center of each riparian plot was established randomly along the selected stream segment; however, some plot-center locations were adjusted slightly to position each riparian plot as close to the adjacent stream as possible, with the streamside plot perimeter along the stream bank edge. Plot location (UTM point), slope, aspect, and elevation were recorded at plot center (Table 1).

Within each plot, information recorded on all live and dead trees ( $\geq 5$  cm diameter at breast height (DBH)) included: species, DBH, percent live crown, and crown base height (noncompacted). Evidence of MPB incidence and damage was recorded for each standing lodgepole pine tree (live or dead); similarly, SB incidence was recorded for each standing Engelmann spruce and Colorado blue spruce tree (*Picea pungens* Engelm.). Trees were categorized as: uninfested (no evidence of beetle); infested with MPB, or infested with SB. Beetle infestation was discernible by the presence of pitch tubes, exit holes in the bark, frass or sawdust around the base of the tree, and/or beetle galleries beneath the bark (Rocky Mountain Region, Forest Health Protection, 2010; Simard et al., 2011). If a dead lodgepole pine or spruce tree was categorized as uninfested (no evidence of beetle), we assumed that it had died prior to the beetle outbreaks. If a dead tree was categorized as infested (by either MPB or SB), we assumed that it had died due to beetle infestation, or was beetle-killed. We combined data for dead-infested trees with live trees to evaluate basal area and other stand conditions prior to bark beetle outbreaks. Stumps were not included in evaluations of stand conditions prior to bark beetle infestation.

Prior to data analysis, the 5–10 cm DBH size class was sorted, removed from the overstory tree dataset, and treated as part of the understory. We refer to this size class of understory trees (5–10 cm DBH) as poles; live poles were analyzed as the largest size class of regeneration, and dead poles were used to assess ladder fuels (Lutes et al., 2006; Ottmar et al., 2007).

We recorded data on smaller size classes in the understory to assess regeneration and live fuels. Saplings were defined as plants that were less than 5 cm in diameter (DBH) and taller than 1.4 m in height. Within each plot, we recorded species, DBH and estimated height for live saplings in two diameter classes (stems  $\geq 2.5$  cm and  $< 2.5$  cm DBH; and stems  $< 2.5$  cm DBH). Seedlings were defined as plants that were less than or equal to 1.4 m in height. Within the inner 0.0125-ha of each plot (radius = 6.31 m), live seedlings were tallied by species and height class ( $< 0.5$  m or  $\geq 0.5$  m). Regeneration data for different size classes of live saplings and seedlings were also used to assess ladder fuels (Lutes et al., 2006; Ottmar et al., 2007).

In each plot, three transects (12.63 m in length) were established from plot center on randomly selected bearings to sample shrubs and surface woody fuels. Shrub cover was estimated for each species using the line intercept method (Lutes et al., 2006). Along each transect, the length of intercept for each species was recorded by noting the point on the tape where the shrub canopy began and ended. Height of the combined shrub + herbaceous layers was measured at every meter along each transect (12 heights per transect; 36 heights per plot). Percent cover of herbaceous vegetation, bare ground, gravel/cobble, bedrock, and litter was visually estimated for the entire 0.05 ha plot. Nomenclature follows the U.S. Department of Agriculture Natural Resources Conservation Service PLANTS database (2014). Shrub and herbaceous cover estimates were also used to assess live understory fuels.

### 2.4. Surface fuels

Surface woody fuel loads were estimated along the same transects described above (3 per plot, 12.63 m) using the planar intercept method for 1-h, 10-h, and 100-h size classes (Brown, 1971, 1974). Along each transect, 1-h fuels were tallied for the first 6.3 m and 10-h and 100-h fuels were tallied along the entire transect length (Lutes et al., 2006; Riccardi et al., 2007). Within each plot, we conducted a complete tally of large woody fuels (1000-h); length and two end diameters ( $> 7.6$  cm) were measured on each piece – or portion of each piece – that occurred within the plot perimeter. For each stump located within the sampled plots, the height, basal diameter (above the root swell), and diameter at the cut surface were measured. Decay status of each large woody fuel piece and stump was noted as either sound or rotten. Depth of litter and duff was measured every meter along each transect (12 depths per transect; 36 depths per plot; Lutes et al., 2006).

### 2.5. Statistical analysis

We compared stand characteristics in 30 pairs of riparian and upland plots in beetle infested stands using generalized linear mixed models (Proc GLIMMIX; SAS, 2011). We used a randomized complete block design with paired riparian and upland plots as blocks, plot type (riparian or upland) as a fixed effect, and plot elevation, aspect, and slope as random effects. Prior to analysis, each type of data (e.g. basal area, shrub cover, etc.) was plotted and examined to assist in assigning the appropriate distribution for that model. For count data, namely density of stumps and understory and overstory stems, we used a negative binomial distribution. In analysis of basal area, tree size class distribution, and crown base height, we used a log-normal distribution.

Percent shrub cover by species was calculated for each plot by first summing the intercept lengths, then dividing by the transect length to obtain percent cover for that transect. The three transect cover values were then averaged to generate a plot cover estimate for each species. We compared total shrub cover and cover by species for 30 pairs of riparian and upland plots using generalized linear mixed models (Proc GLIMMIX; SAS, 2011) as described above, assuming a beta distribution (Smithson and Verkuilen, 2006).

We calculated fuel loads for 1-h, 10-h, and 100-h size classes as described in Brown (1971, 1974). For large woody fuels (1000-h), length and diameters of each piece were used to calculate individual piece volume, approximating the piece as a cylinder (Lienkaemper and Swanson, 1987). For stumps, height, basal diameter and diameter at the cut surface were used to calculate individual piece volume, again approximating the piece as a cylinder. Total volume of sound and rotten large woody fuels and stumps was summed for each plot in cubic meters. For both stumps and large woody fuels, we assumed an average wood density of  $400 \text{ kg m}^{-3}$  for sound pieces and an average wood density of  $300 \text{ kg m}^{-3}$  for rotten pieces (Lamlom and Savidge, 2003), and then converted values to  $\text{Mg ha}^{-1}$  for each plot. The four fuel size classes (1-h, 10-h, 100-h, and 1000-h) were summed for each plot, and then averaged to compare surface woody fuel loads in upland and riparian plots. Similar to stand characteristics, we compared surface fuel loads and stumps using generalized linear mixed models (Proc GLIMMIX; SAS, 2011), assuming a log-normal distribution. Statistical significance was assigned at the  $\alpha = 0.05$  level.

## 3. Results

Of the 30 riparian plots sampled, 16 were located along first order streams and 14 occurred along second order streams (Table 1). Elevation ranged from 2511 m to 3154 m at the riparian

plot centers, and drainage area (derived from the USGS National Hydrography Dataset) ranged from 0.67 km<sup>2</sup> to 55.75 km<sup>2</sup>.

### 3.1. Forest stand characteristics

Basal area of live and dead overstory trees ( $\geq 10$  cm DBH) was highly variable between plot types and among plots. Mean dead basal area was similar in riparian ( $24.64 \pm 2.65$  m<sup>2</sup> ha<sup>-1</sup>; range 2.57–60.46 m<sup>2</sup> ha<sup>-1</sup>) and upland plots ( $25.27 \pm 2.50$  m<sup>2</sup> ha<sup>-1</sup>; range 3.12–65.05 m<sup>2</sup> ha<sup>-1</sup>). Although not significantly different, mean live basal area was higher in riparian plots ( $18.65 \pm 2.25$  m<sup>2</sup> ha<sup>-1</sup>; range 3.15–55.75 m<sup>2</sup> ha<sup>-1</sup>) than in upland plots ( $14.15 \pm 1.34$  m<sup>2</sup> ha<sup>-1</sup>; range 3.71–29.05 m<sup>2</sup> ha<sup>-1</sup>). Mean total basal area (live + dead) was higher in riparian plots ( $43.28 \pm 3.04$  m<sup>2</sup> ha<sup>-1</sup>; range 14.50–77.55 m<sup>2</sup> ha<sup>-1</sup>) than in upland plots ( $39.42 \pm 2.94$  m<sup>2</sup> ha<sup>-1</sup>; range 17.96–85.03 m<sup>2</sup> ha<sup>-1</sup>), but not significantly different.

Despite similarities in basal area between riparian and upland plots, there were differences in the relative contribution of the three dominant species (Fig. 2). Currently, live basal area of lodgepole pine comprises 16% of the live overstory in riparian plots ( $2.88 \pm 1.26$  m<sup>2</sup> ha<sup>-1</sup>) and approximately 33% of the live overstory in upland plots ( $4.69 \pm 1.25$  m<sup>2</sup> ha<sup>-1</sup>). Engelmann spruce dominates riparian plots at 47% of the live basal area ( $8.75 \pm 1.94$  m<sup>2</sup> ha<sup>-1</sup>) but represents only 26% of live basal area in upland plots ( $3.74 \pm 0.86$  m<sup>2</sup> ha<sup>-1</sup>). The proportion of live subalpine fir basal area is more similar between riparian and upland plots, comprising 33% ( $6.05 \pm 1.44$  m<sup>2</sup> ha<sup>-1</sup>) and 39% ( $5.49 \pm 1.10$  m<sup>2</sup> ha<sup>-1</sup>) of the live overstory respectively (Fig. 2). Across all plots, nearly 93% of the lodgepole pine dead basal area was attributed to MPB, and approximately 70% of the Engelmann spruce dead basal area was attributed to SB (Figs. 2 and 3).

Several other species were present in the overstory canopy in both riparian and upland plots but these were minor contributors

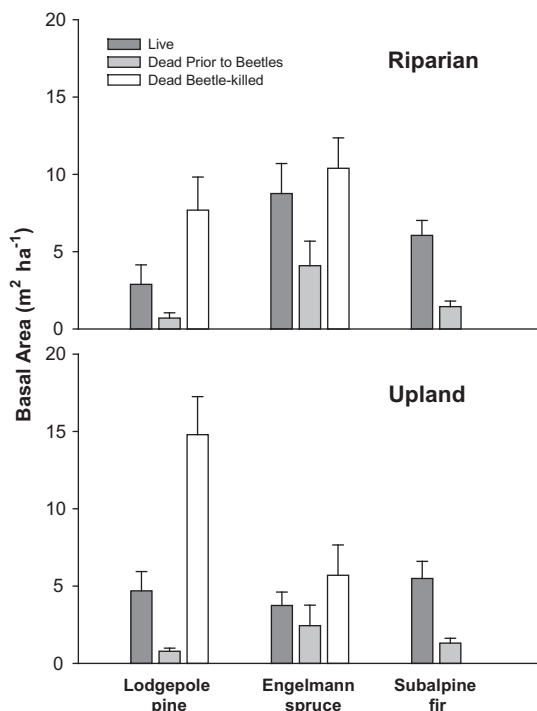


Fig. 2. Basal area (m<sup>2</sup> ha<sup>-1</sup>) for lodgepole pine, Engelmann spruce, and subalpine fir in 30 riparian and 30 upland plots (all trees  $\geq 10$  cm DBH). Data are means and SE for live trees; trees that were assumed dead before the beetle infestations (dead prior to beetles); and trees killed by beetles (dead beetle-killed).

to the overall forest structure. Quaking aspen (*Populus tremuloides* Michx.) and Colorado blue spruce (*P. pungens* Engelm.) contributed about 3% of the total riparian basal area. Additional species in upland plots were ponderosa pine (*P. ponderosa* Lawson ssp. *scopulorum* (Engelm.) A.E. Murray) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), which together contributed about 1% of the total upland basal area.

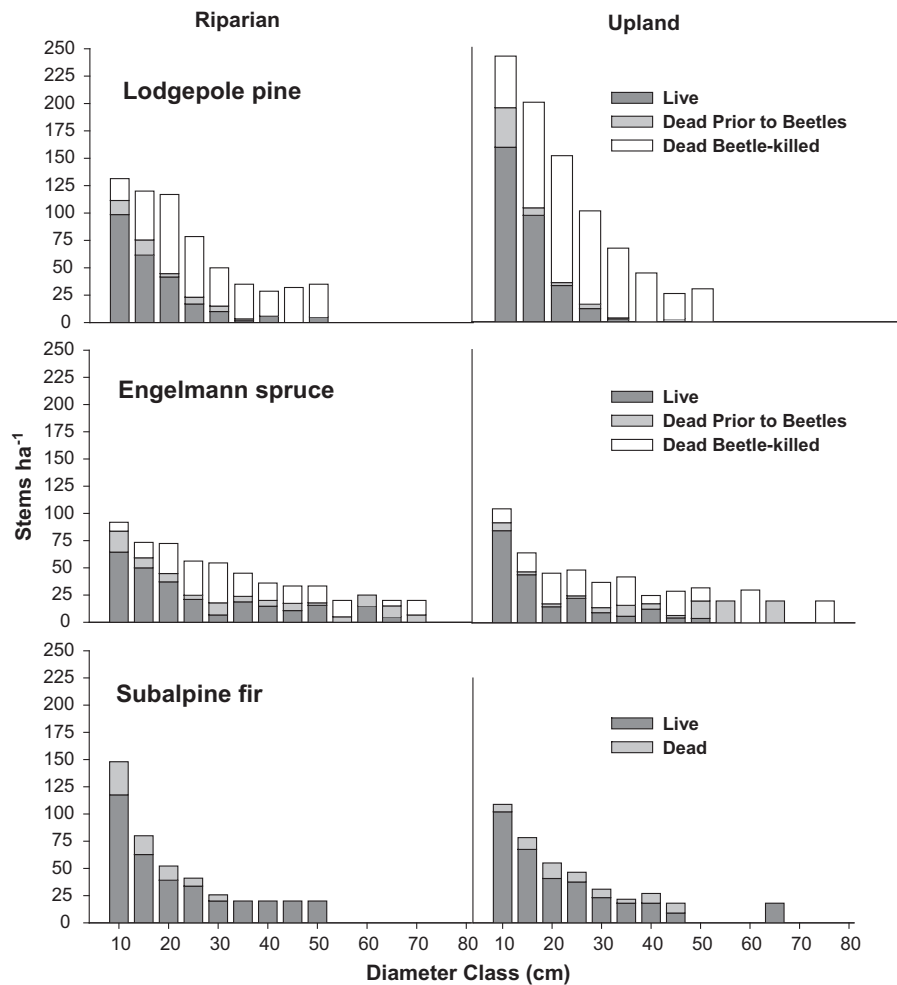
To explore forest stand conditions prior to the bark beetle infestations, we combined live basal area with basal area for lodgepole pine and Engelmann spruce trees that had been categorized as 'dead-infested' (by MPB or SP) during sampling (indicated as 'Dead Beetle-killed' in Fig. 2). Using this approach, we estimated that the live basal area for upland stands prior to the bark beetles was composed of approximately 56% lodgepole pine, 27% Engelmann spruce, and 15% subalpine fir. In contrast, the composition of live basal area for riparian stands prior to the bark beetles was approximately 28% lodgepole pine, 53% Engelmann spruce, and 16% subalpine fir.

The distribution of mean stem densities in diameter size classes illustrates the impacts of bark beetles on the larger diameter classes of lodgepole pine and Engelmann spruce (Fig. 3). Differences in the contribution of the three dominant species to current riparian and upland stands are also evident, and reflect the patterns observed in basal area (Figs. 2 and 3). For lodgepole pine, MPB-induced mortality was significantly higher in trees larger than 20 cm DBH in both upland and riparian plots ( $p < 0.05$ ). However, more live lodgepole pine trees larger than 20 cm DBH remained in riparian plots. Similar results were observed for Engelmann spruce. SB-induced mortality was significantly higher in trees larger than 20 cm DBH in both upland and riparian plots ( $p < 0.05$ ), but more live spruce trees remained across multiple size classes in riparian plots. For subalpine fir, the distribution of live stem diameter classes was roughly similar for riparian and upland plots (Fig. 3). Live subalpine fir stem densities were significantly higher than either lodgepole pine or Engelmann spruce in both riparian and upland plots ( $p < 0.05$ ).

### 3.2. Understory characteristics

Stem densities of regeneration size classes ( $< 10$  cm DBH) were also highly variable between plot types and among plots. General trends in total densities were similar between riparian and upland plots, despite some apparent differences in species composition (Table 2). Colorado blue spruce stems were observed only in riparian plots and ponderosa pine stems only in the uplands. Quaking aspen stems were more abundant in riparian plots in all size classes, but particularly as seedlings. As expected, mountain alder stems were also more numerous in riparian plots. The mesic willow species, *Salix geyeri* and *Salix drummondiana*, occurred only in riparian plots, while the more upland willow, *Salix scouleriana* Barrett ex Hook., was observed only in upland plots.

In riparian plots, the average density of poles and saplings (all species combined) was approximately 400 stems ha<sup>-1</sup> for each diameter size class, slightly lower but not significantly different from densities in upland stands (Table 2). Subalpine fir dominated understory regeneration in all plots, comprising over 50% of the pole-sized stems in riparian plots and nearly 38% in upland plots, and approximately 50% of sapling-sized stems in both riparian and upland plots. Average densities of subalpine fir were similar between riparian and upland plots for poles and both size classes of saplings. Subalpine fir saplings (both size classes combined) were found in nearly 90% of both upland and riparian plots. Average densities of lodgepole pine poles and saplings were 3–4-fold higher in the uplands relative to riparian areas. However, no lodgepole pine saplings were tallied in 30% of the upland plots and 60% of the riparian plots (both sapling size classes combined). Although



**Fig. 3.** Density (stems  $\text{ha}^{-1}$ , live and dead,  $\geq 10$  cm DBH) of Engelmann spruce, subalpine fir, and lodgepole pine stems by diameter class (5 cm increments) for 30 riparian and 30 upland plots. Data shown are means of live stems; stems that were assumed dead before the beetle infestations (dead prior to beetles); and stems killed by beetles (dead beetle-killed).

slightly higher in riparian plots, densities of Engelmann spruce poles and saplings were not significantly different between riparian and upland types. Densities of spruce saplings (both sapling size classes combined) ranged from 0 to 1120 stems  $\text{ha}^{-1}$  in the riparian plots and from 0 to 480 stems  $\text{ha}^{-1}$  in the uplands, and occurred in nearly 90% of both riparian and upland plots.

Seedling densities varied considerably both between plot types and among plots. In the shorter size class ( $<0.5$  m in height), densities ranged from 160 to 14,720 stems  $\text{ha}^{-1}$  in the riparian plots and from 0 to 6160 in the uplands for all species combined; in the taller seedling size class ( $\geq 0.5$  to 1.4 m), densities ranged from 160 to 67,600 stems  $\text{ha}^{-1}$  in the riparian plots and from 0 to 23,280 in the uplands for all species combined. Average stem densities of taller seedlings ( $\geq 0.5$  m and  $<1.4$  m) were higher overall in riparian plots, most notably for Engelmann spruce (Table 2). However, no spruce seedlings were tallied in 20% of the riparian plots and about 45% of the upland plots (both seedling size classes). Subalpine fir dominated the seedling stratum ( $<1.4$  m), comprising approximately 86% of the shorter seedling size class ( $<0.5$  m) in both riparian and upland plots, and 56% (riparian) and 76% (upland) of the taller seedling size class ( $\geq 0.5$  m). No subalpine fir seedlings were tallied in 10% of the riparian plots and nearly 20% of the upland plots. Although average densities of lodgepole pine seedlings were 2-fold higher in the taller size class and 8-fold

higher in the shorter size class in upland plots, stem densities ranged from 0 to 2560 stems  $\text{ha}^{-1}$ , and no lodgepole seedlings were tallied in nearly 50% of the upland plots (both seedling size classes). Lodgepole seedlings were observed in only 20% of the riparian plots.

Riparian and upland plots did not differ in average total shrub cover, although there were some differences in species composition (Table 3). Thirteen taxa were sampled, with 10 occurring in both riparian and upland plots. Eight of the 13 taxa are deciduous, including the dominant *Vaccinium* spp., and 5 of the lower-cover species are evergreen. Although three taxa – *Ribes inerme* Rydg., *Lonicera involucrata* (Richardson) Banks ex Spreng, and *Salix* spp. L. – occurred only in riparian plots, the average number of shrub species per plot (3–4 species/plot) was similar across riparian and upland areas. *Vaccinium scoparium* Leiberg ex Coville was the dominant shrub species in all plots, followed by *Vaccinium myrtillus* L. ssp. *oreophilum* (Rydb.).

Herbaceous cover was significantly higher in riparian plots ( $73 \pm 5\%$ , range: 10–100%) than in upland plots ( $16 \pm 4\%$ , range: 0–85%). The height of the combined shrub + herbaceous layers was also greater in riparian plots ( $0.68 \pm 0.35$  m, range 0.28–1.3 m) than in upland plots ( $0.37 \pm 0.20$  m, range: 0.20–0.78 m). However, percent cover of bare ground, gravel and cobble, bedrock, and litter was similar across all plots.

**Table 2**  
Density (stems ha<sup>-1</sup>) of regeneration in the understory, including poles (stems ≥ 5.0 cm and < 10 cm DBH), two diameter classes of saplings (stems ≥ 2.5 cm and < 5 cm DBH; and stems < 2.5 cm DBH; height > 1.4 m), and two height classes of seedlings (stem height ≥ 0.5 m and ≤ 1.4 m; and stem height < 0.5 m). For each species, data are means and SE for 30 riparian and 30 upland plots. For totals, data are means and SE for sums of all species within 30 riparian and 30 upland plots.

	Poles DBH: ≥ 5.0 cm and < 10 cm		Saplings DBH: ≥ 2.5 cm and < 5 cm		Saplings DBH: stems < 2.5 cm		Seedlings Height: ≥ 0.5 m and < 1.4 m		Seedlings Height: < 0.5 m	
	Riparian	Upland	Riparian	Upland	Riparian	Upland	Riparian	Upland	Riparian	Upland
Lodgepole pine	47 ± 20*	191 ± 71*	39 ± 14*	157 ± 65*	50 ± 25*	140 ± 52*	93 ± 69*	184 ± 91*	24 ± 14*	192 ± 80*
Subalpine fir	213 ± 38	181 ± 42	214 ± 47	264 ± 57	187 ± 39	204 ± 34	1513 ± 317	1200 ± 283	4186 ± 2300	3754 ± 1026
Engelmann spruce	139 ± 38	93 ± 19	113 ± 27	91 ± 16	98 ± 20	71 ± 15	793 ± 274*	187 ± 69*	631 ± 210*	369 ± 106*
Colorado blue spruce	3 ± 2*	0*	3 ± 2*	0*	9 ± 6*	0*	11 ± 7*	0*	8 ± 4*	0*
Ponderosa pine	0	0	0*	1 ± 1*	0*	1 ± 1*	0	0	0*	5 ± 5*
Quaking aspen	10 ± 7*	0*	25 ± 18*	1 ± 1*	27 ± 16*	2 ± 1*	290 ± 190*	0*	72 ± 59*	0*
Mountain alder	3 ± 2*	0*	5 ± 2*	1 ± 1*	17 ± 8*	4 ± 4*	0	0	0	0
Willow spp. <sup>a</sup>	1 ± 1*	0*	1 ± 1*	0	10 ± 6*	0	0	0	0	0
Scouler's willow	0*	4 ± 4*	0*	3 ± 3*	0*	2 ± 1*	0	0	0	0
Total (all species)	415 ± 153	469 ± 71	401 ± 51	517 ± 84	397 ± 47	423 ± 60	2700 ± 512*	1570 ± 310*	4921 ± 2303	4321 ± 1031

<sup>a</sup> Combined stems for Geyer's willow (*Salix geyeri*), Drummond's willow (*Salix drummondiana*), and unidentified *Salix* spp.

\* Significant difference between riparian and upland stands (alpha = 0.05).

**Table 3**  
Percent shrub cover estimated for each taxon using the line intercept method. Unless otherwise noted, data are means, SE, and range of values for 30 riparian and 30 upland plots.

Species	Species common name	Growth habit	Riparian cover (%)	Upland cover (%)
<i>Vaccinium scoparium</i> Leiberg ex Coville	Grouse whortleberry	Deciduous	17 ± 4 (0–76)	24 ± 4 (0–81)
<i>Vaccinium myrtillus</i> L.ssp. <i>oreophilum</i> (Rydb.)	Whortleberry, dwarf bilberry	Deciduous	12 ± 3 (0–49)	9 ± 3 (0–58)
<i>Juniperus communis</i> L.	Common juniper	Evergreen	2 ± 1 (0–19)	2 ± 1 (0–21)
<i>Rosa woodsii</i>	Wood's rose	Deciduous	2 ± 1 (0–7)	<1 (0–5)
<i>Shepherdia canadensis</i> (L.) Nutt.	Russet buffalobery	Deciduous	<1 (0–2)	2 ± 1 (0–16)
<i>Paxistima myrsinites</i> (Pursh) Raf.	Oregon boxleaf, mountain-lover	Evergreen	1 ± 1 (0–10)	1 ± 1 (0–22)
<i>Ribes inerme</i> Rydb.	Common or whitestem gooseberry	Deciduous	1 ± 1* (0–16)	0*
<i>Ribes lacustre</i> (Pers.) Poir.	Prickly gooseberry, prickly currant	Deciduous	3 ± 1 (0–11)	<1 (0–5)
<i>Lonicera involucrata</i> (Richardson) Banks ex Spreng	Twinberry honeysuckle, bush honeysuckle	Deciduous	3 ± 1* (0–10)	0*
<i>Salix</i> spp. <sup>a</sup>	Willow	Deciduous	2 ± 1* (0–10)	0*
<i>Arctostaphylos uva-ursi</i> (L.) Spreng.	Kinnikinnick, bearberry	Evergreen	<1 (0–2)	<1 (0–1)
<i>Chimaphila umbellata</i> (L.) W.P.C. Barton	Pipsissewa	Evergreen	<1 (0–2)	<1 (0–4)
<i>Mahonia repens</i> (Lindl) G. Don	Creeping barberry, creeping Oregon grape	Evergreen	<1 (0–4)	<1 (0–6)
Total shrub cover			35 ± 5 (1–100)	41 ± 4 (2–100)
Total number of shrub taxa sampled			13	10
Average number of shrub taxa sampled per plot			4 ± 1 (1–8)	3 ± 1 (1–6)

\* Significant difference between riparian and upland stands (alpha = 0.05).

<sup>a</sup> Combined cover for Geyer's willow (*Salix geyeri*), Drummond's willow (*Salix drummondiana*), and unidentified *Salix* spp.

### 3.3. Fuels

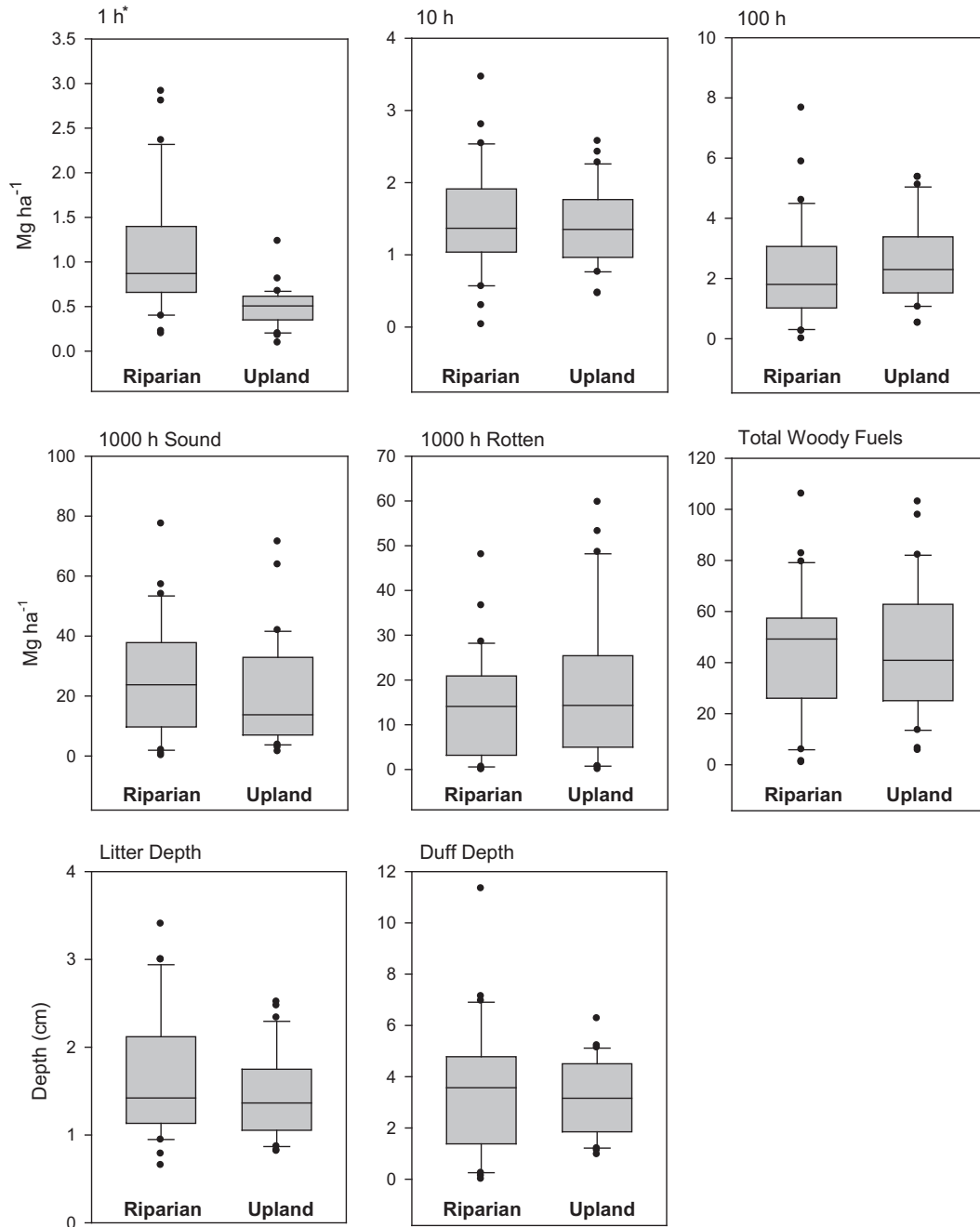
One-hour fuel loads were higher in riparian plots (Fig. 4;  $p = 0.04$ ). However, loads for 10-h, 100-h, and 1000-h fuel size classes were similar in riparian and upland plots, resulting in total woody fuel loads of approximately 45 Mg ha<sup>-1</sup> across all plots. The depths of litter and duff layers were also similar in riparian and upland plots (Fig. 4).

Other fuel characteristics were also similar for riparian and upland plots. Neither the density of dead pole-size stems or estimates of crown base height differed between plot types (Table 4). Since no significant differences were observed in the total density of live poles and saplings (Table 2), these combined results indicate that ladder fuels and fuel continuity are currently similar in riparian and upland plots. Estimates for percent live crown did not differ between riparian and upland plots (Table 4). Since shrub cover was comparable in riparian and upland plots (Table 3), it is reasonable to assume that live fuels attributed to shrubs were also similar. As noted above, herbaceous cover was higher in riparian plots, so this fine-fuels component of the fuel complex was more abundant in riparian areas. Stumps occurred in 53% of the riparian plots and 73% of the upland plots. On a per-area basis, there were no significant differences in stump number or volume between the two

plot types. However, the number of stumps was slightly lower in riparian areas and the volume of stumps slightly greater than in uplands (Table 4).

## 4. Discussion

No significant differences were found in live, dead, or total basal area in overstory trees between riparian and upland plots. The combination of MPB-and-SB-caused canopy mortality has diminished differences between riparian and upland areas, making them more structurally similar than prior to the beetle outbreaks. High stem densities of subalpine fir in the residual overstory and understory indicate that this species will have a more dominant role in future forests across the landscape. Although fuel loads are currently similar, fuel profiles will change over time as dead trees fall, possibly resulting in greater differentiation in distribution of fuels in riparian and upland areas over time. Our inability to detect strong differences between riparian and upland stand characteristics was likely influenced by the high variability in the overstory and understory data (Fig. 2, Table 2). Although this variability could be partly due to small plot size (0.05 ha) and sample size



**Fig. 4.** Fuel loads in 30 riparian and 30 upland plots. Fuel loads were similar for 10 h, 100 h, 1000 h, and total woody fuels; 1 h fuel loads were significantly higher ( $p = 0.04$ ) in riparian plots. Box plots show 25th and 75th percentiles divided at the median, whiskers show the 10th and 90th percentiles, dots are outliers.

**Table 4**

Additional fuel characteristics; density of dead poles (DBH > = 5 cm and < 10 cm); crown fuel base height; percent live crown; and density and volume of stumps. Data are means, SE, and range of values for 30 riparian and 30 upland plots. See Table 2 for stem densities of live ladder fuels.

Fuel characteristic	Riparian	Upland
Dead poles (stems ha <sup>-1</sup> )	108 ± 30 (0–900)	84 ± 13 (0–260)
Crown Base Height (m)	3.4 ± 1.3 (0–24)	3.7 ± 1.4 (0–20)
Percent Live Crown (%)	49 ± 4 (5–100)	46 ± 4 (4–100)
Stumps (No ha <sup>-1</sup> )	37 ± 10 (0–200)	53 ± 10 (0–180)
Stumps (Mg ha <sup>-1</sup> )	1.31 ± 0.47 (0–12.59)	0.78 ± 0.15 (0–2.67)

(30 pairs), it also reflects the heterogeneity of natural conditions that occur across the study area.

#### 4.1. Forest stand characteristics

Bark beetles have significantly impacted forest structure in both riparian and upland stands and will continue to influence overstory stand dynamics over the next years to decades. Prior to the MPB and SB epidemics, uplands were dominated by lodgepole pine, riparian areas were dominated by Engelmann spruce, and subalpine fir occurred as a subdominant species across the landscape. Collectively, MPB and SB have killed between 50% and 60% of the live basal for lodgepole pine and Engelmann spruce that existed



before the beetle outbreaks, thus diminishing differences in composition of current live basal area between upland and riparian stands. Although Engelmann spruce remains dominant in riparian areas, live subalpine fir basal area now exceeds that of lodgepole pine in most upland plots (Fig. 2). Current stem densities of live subalpine fir trees (>10 cm DBH) are greater than either lodgepole pine or Engelmann spruce in both riparian and upland plots (Fig. 3). Because subalpine fir is not directly impacted by MPB or SB, we expect that the proportion of fir will increase in both riparian and upland landscape positions throughout the study area (e.g. Collins et al., 2012). As the canopy continues to open due to continued spruce mortality, subalpine fir trees in the overstory will likely experience an increase in growth, resulting in greater basal area. High densities of subalpine fir poles, saplings, and seedlings will eventually result in more dominance in the overstory. Although MPB infestation has declined substantially in recent years, spruce beetle infestation continues (Colorado State Forest Service, 2012) and will further reduce the proportion of live Engelmann spruce in both uplands and riparian areas. As dead overstory Engelmann spruce and lodgepole pine trees in both riparian and upland stands lose branches and eventually fall (Mitchell and Preisler, 1998), woody fuel loads will increase over time.

The riparian stands sampled in this study are dominated by the same overstory species as surrounding uplands and are drier than most other riparian plant associations in the region, as indicated by the high cover of *Vaccinium* spp. (Carsey et al., 2003). Differences in total live basal area have been attributed to moister site conditions in riparian areas, as well as successional dynamics among the three dominant species following disturbance (Romme and Knight, 1981). Natural disturbance regimes in riparian and upland stands likely differ somewhat in the study area, but have not been studied directly. Generally, fire return intervals are less frequent in valley bottoms (Romme and Knight, 1981; Dwire and Kauffman, 2003). The role of insect infestations on stand development is assumed to be spatially heterogeneous depending largely on site conditions (Kulakowski and Jarvis, 2011).

Canopy fuels, composed of live and dead overstory trees, are important fuelbed variables that can affect crown fire behaviour potential (Riccardi et al., 2007), and are evaluated using stem densities, species and relative cover. Although live and dead basal area did not differ significantly between riparian and upland plots, there were differences in relative species composition (Fig. 2). Since snag fall rates for lodgepole pine and Engelmann spruce are different and local topography (valley bottom vs. upland landscape position) influences wind patterns, fuel distribution may become increasingly different over time in uplands compared to streamside areas.

#### 4.2. Understory characteristics

The unprecedented nature of the MPB and SB outbreaks has raised questions regarding forest regeneration and trajectories of stand development. Research has shown that small trees and saplings in the understory are rarely killed during insect outbreaks (Veblen et al., 1991; Nigh et al., 2008; Collins et al., 2011), and that understory regeneration response largely depends on the species, extent of canopy mortality, and site conditions (Nigh et al., 2008; Kayes and Tinker, 2012). In a retrospective study of a 1940s SB outbreak in Colorado subalpine forests, Veblen et al. (1991) found a strong regeneration response from subcanopy Engelmann spruce and subalpine fir. Growth of released regeneration remained high for over 40 years following the outbreak, and dominance in basal area shifted from Engelmann spruce to subalpine fir. Following the recent MPB-outbreak in untreated stands in northern Colorado, Collins et al. (2011) predicted that subalpine fir will become the most abundant species based on growth simulations of regeneration data. In contrast, Kayes and Tinker (2012) concluded that

the continued presence of surviving lodgepole in the overstory will likely retain the dominance of this species as post-MPB-outbreak stands develop in southern Wyoming. In subalpine forests of the southern Rocky Mountains that have been impacted by both MPB and SB, interactions between the amount and composition of the residual overstory, establishment requirements of individual species and relative site conditions may be particularly important and may differ in riparian and upland stands. In addition, rates of growth, recruitment, and survival will also vary among species and influence future stand composition. Research to date has primarily focused on either MPB or SB outbreaks, rather than the combined influence of both bark beetles.

We observed that riparian and upland stands contained high densities of tree regeneration in all size classes, similar to results reported in other studies of post-outbreak upland forest conditions (Table 2; Simard et al., 2011; Collins et al., 2011, 2012; Kayes and Tinker, 2012). In this study, we infer that higher densities of lodgepole pine in upland plots reflect the influence of site conditions and overstory composition (Fig. 3). Similar to other studies throughout post-outbreak forests in Colorado and southern Wyoming (Klutsch et al., 2009; Collins et al., 2011, 2012; Kayes and Tinker, 2012; Pelz and Smith, 2012), we found that subcanopy strata were dominated by subalpine fir in all regeneration size classes; nearly half of the total understory stem density across both riparian and upland plots was attributed to subalpine fir (Table 2). In previous studies, aspen was an important component of the regenerating understory, accounting for 10–40% of the stem density (Collins et al., 2011, 2012; Kayes and Tinker, 2012; Pelz and Smith, 2012), whereas we found that aspen accounted for less than 5% of the understory stem densities for all size classes combined.

Current differences between riparian and upland stands in live canopy and understory species composition and site conditions may lead to stronger differentiation over time. Across both riparian and upland plots, we observed considerable variability in the distribution of stem densities in different regeneration size classes, as would be expected given the heterogeneous environment and latitudinal range sampled in this study. However, all plots had a combination of poles, saplings and seedlings that will contribute to stand development. Regeneration stem densities are considered adequate to form well stocked new stands, even if more canopy trees succumb to bark beetles. At the time of sampling, approximately 36% of the basal area was composed of live overstory trees in the uplands, and about 43% of the riparian overstory basal area was live. However, it is difficult to predict how many of the remaining overstory trees will survive, particularly spruce trees with the ongoing SB outbreak.

Beetle-caused mortality of overstory trees opens portions of the canopy, and releases resources, including light, space, soil moisture, and nutrients to surviving plants. This release results in increased growth of small trees, saplings, and seedlings, but can also initiate a release of shrub and herbaceous growth, especially during the early part of the post-epidemic period (Stone and Wolfe, 1996; Jorgensen and Jenkins, 2011). Although shrub cover was similar in riparian and upland plots, the greater diversity of riparian shrub taxa, increased canopy openings adjacent to the stream channels, and moister site conditions may lead to greater release of shrubs in streamside areas. In these conifer-dominated riparian stands, the *Salix* and *Ribes* species grow in a narrow band along the stream banks, and could expand in cover. Herbaceous cover, already considerably higher in riparian plots, is also likely to increase. Although increased cover of shrubs and herbaceous species may reduce growth of regenerating trees, it is unlikely to have a strong impact on stand trajectories.

In forest ecosystems, the shrub component is important for differentiating forest plant associations in both upland and riparian forest types. The species composition and abundance of shrubs

that we observed are consistent with descriptions of undergrowth commonly observed in mature spruce-fir and lodgepole upland forests. In the most thorough treatment of riparian vegetation for the study area (Carsey et al., 2003), there are seven recognized subalpine fir-Engelmann spruce plant associations, which are differentiated based largely on shrub and herbaceous components of the understory. Three of these plant associations include lodgepole pine with cover ranging from 2% to 48%. Five of these conifer-dominated riparian plant associations include *Vaccinium* spp. as contributing from 1% to 34% cover, as well as variable coverage (10% or less) by *Ribes* spp., *Rosa woodsii*, *L. involucrata*, and *Salix* spp., as observed in this study. The riparian shrub component sampled in this study, particularly the similarity in species composition to upland stands and high cover of *Vaccinium* species, indicate that these riparian forests are among the driest riparian vegetation types in the region.

### 4.3. Fuels

#### 4.3.1. Surface fuel loads

Surface fuel loads and depths of litter and duff were surprisingly similar in riparian and upland stands (Fig. 4). We anticipated that fine surface fuels, primarily litter layer and 1-h fuels due to high needle and small twig input, may be greater in upland stands due to the condition of the overstory strata, which had a high number of dead lodgepole pine in the 'gray stage' of post-outbreak (Simard et al., 2011; Page et al., 2013). Fine woody fuels generally reach their highest levels in the first few years following a bark beetle epidemic (Jenkins et al., 2008), which is the case for MPB in most of the upland plots we sampled. Our estimates for 1-h fuel loads are generally comparable with reported values for MPB-impacted lodgepole stands in the Greater Yellowstone area, Wyoming (Simard et al., 2011), northeastern Utah (Page and Jenkins, 2007), and northern Colorado (Collins et al., 2012), while our estimates for 10-h and 100-h are either comparable (Klutsch et al., 2009) or 2–4-fold lower than observed in other studies (Page and Jenkins, 2007; Simard et al., 2011; Collins et al., 2012). Variability in accumulated fuels of different sizes is likely related to differences in level of mortality, stand structure and post-outbreak stages (Hicke et al., 2012; Donato et al., 2013).

Large woody fuels (1000-h) loads were also similar in riparian and upland plots (Fig. 4), reflecting similarities in current live and dead basal area and stem densities in the overstory (Figs. 2 and 3). Although not significantly different, the proportion of sound 1000-h fuels in riparian plots (65%) was slightly greater than in upland plots (53%), likely indicating differences in decay rates among species and environmental conditions, as well as time since tree fall and other factors related to management history. In a few riparian and upland plots, we observed recently toppled MPB-killed lodgepole pine trees. However, most beetle-killed trees were still standing at the time of sampling. Published values for 1000-h fuels are highly variable for both MPB and SB-affected stands depending on the extent of the outbreak (endemic or epidemic), the timing of sampling relative to the outbreak, and species composition of the sampled stands. Although our values for both sound and rotten coarse woody fuel components are similar to those reported for SB-affected spruce stands in southern Utah (Jorgensen and Jenkins, 2011), they are 2–4-fold lower than those reported for MPB-affected lodgepole stands in Utah and Wyoming (Page and Jenkins, 2007; Simard et al., 2011) and 2–4-fold higher than reported for other studies in northern Colorado (Klutsch et al., 2009; Collins et al., 2012). The accumulation of coarse woody fuels largely depends on the rate at which dead overstory trees fall to the surface, which can vary widely due to site features, incidence of disease, and tree species (Mielke, 1950; Mitchell and Preisler, 1998; Jenkins et al., 2008, 2012; Lewis and Thompson,

2011). Although stumps only contribute an additional 1 Mg ha<sup>-1</sup> to the coarse woody fuel totals, their numbers and characteristics suggest differences in past management of upland and riparian plots. Stumps in riparian plots were generally taller, had wider diameters and were more rotten than those in upland plots (data not shown), likely remnants of tie-drive activities that peaked in the late 1800s (Thybonny et al., 1986; Young et al., 1994; Ruffing et al., in press).

#### 4.3.2. Ladder fuels

The high stem densities of all regeneration size classes, as well as comparable densities of dead pole-size trees (Table 4), indicate the abundance of ladder fuels across both plot types. When considered in combination with comparable crown base heights (Table 4), the vertical fuel continuity between strata is similar in riparian and upland plots. The mean canopy-base heights – 3.4 m in riparian plots and 3.7 m in upland plots – may currently be high enough to reduce probability of fire transition into crowns (torching) in most sampled locations. However, as different size classes of regeneration continue to grow and the lower canopy strata increases in foliar cover at different heights, the base of the canopy will effectively decrease. In a study comparing a chronosequence of MBP-affected lodgepole forests in the Greater Yellowstone area, Simard et al. (2011) found that canopy base height decreased from approximately 3 m during the MPB red stage to nearly zero at 35 years post-outbreak, while sapling density increased nearly 10-fold from about 400 to 4000 stems/ha. In this study, it appears that beetle-triggered acceleration of the release and recruitment of regeneration is occurring in both upland and riparian areas. While such changes in ladder fuels and fuel continuity could potentially increase torching potential, changes in future fire behaviour will depend on how other components of the fuels complex develop over time, as well as climatic and topographic variables (Bebi et al., 2003).

#### 4.3.3. Fuel moisture

We did not measure moisture content of live biomass or other fuel components, although differences in moisture content of various fuel strata may be a critical feature in determining how some riparian stands may burn relative to uplands (Dwire and Kauffman, 2003). Riparian microclimates, mostly higher humidity and cooler temperatures (Broszofski et al., 1997), could slow the rates of fine fuel drying and decay of coarse wood, thus reducing the probability of fire ignition and spread. In a Wyoming subalpine forest, Romme and Knight (1981) found that late season moisture of fine woody surface fuels (1–10 cm, which includes 1-h, 10-h, and 100-h fuels) were consistently higher in valley bottoms relative to uplands. Foliar moisture in the tree canopies will continue to change as lodgepole pine and Engelmann spruce trees respond to beetle infestation in both riparian and upland stands (Jolly et al., 2012).

Since shrub cover was comparable in riparian and upland plots (Table 3), it is reasonable to assume that live fuels attributed to shrubs are also similar. However, even though the shrub component was dominated by *Vaccinium* spp. in both riparian and upland plots, differences in shrub foliar moisture may occur, particularly late in the growing season. The occurrence of more deciduous shrubs in riparian plots also indicates that foliar moisture of shrubs differs between upland and streamside areas in some locations. As noted above, herbaceous cover was higher in riparian plots, and several of the observed species, notably *Senecio triangularis* Hook., *Mertensia ciliata* (James ex Torr.) G. Don, and *Cardamine cordifolia* A. Gray are considered indicators of mesic conditions and are known to have high foliar moisture content (Cronk and Fennessy, 2001). In Douglas-fir stands (Blue Mountains, northeastern Oregon), Agee et al. (2002) found that understory shrub and herbaceous foliar moisture was considerably higher in riparian areas relative to

uplands. Fuel moisture can affect the rate of spread, fuel consumption, and fire-caused mortality for wildland and prescribed fires. Since herbaceous cover can either inhibit or carry fire, depending on foliar moisture and other factors, this difference between riparian and upland fuelbeds could influence fire behaviour. More data are needed on relative moisture content of riparian and upland fuelbeds, especially during drought years, late in the wild-fire season, and during prescribed fire season.

#### 4.4. Implications for management

Riparian areas cover a relatively small area, yet they are disproportionately important for maintenance of water quality and quantity, habitat for aquatic and terrestrial biota, sediment retention, stream bank building and maintenance, and provision of other ecosystem services (Naiman and Decamps, 1997; NRN, 2002; Naiman et al., 2005). On National Forest lands, protection of riparian areas is usually governed by standards and guidelines in the forest plan for each National Forest, which frequently include specific best management practices (BMPs) and a designated riparian buffer width (Belt et al., 1992; Gregory, 1997; USDA Forest Service, 2012). In the Rocky Mountain Region of the US Forest Service (Region 2), where this study was conducted, the default riparian buffer distance, or 'water influence zone' is 100 feet (30.48 m) from the stream bank, an area where only actions that "maintain or improve long-term stream health and riparian conditions" can be conducted (USDA Forest Service, 2006). The riparian plots sampled in this study were all within the designated 100 feet (30.48 m) buffer zone. Management of riparian areas in beetle-infested watersheds presents new challenges for resource managers, particularly with respect to maintenance of water quality and aquatic habitat within the context of increased fire risk (Dwire et al., 2010; Luce et al., 2012). Implementation of BMPs and establishment of riparian buffers have generally decreased the negative effects of forest harvest activities on surface water quality (Belt et al., 1992; Norris, 1993; Osborne and Kovacic, 1993). However, less is known regarding BMP effectiveness in protecting other riparian functions, especially given the streamside levels of beetle-caused canopy mortality observed in this study.

A recent study compared the influence of different natural forest disturbances on stream water nitrate concentrations, and found no significant increase following extensive beetle-caused tree mortality in streams of Colorado (Rhoades et al., 2013). The authors attributed this finding to a combination of factors: relatively low atmospheric nitrogen deposition in the region, tree mortality occurring over a number of years, and high compensatory capacity of residual overstory, understory and undisturbed soils to retain nitrate despite high levels of canopy mortality. It is likely that the riparian forests observed in this study, with approximately 30% of live basal area in the overstory, abundant understory regeneration and high herbaceous cover, contribute to nitrate uptake. Although concerns regarding potential for increased stream water nitrate levels in beetle-infested watersheds may have been alleviated, other water quality parameters, notably stream temperature, require increased consideration (Luce et al., 2012).

An outcome of canopy mortality in riparian areas will be increased recruitment of large wood to stream channels. Instream large wood provides numerous beneficial and ecologically important functions, especially in low-order streams. Large wood shapes channel morphology and contributes to channel complexity, and shapes the geometry, number, and distribution of pools, thus creating aquatic habitat diversity; large wood slows flow, dissipates energy, and reduces downcutting; instream large wood also traps and stores organic matter, providing food and habitat for aquatic biota (Gregory et al., 2003). In forested watersheds, riparian zones are a primary source of instream large wood, and forest distur-

bance events, such as fire and insect-caused canopy mortality, can result in considerable inputs of large wood to streams over time (Benda et al., 2003). Large wood loads in many streams in Wyoming and Colorado have been reduced by past management and land use activities (Young et al., 1994; Wohl, 2001; Ruffing et al., in press). With the exception of anecdotal reports, the recruitment of beetle-killed trees to streams has not yet been observed in the study region (Jackson, 2014), and will vary with tree species, exposure to wind, and hillslope features. Large wood inputs to streams can be considered one beneficial outcome of the bark beetle infestations, although recruitment will require managerial oversight in locations close to infrastructure.

Perhaps the most pressing management issues surrounding the bark beetle infestations are related to fuels reduction and salvage logging treatments. Although most treatments are occurring in uplands, there are valid concerns about fuel load distribution and potential fire behaviour when uplands are treated and riparian areas are left untreated (Murphy et al., 2007; Dwire et al., 2010). Whereas riparian areas and BMPs will likely assist in mitigating some impacts of upland fuel reduction treatments, additional precautions and actions may be necessary to protect particular riparian functions. Since our results show that riparian buffers in beetle-infested watersheds have comparable levels of canopy mortality and fuel loads to surrounding uplands, there is justifiable concern regarding fire risk, potential fire behaviour, and impacts on streams and aquatic biota. Along low order streams, where the vegetation composition of riparian areas is similar to that of adjacent uplands, streamside areas have been observed to burn similar to uplands, particularly on south-facing aspects (Hemstrom and Franklin, 1982). It is likely that, given certain weather conditions, riparian areas in the study area may burn with similar severity, intensity, and frequency to surrounding uplands. Protective rules for riparian management are restrictive but allow for active riparian management, and fuels reduction treatments are being applied in some riparian areas, although cautiously (Stone et al., 2010; Meyer et al., 2012). In cases where treatments prescriptions are being planned and conducted within riparian areas, managers may need to develop and implement additional on-site BMPs and riparian-specific precautions to protect streams and valued riparian functions.

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