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Pre-outbreak forest conditions mediate the effects of spruce beetle outbreaks on fuels in subalpine forests of Colorado

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Abstract. Over the past 30 years, forest disturbances have increased in size, intensity, and frequency globally, and are predicted to continue increasing due to climate change, potentially relaxing the constraints of vegetation properties on disturbance regimes. However, the consequences of the potentially declining importance of vegetation in determining future disturbance regimes are not well understood. Historically, bark beetles preferentially attack older trees and stands in later stages of development. However, as climate warming intensifies outbreaks by promoting growth of beetle populations and compromising tree defenses, smaller diameter trees and stands in early stages of development now are being affected by outbreaks. To date, no study has considered how stand age and other pre-outbreak forest conditions mediate the effects of outbreaks on surface and aerial fuel arrangements. We collected fuels data across a chronosequence of post-outbreak sites affected by spruce beetle (SB) between the 1940s and the 2010s, stratified by young (<130 yr) and old (>130 yr) post-fire stands. Canopy and surface fuel loads were calculated for each tree and stand, and available crown fuel load, crown bulk density, and canopy bulk densities were estimated. Canopy bulk density and density of live canopy individuals were reduced in all stands affected by SB, though foliage loss was proportionally greater in old stands as compared to young stands. Fine surface fuel loads in young stands were three times greater shortly (<30 yr) following outbreak as compared to young stands not affected by outbreak, after which the abundance of fine surface fuels decreased to below endemic (i.e., non-outbreak) levels. In both young and old stands, the net effect of SB outbreaks during the 20th and 21st centuries reduced total canopy fuels and increased stand-scale spatial heterogeneity of canopy fuels following outbreak. Importantly, the decrease in canopy fuels following outbreaks was greater in young post-fire stands than in older stands, suggesting that SB outbreaks may more substantially reduce risk of active crown fire when they affect stands in earlier stages of development. The current study shows that the effects of SB outbreaks on forest structure and on fuel profiles are strongly contingent on pre-outbreak conditions as determined by pre-outbreak disturbance history.

Key words: conifer forests; Dendroctonus rufipennis *Kirby; disturbance interactions; disturbance legacies; fuel heterogeneity; linked disturbances; natural disturbances;* Picea engelmannii; *Rocky Mountains, USA; western U.S. forests.*

Introduction

Assessing the impacts of large, infrequent disturbances on post-disturbance stand structure and dynamics is an important frontier in ecology. This is especially important as vegetation properties are theoretically expected to become less important in determining disturbance regimes as climate-related disturbances intensify. However, the consequences of the potentially declining importance of vegetation in determining future disturbance regimes are not well understood. It is well established that an initial disturbance may dampen or enhance the occurrence, extent, or severity of a subsequent disturbance through positive or negative feedbacks (Buma 2015, Seidl et al. 2017). For instance, stand-replacing fires have been shown to reduce the likelihood of subsequent spruce beetle outbreaks (Veblen et al. 1994, Kulakowski et al. 2003) and prior spruce beetle outbreak to limit occurrence of subsequent spruce beetle outbreak (Hart et al. 2015*b*). Additionally, pre-spruce-beetle-outbreak forest structure has been shown to mediate the effects and likelihood of wildfire following outbreaks in boreal spruce–fir forests (Hansen et al. 2016) and in lodgepole and spruce–fir forests of the U.S. Pacific northwest (Meigs et al. 2016). Wind blowdown events have been shown to increase the amount of spruce beetle host material, thus amplifying the likelihood of subsequent outbreaks (Schmid 1981). Furthermore, the relative timing and severity of disturbances (e.g., wildfire) can either increase (Kulakowski and Jarvis 2013, Agne et al. 2016) or decrease (Kulakowski et al. 2012) susceptibility of forests to future outbreaks of mountain pine beetle. Disturbance combinations in quick succession can also have

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negative impacts on post-disturbance regeneration at landscape to continental scales (Cohen et al. 2016, Carlson et al. 2017). Over the past decades, much has been learned about interacting disturbances, however, climate change is dramatically affecting disturbance regimes, post-disturbance regeneration, disturbance interactions.

The native spruce beetle (SB; *Dendroctonus rufipennis* Kirby) is one of the most widely distributed bark beetles in North America, ranging from Arizona to Alaska (Raffa et al. 2008). Though spruce beetles are endemic across subalpine forests, widespread and epidemic outbreaks can occur due to a combination of susceptible host trees (Veblen et al. 1991*a*), high beetle population density (Raffa et al. 2008), warm and dry weather (Hart et al. 2014*a*), and low beetle predation (Fayt et al. 2005). Here we define endemic conditions as those under which beetle-caused tree mortality is limited to weakened trees and beetle populations do not vary substantially from year to year, whereas epidemic conditions are defined as those under which increased spruce beetle populations result in widespread tree host mortality that can exceed 80% of susceptible individuals (Schmid and Amman 1992, Safranyik and Carroll 2006, Jenkins et al. 2008). In general, spruce beetles preferentially attack older trees and stands in latter stages of development (>23 cm diameter at breast height [DBH]), but during extreme outbreaks, spruce trees as small as ~14 cm can be attacked (Hart et al. 2014*b*, Bakaj et al. 2016).

Given that stand structure and composition is strongly shaped by disturbance history (e.g., spruce beetle, blowdown, stand-replacing fire), susceptibility to spruce beetle outbreak is similarly influenced by these lasting disturbance legacies (Schmid and Frye 1977, Veblen et al. 1994, Bebi et al. 2003, Kulakowski et al. 2003, DeRose and Long 2012, Hansen et al. 2016). Prior disturbances can alter stand structure in a manner that either reduces or amplifies overall susceptibility of the stand to future outbreak. For instance, retrospective studies have found that spruce beetle outbreaks in the 19th and mid-20th century were less likely to occur in young stands that recently (within ~70 yr) established following stand-replacing fires (Veblen et al. 1994, Bebi et al. 2003, Kulakowski et al. 2003, Kulakowski and Veblen 2006*b*). Generally, young spruce stands are characterized by even-aged populations of relatively small trees, whereas older spruce stands are characterized by uneven-aged populations and larger diameter individuals, which are more suitable hosts for spruce beetles. However, as climate continues to intensify outbreaks by promoting growth of beetle populations and compromising tree defenses, smaller diameter trees and stands in early stages of development are being affected by outbreaks (Raffa et al. 2008, Hart et al. 2014*a*).

The net effect of spruce beetle outbreak on forest fuels is normally a reduction of live trees and canopy bulk density, and an increase in surface fuels and canopy openness, especially as time since outbreak increases. Immediately following tree mortality (~<1 yr), foliar moisture content decreases and leaf chemistry changes, turning foliage yellow (Page et al. 2015). Eventually, foliage (~2–5 yr), twigs (~5–10 yr), branches (~10–25 yr), and the tree itself will fall (~>30 yr; Table 1; Klutsch et al. 2009, Jolly et al. 2011, Page et al. 2014). This transference of aerial fuels to surface fuels reduces overall canopy bulk density (Jorgensen and Jenkins 2011), resulting in a one-to-one fuel load transference rate, minus any fine fuel decomposition that occurs (Bigler and Veblen 2011). Canopy mortality results not only in changes in canopy and surface fuels, but also in the growth release of shrubs, forbs, sub-canopy trees, and saplings, especially in the decades following outbreaks (Jorgensen and Jenkins 2011). The accumulation of coarse (1,000-h) fuels is highly influenced by the rate at which dead overstory snags fall to the ground, and can be correlated with increased time since outbreak (e.g., >30 yr post-outbreak; Mielke 1950, Schmid and Hinds 1974).

Previous work in the southern Rockies has evaluated the relative influence of environmental setting (e.g., riparian vs. upland) on mountain pine beetle (MPB; Dendroctonus ponderosae) and SB outbreaks (Dwire et al. 2015). Other studies have examined the influence of Douglas-fir beetle (Donato et al. 2013) or MPB (Pelz and Smith 2012, Schoennagel et al. 2012) on fuels arrangements along a chronosequence of outbreaks. To date, no study has considered the consequences of the novel phenomenon of SB outbreaks affecting younger trees and stands in early stages of development on surface and aerial fuel arrangements, nor, more generally, how pre-outbreak forest conditions (e.g., stand age) mediate fuels consequences following outbreaks.

Table 1. Qualification of spruce beetle time since outbreak classes.

Status	Description	Estimated time since outbreak
Live stage (Li)	trees with no evidence of SB activity	>100 yr
Green stage (Gr)	needles are still green and no signs of yellowing; pitch tubes, entrance holes, and frass visible on tree bole	<1 yr
Yellow stage (Ye)	visible signs of yellow needles in canopy; pitch tubes, entrance holes and frass on tree bole	1–2 yr
Needle drop (Nd)	>50% retention of dead needles in the canopy; needles are predominately red	2–5 yr
Twigs (Tw)	<50% red needles retained in the canopy; >50% 1-h twigs remain but are devoid of needles	5–10 yr
Branches (Br)	<50% 1-h twigs remain; canopy has dropped all needles	10–25 yr
Snag (Sn)	no branches present; bole >1.3 m tall	>25 yr
Dead (De)	dead tree not killed by SB	

Empirical studies in lodgepole and mixed conifer forests of the northern U.S. Rockies have shown that fire severity has been largely unaffected by pre-fire bark beetle activity and that weather during the time of fire strongly influenced fire severity (Harvey et al. 2013, 2014*a*, *b*). Additionally, modeling studies further suggest that the probability of fire is unchanged following low to moderate outbreaks and is reduced following high severity outbreaks due to the reduction of canopy fuels (Derose and Long 2009). Modeling studies have also indicated that passive fires may be more likely following outbreaks whereas active crown fires, which are most important ecologically and socially, are less likely due to decreased continuity of the canopy fuels (Jenkins et al. 2008).

Forest disturbances both respond to and create environmental structural variability that drives the spatial and temporal heterogeneity of forested landscapes (Schoennagel et al. 2012, Donato et al. 2013, Jenkins et al. 2014). For example, whereas beetle outbreaks in monospecific and structurally homogenous stands can result in very high total tree mortality, the proportion of trees killed is likely to be lower in mixed-species and structurally heterogeneous stands. Consequently, the magnitude of overall change in structure and fuels should be expected to be a function of pre-outbreak stand structure. However, this hypothesis has not been adequately explored because, until recently, outbreaks of spruce beetle have mostly been limited to stands in late stages of structural development. Here we hypothesize the following:

> Hypothesis 1**.** Effects of SB outbreaks on fuels are greater in young stands (<130 yr) than in older stands (>130 yr) characterized by more heterogeneous pre-outbreak structure.
> Hypothesis 2. Within-stand surface-to-crown fuel continuity decreases as time since SB outbreak increases.
> Hypothesis 3. Crown fuels and canopy bulk density are reduced as time since SB outbreak increases, potentially for decades after the outbreak.

Locations of well-documented spruce beetle outbreaks during the 20th and 21st century and stand-replacing fires during the late-19th century in northwestern Colorado (Veblen et al. 1991*c*, Eisenhart and Veblen 2000, Bebi et al. 2003, Kulakowski et al. 2003, Kulakowski and Veblen 2006*a*, 2007) provided an ideal opportunity to compare the effects of spruce beetle outbreaks on fuels in relatively young post-fire (i.e., established following stand-replacing fires in the late 19th century) with older stands (i.e., no stand-replacing disturbance for >200 yr). Here we present the results of an empirical study that examined fuel consequences across a chronosequence of spruce beetle outbreaks during the 20th and 21st century in stands that were burned (i.e., young) and unburned (i.e., old) by stand-replacing fires in the late-19th century.

Materials and Methods

Study area

Study sites were located in north-central Colorado in the subalpine forests of White River National Forest, Routt National Forest, Grand Mesa National Forest, and Arapahoe-Roosevelt National Forest (Fig. 1, Table 2). Sampled sites ranged in elevation from 2,750 to 3,950 m above sea level and were dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa)*.

All four national forests within our study area were partly burned by extensive stand-replacing fires in the early 18th century and late 19th century (Sudworth 1900, Kulakowski and Veblen 2002, 2006*a*, Sibold and Veblen 2006, Veblen and Donnegan 2006).

Site selection

All stands that established after the extensive late 19th-century fires were classified in this study as young stands, and all stands unburned by these or subsequent fires were classified as old stands. Selecting sites in this manner allowed us to examine how pre-outbreak stand structure, as shaped by previous fires, influenced post-outbreak fuels.

In both young and old forests, we sampled four stands in endemic (i.e., non-epidemic) conditions and four stands in each of the major spruce beetle epidemics of the past 100 years in western Colorado: 1940s, 1960s, 1990s, 2000s, and 2010s, for a total of 32 stands. Stands burned in the late 19th century were not affected by the 1940s and 1960s spruce beetle outbreak (Kulakowski et al. 2016), therefore these outbreaks are only represented in old stands. Outbreaks were classified based on the time since initiation of outbreak in a given stand. Outbreak that began in the 1990s spread across the state during the 2000s and 2010s and could be considered a single outbreak at the landscape scale, but the initiation of outbreak in individual stands varied across the landscape. We used categorical tree status attributes (Appendix S1: Fig. S1) and dendrochronological reconstructions to validate that the time of outbreak initiation coincided with the decadal classes. Site selection was based on existing SB reconstructions for this region and stratified by pre-outbreak stand age, biophysical setting, and outbreak severity (Veblen et al. 1991*c*, Eisenhart and Veblen 2000, Bebi et al. 2003, Kulakowski et al. 2003, Kulakowski and Veblen 2006*a*).

Canopy fuel sampling

Field methods were based on similar studies previously employed to quantify the effects of other bark

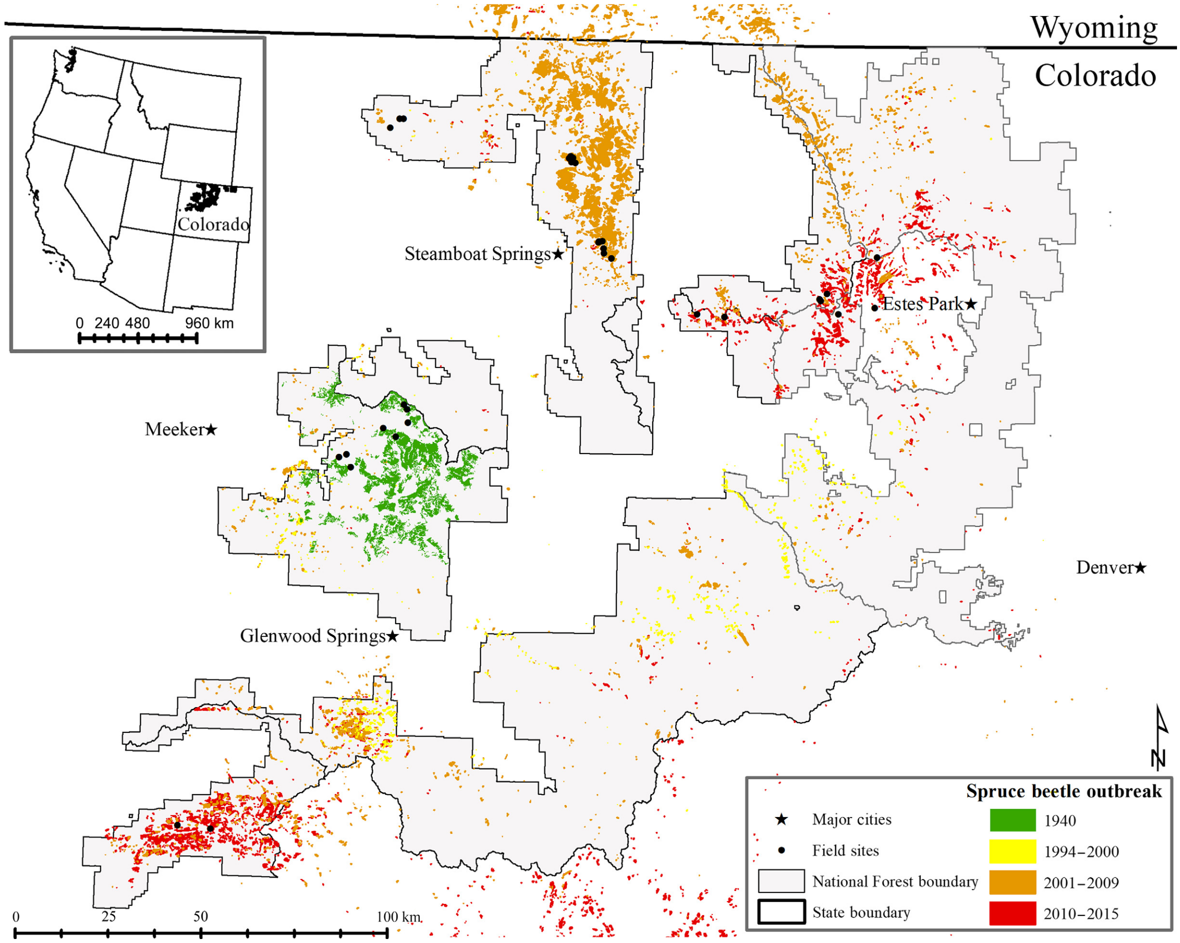

FIG. 1. Locations of fuels site across north-central Colorado, USA, stratified by onset of spruce beetle outbreak.

TABLE 2. Descriptors of the National Forests containing the study sites (based on long-term mean from 1980 to 2014; Colorado Climate Center 2014).

National Forest	Weather station	Elevation (m)	Latitude (°N)	Longitude (°W)	Mean temperature (°C) January	Mean temperature (°C) July	Annual mean precipitation (mm)
Routt	Steamboat Springs	2,090	40.48833	106.82333	−4.1	12.4	608
White River	Meeker	2,380	40.03583	107.90584	−2.4	15.4	416
Arapaho	Gould	2,745	40.50917	106.00556	−6.7	10	603
Grand Mesa	Bonham Reservoir	3,000	39.1025	107.89889	6.5	−6.5	774

beetles in subalpine forests (Schoennagel et al. 2012). Ten variably-sized plots (0.01, 0.02, 0.04 ha, density dependent), were established at each site. Four live and dead canopy trees (total of 40 per stand) were cored in each plot to determine stand age and stand structure, and to verify timing of spruce beetle attack. To verify timing of spruce beetle outbreak, cored trees were chosen according to two criteria: (1) fallen or standing dead spruce that show evidence of spruce-beetle-caused mortality, and (2) live fir or spruce canopy trees that exhibit no signs of spruce beetle damage but that could exhibit growth release corresponding to estimated timing of spruce beetle outbreak.

At each stand, we recorded general site attributes including elevation, aspect, slope (%), canopy density, estimated time since spruce beetle outbreak, and a visual assessment of stand structure (e.g., open vs. dense and single vs. multi-storied canopy). Within each plot, for all trees >4 cm diameter at breast height (DBH), species, position of the tree (standing or fallen), tree height, canopy base height (CBH), and status were recorded. CBH is defined as the height above the ground of the lowest fuel on the individual's main stem above which there is sufficient canopy fuel to propagate fire vertically through the canopy (Reinhardt et al. 2006). Effective crown base height was recorded if adjacent ladder fuels (sapling, seedling, or nearest tree) were lower than CBH and could successfully carry fire into the canopy. Here we define ladder fuels as the three closest individuals (i.e., seedlings, saplings, or trees) to the main stem that could successfully propagate fire from the surface to the crown. Crown ratio was recorded for all standing trees as defined by the ratio of the tree length that is occupied by the crown. Photographs were taken to visually describe each plot.

Surface fuel sampling

Surface fuels.—Following Brown (1974), two litter subplots were established at the 10- and 18-m marks along each of the two transect lines (n = 4). As such, there are four litter subplots per site, and 10 canopy fuels plots in total. Therefore, each of the stand age/time since outbreak category had 40 litter subplots. Data were collected on fuel size, arrangement, and type. Fuels that intercept the transects were tallied as (1) 1-h (<0.6 cm diameter) and 10-h (0.6–2.5 cm diameter) from 0 to 2 m along the transect, (2) 100-h (2.5–8 cm diameter) pieces from 0 to 5 m, and (3) 1,000-h (>7.6 cm) pieces from 0 to 20 m. Additionally, decay class and species were recorded for each intercepted 1,000-h fuel. At 10 m and 18 m along each transect, the depth of fuel bed, litter, and duff, as well as the height and percent cover of live/dead shrubs, grasses, litter, bare ground, and herbs were measured in 1-m^2 plots (Brown 1974).

Saplings.—In each plot, 5 × 1 m subplots were systematically established to tally the number and height of all saplings (<4 cm DBH but >1.4 m tall) by species. The number of subplots was determined such that a minimum of 50 saplings were tallied at each plot (e.g., average five saplings per plot). To account for regeneration heterogeneity within each plot, there was at least one, but no more than three, sapling subplots in any one plot. Subplots were established at equal intervals at the center of the plot.

Seedlings.—In each plot, 2 × 1 m subplots were systematically established to tally the number, species, and height of tree seedlings (<1.4 m tall). The number of subplots was determined such that at least 100 tree seedlings are tallied at each site (i.e., average 10 per plot). There was at least one, but no more than three seedling subplots in any plot. Subplots were established at equal intervals at the center of the plot.

Dendrochronological reconstruction

Tree cores were processed and crossdated according to standard dendrochronological techniques (Stokes and Smiley 1968). Tree rings were counted to determine establishment dates, growth suppressions, and releases (an increase or decrease of ≥125% in mean ring width, respectively, compared to the mean of the previous 10 yr and lasting ≥10 yr; Eisenhart and Veblen 2000, Schoennagel et al. 2012, Smith et al. 2012). All cores from dead trees were quantitatively crossdated using the program COFECHA (Holmes 1983, Grissino Mayer 2001). Cores from live trees for each site were measured to create a master chronology for crossdating the dead trees. Trees that could not be crossdated with statistical confidence were not included in the analysis. Each crossdated series was standardized and fit to a horizontal line to preserve low-frequency trends, which facilitate the detection of a canopy disturbance (Veblen et al. 1991*b*).

Surface and canopy fuels calculation

Surface fuels were calculated following the protocol outlined in Schoennagel et al. (2012). Dry biomass of understory vegetation was estimated by

$$\mathrm{UVB} = \text{percent cover class} \times \text{vegetation height} \times \text{bulk density}$$

where bulk density of shrubs = 1.8 kg/m^3 and herbs and grasses = 0.8 kg/m^3 (Lutes et al. 2006). Total biomass per site of seedlings and saplings was estimated using established regression equations based on species and height (Brown 1978, Brown et al. 1982). Duff and litter fuel loads were derived by

$$\frac{\text{Average Stand Duff Depth}}{\text{Bulk Density}}$$

where bulk density of duff = 139 kg/m^3 (Brown 1974) and litter = 45 kg/m^3 (Lutes et al. 2006). Surface fuel loads of 1, 10, 100, and 1,000-h fuel loads were calculated using regression equations, based on fuel type and time lag, as derived by Brown (1978). We explicitly accounted for sound and rotten 1,000-h fuels by treating them as disparate fuel classes based on relative decay class. All 1,000-h fuels with decay class 1–3 were treated as sound fuels; all 1,000-h fuels with decay class 4–5 were treated as rotten fuels.

For each site, crown masses of foliage and woody fuels were calculated using species-specific equations for subalpine conifers based on DBH, height, and crown length (Brown 1978). Estimated crown mass was used to calculate fuel loads of the tree and stand and available crown fuel load, crown bulk density, and canopy bulk density (Reinhardt and Crookston 2003, Reinhardt et al. 2006). Following Donato et al. (2013), biomass of needle loss was corrected based on a general multiplier of crown needle retention per status class: 1.0, 0.75, 0.25, and 0.0, respectively, for the specific status classes (Table 1). Fuel masses were corrected to represent the true live or dead mass based on the tree status observed in the field. For example, this correction was applied to crown fuel loads for trees with dropped needles by reclassifying the calculated live needle mass, corrected for needle loss, as dead fuel load. ANOVAs with pairwise comparison of the means using the Tukey HSD function were used to test for differences in estimated surface and canopy fuel loads among the eight status classes.

Available crown fuel load (ACFL) was estimated based on the sum of live and dead foliage, plus 50% of the live 1-h fuels and 100% of dead 1-h fuels, across all trees (Donato et al. 2013). Crown bulk density was then estimated for each tree, by dividing by crown length and area sampled (kg/m^3). According to convention, we use crown as a tree-level term and canopy as a stand-level term. Canopy bulk density (CBD) per site was estimated by assigning the crown bulk density value to each 0.25-m increment of each crown, then summing the crown bulk density values within 0.25-m increments across all trees in a stand, then averaging across stands (subplots), to produce vertical profiles of canopy bulk density for each site (Reinhardt and Crookston 2003). Canopy bulk density is estimated as the maximum value of a 3-m running mean of crown bulk density (Reinhardt et al. 2006).

Fine scale spatial heterogeneity of within-stand canopy and surface fuels were assessed using the coefficient of variation (CV) in fuels among subplot measurements (i.e., per tree if canopy or per transect if surface fuel) for each plot (Fraterrigo and Rusak 2008, Donato et al. 2013). The coefficient of variation was computed for within-stand CV for litter and duff, fine surface fuels, sound coarse surface fuels, rotten surface fuels, the vertical canopy column of available crown fuel load (ACFL), and the ACFL of three horizontal strata within the vertical canopy column. Similar to calculating the vertical CBD profile, we binned the ACFL into 0.25-m bins from the surface to crown peak for each tree to produce a vertical within-stand heterogeneity based on the CV. Using this vertical fuel profile, the available crown fuel load heterogeneity was assessed separately for the lower (0–5 m), middle (5–10 m), and upper (>10 m) horizontal canopy strata.

Results

Basal area

Average spruce basal area in young and old stands increased with time since outbreak initiation (Fig. 2). Average live basal area was greatest in old endemic stands (162.94 m^2/ha), which was greater than ($P < 0.0001$) in any stands affected by outbreaks, regardless of stand age (Fig. 2a). Basal area of dead spruce trees with >50% needle retention was greatest in stands affected by recent outbreaks (1990s, 2000s, and 2010s), and declined as time since outbreak increased (Fig. 2b). Average basal areas of dead spruce trees in stands affected by outbreaks in the 1990s (old, 10.16 m^2/ha; young, 16.61 m^2/ha); 2000s (old, 19.89 m^2/ha; young, 14.09 m^2/ha), and 2010s (30.46 m^2/ha) were higher than ($P = 0.0018$) in stands affected by outbreaks in the 1940s (4.46 m^2/ha), 1960s (4.40 m^2/ha), and endemic stands (young, 0.55 m^2/ha; old, 2.16 m^2/ha; Fig. 2b). Basal areas of dead trees with <50% needle retention and >50% 1-h fuels were greatest in the young stands affected by outbreak in the 2010s (74.71 m^2/ha) and were similar to old stands affected by spruce beetle in the 2000s (51.74 m^2/ha), but different ($P < 0.0001$) than all other time since outbreak and stand age classes (Fig. 2c). Basal area of dead trees with <50% needle retention and >50% 1-h fuels for young stands decreased with increasing time since outbreak (Fig. 2c). Old stands were more variable, such that basal area of dead spruce trees in stands affected by spruce beetle outbreak peaks in the 2000s and decreases with increasing time since outbreak (Fig. 2c). Basal area of dead spruce trees with <50% 1-h fuels increased with increasing time since outbreak in old stands, followed by an abrupt decline in stands affected by the 1940s and 1960s outbreaks. Average basal area of old stands affected by outbreak in the 1940s (13.67 m^2/ha) was not different than of endemic old stands (10.79 m^2/ha). Basal area of dead spruce trees that retained <50% of 1-h fuels in the canopy was greatest in old stands affected by spruce beetle in the 1990s ($P < 0.0001$; 63.98 m^2/ha; Fig. 2d). Dead spruce trees that retained <50% of 1-h fuels were less abundant in young stands as compared to old stands ($P < 0.0001$; Fig. 2d).

In all categories of stands, the severity of spruce beetle outbreak was >40% mortality of canopy trees (Appendix S1: Fig. S1). The severity of the 1960s outbreak was lower than that of other outbreaks (41% mortality; Appendix S1: Fig. S1; $P < 0.0001$). Severities of the 1990s and 2010s outbreaks were not different in old and young stands ($P < 0.0001$). Severity of the 2000s outbreak in old stands was not different than the severity of the 1990s outbreak in old stands, but greater than the 2010s outbreak in old stands ($P < 0.0001$; Appendix S1: Fig. S1a). Endemic sites were affected by spruce beetle but at very low levels (16% for old stands, 8% for young stands; Appendix S1: Fig. S1).

Canopy fuel loads

Canopy fuels (all live foliage, and dead 1-, 10-, and 100-h canopy fuels) in old endemic stands were greater ($P < 0.0001$) than in all other time-since-outbreak classes for young and old stands (Fig. 3a, d, g, j). Live canopy fuels were lower in young and old stands affected by outbreaks in the 1990s, 2000s, and 2010s as compared to endemic stands and stands affected by spruce beetle in the 1940s and 1960s. Live 100-h canopy fuels in both young and old stands affected by

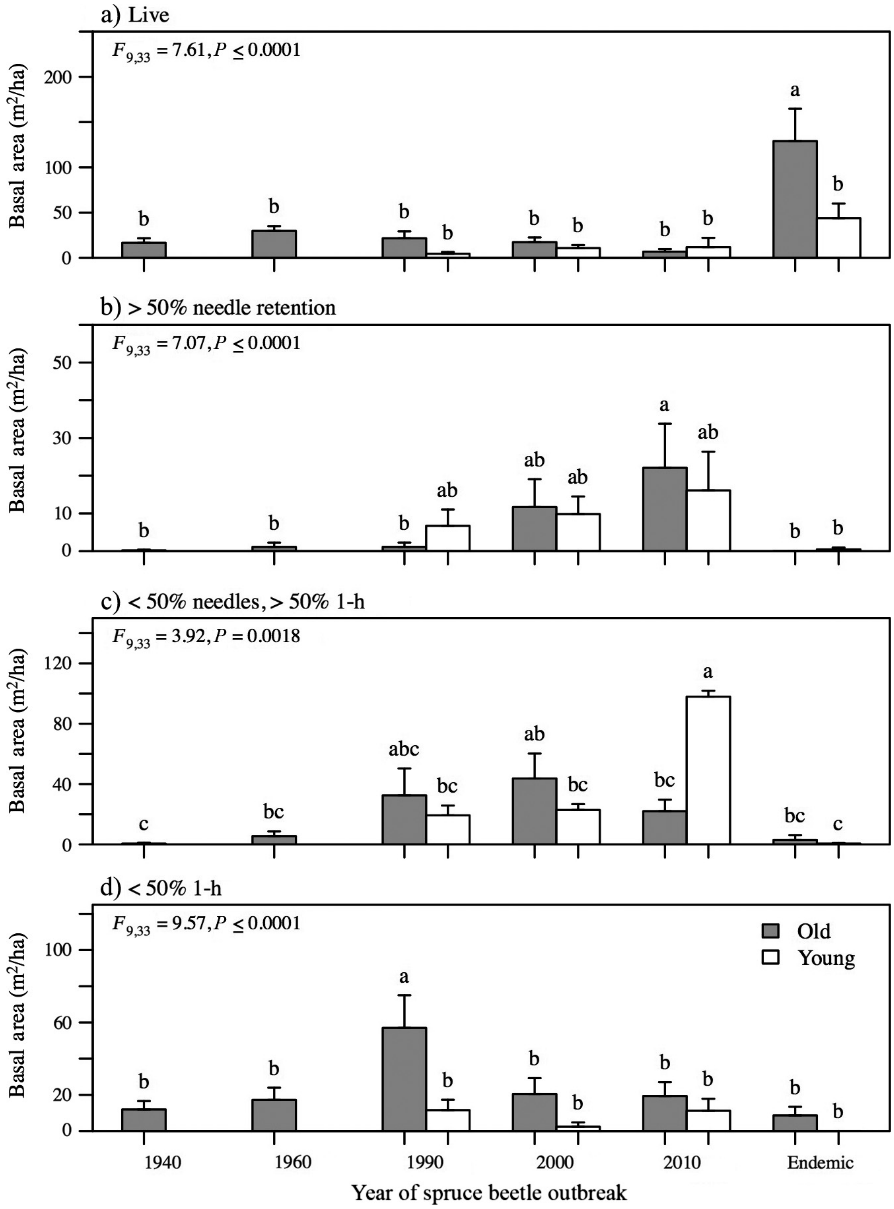

FIG. 2. Comparison of basal area of individuals in classes of (a) live, (b) >50% needle retention, (c) <50% needle retention and >50% 1-h fuels remaining in canopy, and (d) no needles and <50% 1-h remaining among the five spruce beetle outbreaks (1940, 1960, 1990, 2000, 2010, and control sites) stratified by stand age (old and young), with bars representing standard errors. Statistics from ANOVAs are reported in the top left of each graph, with letters indicating significant difference among groups based on Tukey's HSD pairwise comparison of the means.

recent spruce beetle outbreak (1990s, 2000s, and 2010s) were not different among groups ($P > 0.0001$). Within all old stands affected by spruce beetle, live foliage, 1-, and 10-h canopy fuels increased with increasing time since outbreak (Fig. 3a, d, g). Live 100-h canopy fuels increased in old stands affected by spruce beetle as time since outbreak increased until it peaked in stands affected by spruce beetle in the 1960s (Fig. 3j); the live canopy fuels were lower in stands affected by spruce beetle in the 1940s as compared to endemic stands.

Dead canopy foliage in old and young stands affected by spruce beetle increased shortly following outbreak (<4 yr) and decreased with increasing time since outbreak (>4 yr; Fig. 3b, e, h, k). Dead 1-h ($P = 0.0113$; Fig. 3e) and 10-h (Fig. 3h) canopy fuels in stands affected by spruce beetle outbreaks in the 1940s were not different than old endemic fuel loads. Dead 10-h fuels in old stands affected by spruce beetle in the 2010s were greater than in young stands ($P = 0.0037$; Fig. 3e). Dead 1-h fuels were not different ($P = 0.0113$) among any stands affected by outbreaks (Fig. 3e).

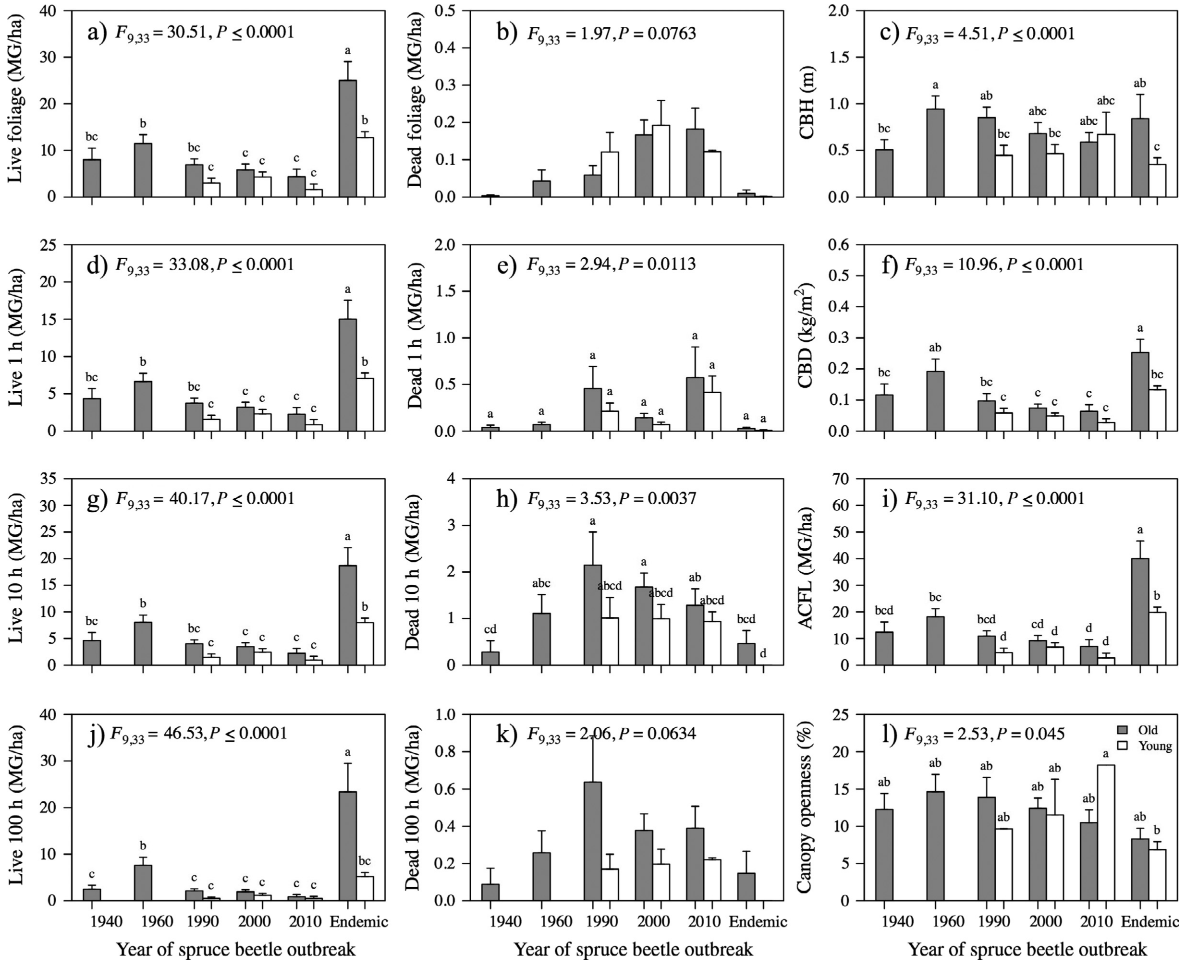

Fig. 3. Comparison of canopy fuels for each spruce beetle outbreak (1940, 1960, 1990, 2000, 2010, and control sites) stratified by stand age (old and young). Bars represent the mean values for each canopy fuel metric, where lowercase letters above the standard error bars indicate significant differences based on the Tukey HSD pairwise comparison of the means ($\alpha = 0.05$). Fuel size classes are standard time-lag classes: 1-h fuels, 0.64 cm diameter; 10-h fuels, 0.64–2.54 cm; 100-h fuels, 2.54–7.62 cm. CBH, Canopy base height; CBD, Canopy bulk density; ACFL, Available crown fuel load.

Canopy base height (CBH) was highest among old stands and lowest among young stands (Fig. 2c). CBH of old stands doubled (0.58–0.94 m) up to 50 years following initial spruce beetle outbreak (Fig. 3c). CBH increased in young stands affected by spruce beetle outbreak in 2010 as compared to young endemic stands, but decreased in stands affected by spruce beetle in the 2000s and 1990s (0.67–0.45 m). CBH of old stands affected by spruce beetle in the 1940s dropped below any previously observed old stand CBH, regardless of spruce beetle outbreak (Fig. 3c).

Available crown fuel load (ACFL) was lower ($P < 0.0001$) in stands more recently affected by outbreaks (1990, 2000, and 2010) as compared to stands affected by spruce beetle outbreaks in the 1940s and 1960s and old endemic stands (Fig. 3i). ACFL was lower in young stands affected by spruce beetle as compared to old stands affected by spruce beetle. Old and young endemic stands had the greatest ACFL as compared to all stands affected by spruce beetle outbreaks (Fig. 3i). ACFL of old stands recently affect by spruce beetle (in the 1990s, 2000s, 2010s) increased with increasing time since outbreak ($P < 0.0001$). Stands affected by spruce beetle outbreaks in the 1940s and 1960s and young endemic stands all had similar ACFL means, 20.15, 23.41, 22.87 Mg/ha, respectively, all of which were lower ($P < 0.0001$) as compared to old endemic stands (45.10 Mg/ha).

Canopy bulk density (CBD) was lowest among spruce beetle affected stands as compared to endemic stands of similar stand age ($P < 0.0001$). CBD was greatest in old endemic stands (0.33 kg/m^2). CBD in old stands affected by spruce beetle outbreaks (1940s, 0.19 kg/m^2) trended toward young endemic CBD loads (0.16 kg/m^2) with increasing time since outbreak (Figs. 3f, 4a,b).

There was an inverse relationship of canopy openness in young vs. old stands (Fig. 3l), such that young stands significantly decreased in canopy openness with

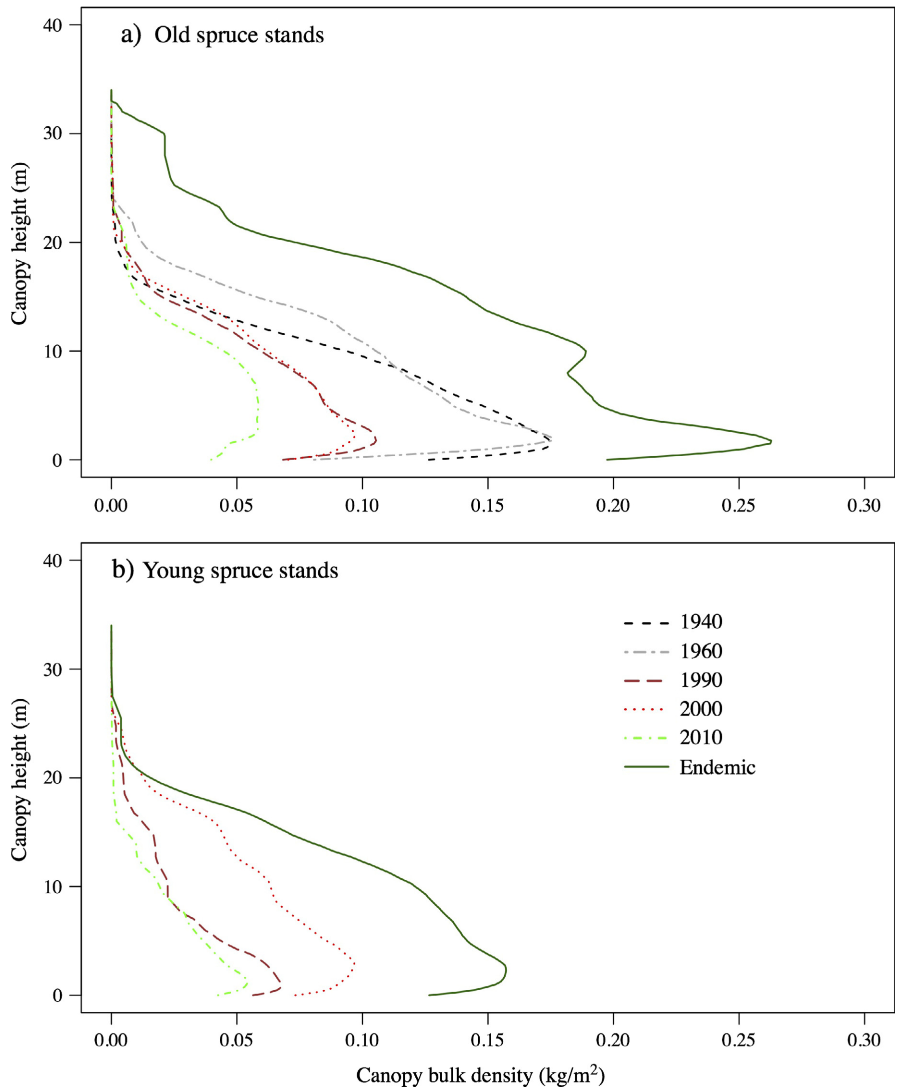

FIG. 4. Vertical profiles of available canopy fuels in (a) old and (b) young spruce–fir stands. Fuel profile classes are spruce beetle outbreaks from the 1940s, 1960s, 1990s, 2000s, 2010s, and endemic populations.

increasing time since outbreak, trending toward canopy closure typical of endemic stands. Old stands increased in canopy openness with increasing time since outbreak (P = 0.0450).

Sapling fine fuels (e.g., foliage, 1-, 10-, and 100-h) were greatest in stands affected by spruce beetle in the 1940s as compared to all other time-since-outbreak and stand age classes (Appendix S1: Fig. S2a–c). Old endemic and young and old stands affected by spruce beetle outbreaks in the 2010s all had similar sapling fine fuels and sapling densities ($P > 0.0001$). Coarse 1,000-h sapling fuels in old stands decreased over the first 20 years after outbreak, followed by a gradual increase with increasing time since outbreak (Appendix S1: Fig. S2e). Though sapling coarse fuels were greatest in stands affected by spruce beetle in the 1940s, the density of saplings was not different than those in stands affected by spruce beetle in the 1960s, 1990s (both young and old), young 2000s, and young endemic sites ($P > 0.0001$; Appendix S1: Fig. S2f). Following related studies (Schoennagel et al. 2012, Donato et al. 2013) we did not collect data on shrub and grass infill, and instead only evaluated how tree species affect fuel load arrangements.

Surface fuels

Coarse fuels.—The general structure of old stands is characteristic of the old-growth developmental stage described by Oliver and Larson (1996), where the canopy is multi-tiered and uneven in age and the subcanopy is heterogeneous in the type and quantity of woody material. Coarse surface fuels in old stands were

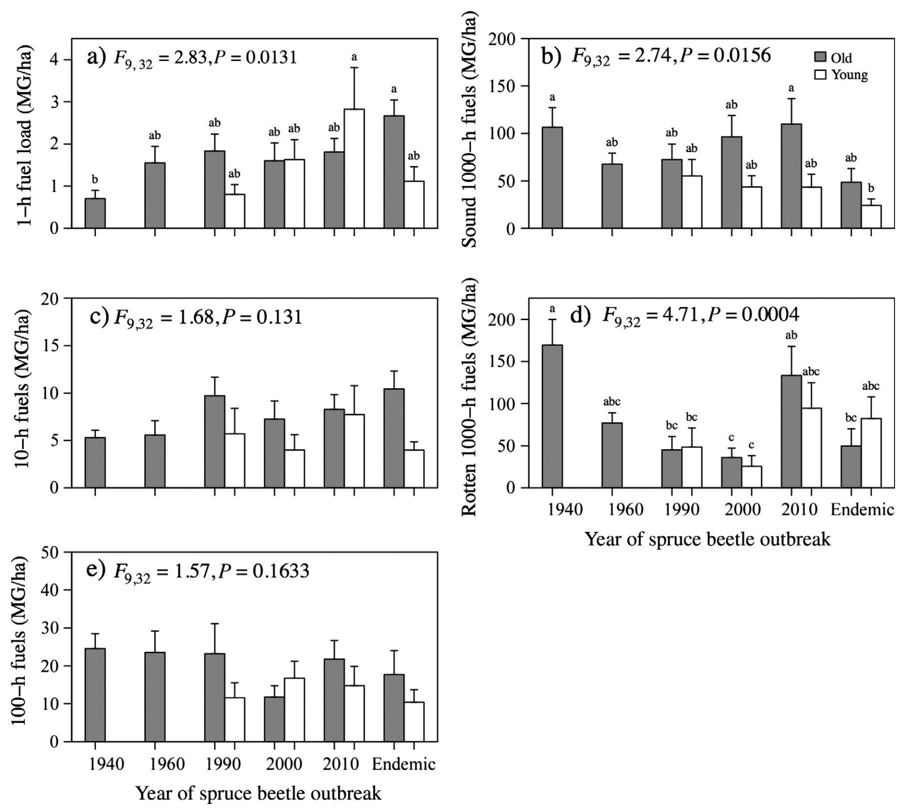

FIG. 5. Comparison of coarse surface fuels for each spruce beetle outbreak (1940, 1960, 1990, 2000, 2010, and control sites) stratified by stand age (old and young). Bars represent the mean values for each surface fuel metric, where lowercase letters above the standard error bars indicate significant differences based on the Tukey HSD pairwise comparison of the means (α = 0.05). Different letters above the bars indicate statistically significant differences among groups. Fuel size classes are standard time-lag classes: 1-h fuels, 0.64 cm diameter; 10-h fuels, 0.64–2.54 cm; 100-h fuels, 2.54–7.62 cm; 1,000-h fuels, >7.62 cm.

variable across time since outbreak, but showed consistent trends among different fuel sizes (Fig. 5). The 1- and 10-h (finer) coarse fuels decreased in abundance with increasing time since outbreak in both old and young stands. Particularly for old stands, endemic sites and stands affected by spruce beetle in the 1940s differed greatly (P = 0.0131); 1-h fuel loads (2.66 Mg/ha) were highest in endemic sites, and lowest in stands affected by the 1940s outbreak (0.70 Mg/ha). Sound 1,000-h fuels in young stands affected by spruce beetle were lower compared to endemic stands (P < 0.0156). Rotten 1,000-h fuel loads were greatest in stands affected by the 1940s outbreak, and were different than all other age and time-since-outbreak classes (P < 0.0004). Rotten 1,000-h fuels increased as time since outbreak increased (P = 0.0004; Fig. 5e).

Fine fuels.—Fine surface fuels were highly variable among time since outbreak and stand age classes (Fig. 6a, c, e). Duff was greatest in the old stands affected by 2010s outbreak (8.35 cm) and significantly different than all age and time-since-outbreak classes (P = 0.0016; Fig. 6a). Duff depths in stands affected by the 1940s outbreaks were similar to depths in old endemic stands (1940s, 2.96 cm vs. endemic, 4.50 cm). Litter depths were greatest in old stands affected by the 1940s and 1960s spruce beetle outbreaks and lowest in young stands affected by the 1990s and 2000s spruce beetle outbreaks (Fig. 6c). Old and young stands affected by spruce beetle in the 2010s had greater litter loads than stands affected by spruce beetle in the 1990s and 2000s and endemic stands (P = 0.0018). Overall fuel bed depths decreased consistently in old and young stands affected by spruce in the 2010s, 2000s, and 1990s; followed by a rapid increase in stands affected by spruce beetle in the 1940s and 1960s (Fig. 6e). Grass and herbaceous biomass in both old and young stands was lower soon after outbreak (2010s) as compared to endemic sites. As time since outbreak increased, grass and herbaceous biomass doubled and stabilized after 30 years after outbreak (Fig. 6b). Shrub biomass was greatest in young stands affected by spruce beetle in the 2010s (Fig. 6d).

Fine scale heterogeneity in fuels

Within-stand coefficients of variation (CV) indicated increased canopy heterogeneity as time since outbreak increased in both young and old stands (Fig. 7a–h). CV

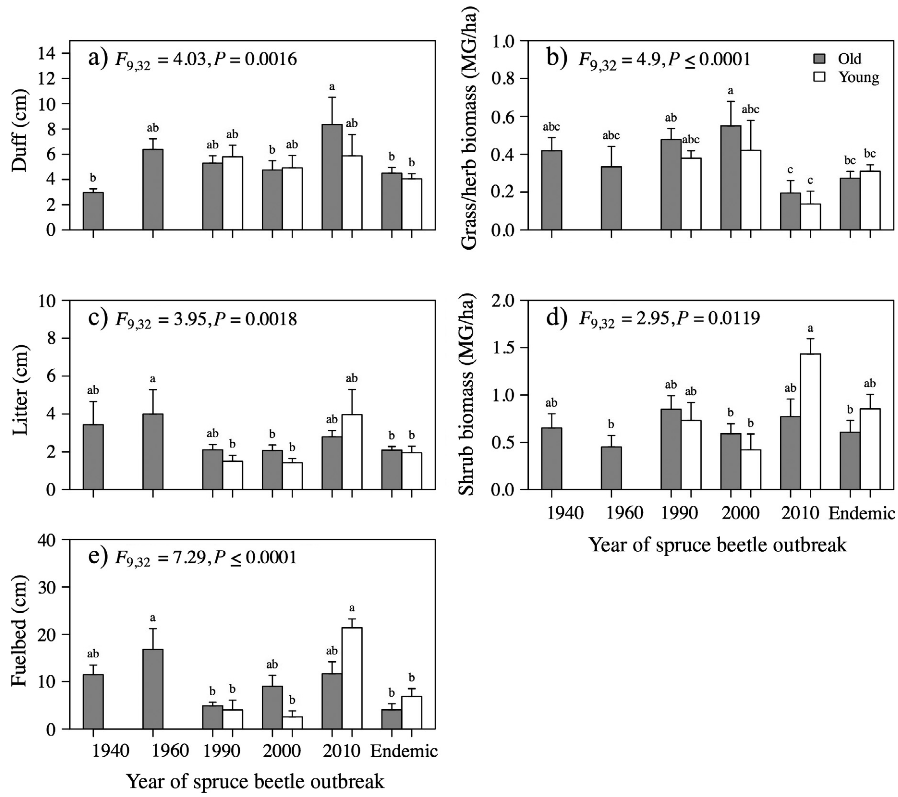

FIG. 6. Comparison of fine surface fuels for each spruce beetle outbreak (1940, 1960, 1990, 2000, 2010, and control sites) stratified by stand age (old and young). Bars represent the mean values for each surface fuel metric, where lowercase letters above the standard error bars indicate significant differences based on the Tukey HSD pairwise comparison of the means (α = 0.05). All ANOVA statistics are reported in the top left of each graph.

was lowest in old and young endemic stands across the horizontal stratum and vertical canopy column (Fig. 7a–h). Available crown fuel in the lower (P = 0.0169) and upper canopy (P = 0.0013) stratum varied most in young stands affected by 2010s spruce beetle outbreak (Fig. 2e, g). Vertical heterogeneity increased with time since outbreak among both young and old stands as compared to endemic stands (Fig. 7d, h).

Within-stand variation of surface fuels increased in heterogeneity with time since outbreak, but no differences were significant (P > 0.113; Fig. 7i–p). Surface heterogeneity of fine and sound coarse fuels in old stands followed a bell-shaped progression, peaking 20–30 years following outbreak (Fig. 7j, k). Sound coarse fuels in stands affected by spruce beetle outbreaks in the 1960s and 1940s peaked in heterogeneity (Fig. 7k) due to beetle-killed snag-fall and spatial fragmentation at the stand scale.

Discussion

The current study shows that the effects of spruce beetle outbreaks on forest structure, and hence on fuel profiles, are strongly contingent on pre-outbreak conditions as determined by pre-outbreak disturbance history. In both young and old stands, the most significant effect of spruce beetle outbreaks during the 20th and 21st century was a decrease in canopy fuels and an increase in spatial heterogeneity of canopy fuels following outbreak. Importantly, the decrease in canopy fuels following outbreaks was greater in young post-fire stands than in older stands, suggesting that spruce beetle outbreaks more substantially reduce risk of active crown fire when they affect stands in earlier stages of development. These findings highlight the importance of pre-outbreak stand history and stand structure in modulating the effects of disturbances on fuel profiles.

Canopy fuels

Our findings are consistent with studies of lodgepole pine (Page and Jenkins 2007, Klutsch et al. 2009, Schoennagel et al. 2012), Douglas-fir (Donato et al. 2013), and Engelmann spruce (Derose and Long 2009, Jorgensen and Jenkins 2011, Hansen et al. 2016) forests that found reduced canopy bulk density and fewer live canopy individuals following bark outbreaks. Canopy bulk density (CBD) is critically important in shaping fire regimes and fire behavior because it governs (1) how

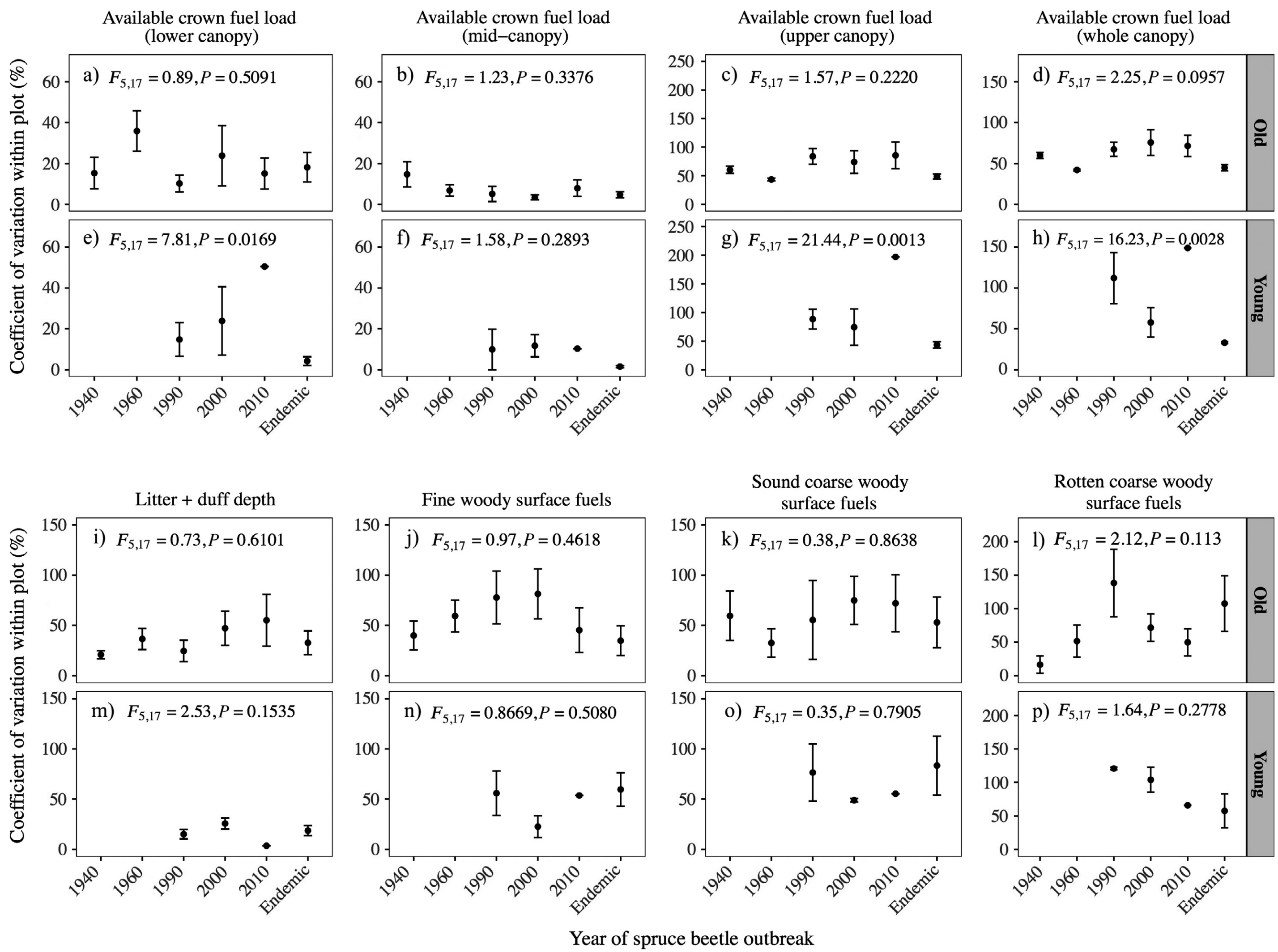

FIG. 7. Within-stand spatial heterogeneity of canopy and surface fuels for each age and time since outbreak class (data are mean ± SE). Horizontal canopy stratum of available crown fuel load are shown for the lower (<5 m), middle (5–10 m), and upper (>10 m) canopy layers for both old (a, b, c) and young (e, f, g) stands. The vertical dimension depicts available crown fuel load variation among 0.25-m canopy increments (d, h). Surface fuel variation was aggregated by size class and fuel quality (i–p) (fine woody fuels are those with 1–100-h particles [<7.6 cm]; coarse woody fuels comprise all 1,000-h particles [>7.6 cm]). Statistical outputs are the results from one-way ANOVAs between the fuel characteristic and outbreak year for both young and old stands.

much material can be consumed to sustain active crown fires and (2) the overall canopy continuity of aerial fuels for horizontal movement of fire. In the current study, pre-outbreak CBD was lower in young stands compared to older stands, which is consistent with characteristic fuel development across stages of stand development. These pre-outbreak differences contributed to the effect of outbreaks. Our data also show that spruce beetle outbreaks increased canopy heterogeneity of both young and old stands. Interestingly, the net effect of spruce beetle outbreak on the heterogeneity and continuity of canopy fuels is greater in young as compared to old stands (Fig. 7).

Previous work in northwestern Colorado has found that spruce beetle outbreaks do not increase fire occurrence (Bebi et al. 2003), extent (Kulakowski et al. 2003, Kulakowski and Veblen 2006*a*), or severity (Bigler et al. 2005). Similarly, outbreaks of mountain pine beetle have been found to not increase fire occurrence (Hart et al. 2015*a*, Mietkiewicz and Kulakowski 2016) or severity (Meigs et al. 2016), likely due to the dominant effects of reduced canopy fuels following outbreaks (Black et al. 2013, Stalling et al. 2017). In this context, our research suggests that the effect of spruce beetle outbreaks on reducing canopy fuels is most pronounced in stands in early stages of development and more generally, that pre-outbreak stand structure, as shaped by pre-outbreak disturbances, modulates the effect of spruce beetle outbreaks on canopy fuels and, possibly, crown-fire potential. Very low mean CBD and density of live canopy trees in young stands affected by outbreak (Fig. 4) translates to (1) less fine flammable materials in the crown to promote and sustain fire and (2) less canopy connectivity to facilitate fire spread across the crown, thus effectively lowering the potential for active crown fire (Reinhardt and Crookston 2003, Reinhardt et al. 2006).

Our data also show that the heterogeneity of available crown fuel load (ACFL) within the vertical column and horizontal stratum increase with time since outbreak, likely due to survivorship of subalpine fir and advanced regeneration of sub-canopy individuals that survived the outbreak. This spatial intermixing of live and dead crowns may be important for fine-scale fire behavior such as individual tree torching, though the effect is variable and contingent on tree and site condition, including weather and biophysical setting.

Surface fuels

Surface 1-h fuels and 1,000-h fuels and ground litter/fuel bed varied significantly across the chronosequence of spruce beetle outbreaks and stand ages. Fine surface fuels in young stands were three times higher during the three decades (<30 yr) following spruce beetle outbreak, after which the abundance of these fuels decreased to below endemic levels. These findings are consistent with studies in lodgepole pine forests affected by mountain pine beetle (Pelz and Smith 2012, Schoennagel et al. 2012) that reported increases in fine fuels directly following bark beetle attack. In both young and old stands, the increase in fine fuels (1-, 10-, 100-h fuels) soon after outbreak, followed by a sharp decrease with time since outbreak, can be explained by the fall of fuels from killed trees and its gradual decomposition.

Solid 1,000-h fuels were more abundant in stands affected by outbreak as compared to endemic stands, though as time since outbreak increased, solid 1,000-h fuels increased in young stands but decreased in old stands. This trend is likely due to the generally smaller bole size and fewer large fallen logs in younger stands (e.g., Donato et al. 2013). While rotten 1,000-h fuels were greatest in stands unaffected by outbreaks (endemic stands) and stands affected by the 2010s outbreak, these fuels were >60% lower in stands affected by outbreaks in the 2000s but much higher in stands affected by outbreaks in the 1990s. As the rate of fall of large fuels is slow (1.3–1.5% per year (Schmid and Hinds 1974); >50 yr this study), this variation may suggest that the abundance of coarse fuels during the initial decades following outbreak is largely controlled by underlying stand heterogeneity, rather than the effects of outbreaks. The largest fuels (i.e., 1,000-h fuels) were most abundant in old stands (that did not burn in the 19th century), independent of year of outbreak (Fig. 5b), which is expected for stands in later stages of development. These coarse fuels are especially important in increasing potential fireline intensity at the flaming front of a wildfire, yet only few studies have attempted to model the effects of coarse 1000-h fuels on wildfire behavior (e.g., Schoennagel et al. 2012, Donato et al. 2013, Keane et al. 2015). More importantly, our results suggest that the spatial heterogeneity of 1,000-h coarse fuels peak at >50 yr following epidemic beetle outbreak, yet modeling studies that have incorporated 1,000-h fuels into their fireline intensity calculations have been based only on shorter chronosequences. Therefore, modeling studies conducted on disturbance interactions should account for the continuum of landscape disturbance legacies, including long-term forest development following disturbances.

Conclusions

The most significant effect of spruce beetle outbreaks during the 20th and 21st centuries was a decrease in canopy fuels and increase in spatial heterogeneity of canopy fuels in affected stands. In contrast, surface fuel loads were more variable with increased time since outbreak and did not return to pre-outbreak conditions during the period considered in this study. Importantly, reductions in canopy fuels were most pronounced in younger post-fire stands than in older stands. The current study shows that the effects of outbreaks on fuels are highly contingent on pre-outbreak stand structure, which is largely shaped by long-term disturbance history. Although outbreaks reduce canopy fuels in all stands, this effect is relatively minor in old spruce–fir stands. In contrast, the potential for outbreaks to reduce canopy fuels that may reduce the probability of active crown fires is greater in young post-fire spruce–fir stands. Pre-outbreak disturbance legacies have long-term effects that modulate subsequent disturbance interactions.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1661/full

Data Availability

Data available from Github: https://doi.org/10.5281/zenodo.1043606