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Beyond red crowns: complex changes in surface and crown fuels and their interactions 32 years following mountain pine beetle epidemics in south-central Oregon, USA

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Abstract

Background: Mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB), a bark beetle native to western North America, has caused vast areas of tree mortality over the last several decades. The majority of this mortality has been in lodgepole pine (*Pinus contorta* Douglas ex Loudon) forests and has heightened concerns over the potential for extreme fire behavior across large landscapes. Although considerable research has emerged concerning influence of MPB on forest fuels, there has been little work in the climax lodgepole pine forests of south-central Oregon, USA. Specifically, we assessed changes in forest structure and crown and surface fuels across a chronosequence of time since mountain pine beetle (TSB) epidemics in south-central Oregon (1979 to 2008).

Results: We classified four distinct periods in which significant changes occur in fuels: overstory mortality stage (2 to 4 years TSB), standing snag and snag fall stage (5 to 13 years TSB), regeneration stage (14 to 25 years TSB), and overstory recovery stage (26 to 32 years TSB). Multivariate analyses indicated changes in crown fuels and forest structure following MPB epidemics were driven primarily by basal area of live and standing dead trees, canopy bulk density, canopy base height, and canopy height. Substantial declines in canopy bulk density occurred early (2 to 5 yrs) following beetle activity and slowly recovered over time. The pattern of succession of surface fuels following a MPB epidemic was largely determined by changes over time in 10-h, 100-h, and 1000-h fuel loads, in addition to increasing fuel bed depth. The 100-h fuel load increased over the entire 30-year period, while 1000-h fuel load reached an asymptote 14 to 26 years following epidemic initiation. Live woody fuels increased through the initial overstory mortality stage and began to decrease during the overstory recovery stage.

Conclusions: Our key findings concerning changing fuels and forest structure following a MPB epidemic in south-central Oregon lodgepole pine forests include: 1-h fuels and litter changed little over time, surface fuel loads changed dramatically between the standing snag and the regeneration stages, lodgepole pine remained dominant, and canopy bulk density was low throughout the chronosequence. These factors point to the perpetuation of a lodgepole pine dominated system with a mixed-severity fire regime well into the future.

Keywords: bark beetles, *Dendroctonus ponderosae*, fuels, lodgepole pine, *Pinus contorta* var. *murrayana*

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Resumen

Antecedentes: El escarabajo del pino montaña (*Dendroctonus ponderosae* Hopkins; MPB), un escarabajo de la corteza nativo del oeste de Norteamérica, ha causado la mortalidad de árboles en vastas áreas durante las últimas décadas. La mayoría de esta mortalidad ha sido en bosques de pino contorta (*Pinus contorta* Douglas ex Loudon), lo que ha aumentado la preocupación por su potencial de generar incendios de comportamiento extremo a través de grandes paisajes. Aunque muchas investigaciones han surgido concernientes a la influencia de MPB sobre los combustibles forestales, muy pocos trabajos se han realizado en los bosques climáxicos del centro-sur de Oregón, EEUU. Específicamente, determinamos cambios en la estructura del bosque y en los combustibles de la corona y superficiales a través de una crono-secuencia desde la ocurrencia de epidemias de escarabajo del pino de montaña (TSB) en el centro-sur de Oregón (1979 a 2008).

Resultados: Clasificamos cuatro períodos distintos en los cuales ocurrieron cambios significativos en los combustibles: el período de mortalidad del dosel superior (2 a 4 años TSB), el período de muerto en pie y caído (5 a 13 años TSB), el período de regeneración (14 a 25 años TSB), y el período de recuperación del dosel superior (26 a 32 años TSB). Los análisis multivariados indicaron que los cambios en los combustibles de la corona y en la estructura del bosque después de una epidemia de MPB ocurrieron primeramente en el área basal de árboles vivos y muertos en pie, en la densidad de la masa del dosel, en la altura de la base del dosel, y en la altura del dosel. Una sustancial declinación en la densidad de la masa del dosel ocurrió tempranamente (2 a 5 años) después de la actividad del escarabajo y se recuperó lentamente con el tiempo. El patrón de la sucesión de combustibles superficiales después de una epidemia de MPB fue largamente determinado por los cambios en la carga de combustibles de 10, 100, y 1000 horas, en adición a un incremento en la profundidad de la cama de combustible. La carga de los combustibles de 100 h se fue incrementando durante el período de 30 años, mientras que los combustibles de 1000 h alcanzaron una asíntota entre 14 y 26 años después del inicio de la epidemia. Los combustibles vivos leñosos se incrementaron desde la mortalidad inicial del dosel y comenzaron a decrecer durante el período de recuperación del dosel.

Conclusiones: Nuestros descubrimientos clave concernientes a los cambios en los combustibles y en la estructura del bosque luego de una epidemia de MPB en bosques de pino contorta en el centro-sur de Oregón incluyen: a) los combustibles de 1 h y la broza cambiaron muy poco a través del tiempo; b) la carga de combustibles superficiales cambió dramáticamente entre los períodos de muerto en pie y de regeneración; c) el pino contorta permanece como especie dominante; y d) la densidad de la masa del dosel fue baja durante toda la crono-secuencia. De cara al futuro y con un régimen de fuegos de severidad mixta, estos factores apuntan a la perpetuación del sistema dominado por pino contorta.

Background

Bark beetles (Coleoptera: Curculionidae, subfamily Scolytinae), especially mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB), are important mortality agents in North American coniferous forests (Negron et al. 2008; Raffa et al. 2008). Over the past several decades, MPB has caused mortality on over 30 million ha of lodgepole pine (*Pinus contorta* Douglas ex Loudon) forests in the western United States and Canada (Raffa et al. 2008), which has raised concerns about potential for extreme fire behavior following this widespread mortality (Page et al. 2014). Fire behavior is driven in part by forest structure and fuels characteristics; the influence of MPB on forest structure and fuels has become the focus of intense study due to differing hypotheses of potential effects on fire behavior (Hicke et al. 2012; Jenkins et al. 2014; Perrakis et al. 2014). Mountain pine beetle has been a cyclical and natural disturbance across lodgepole pine forested landscapes for as long as records indicate (Roe and Amman 1970). However, the spatial and temporal scales of recent epidemics are unprecedented over the last 100 years (Bentz et al. 2009, Raffa et al. 2008, Brown et al. 2010, Edburg et al. 2012, Kautz et al. 2017).

Previous work in lodgepole pine forests has shown that the influence of MPB epidemics on fuels and forest structure is related to stand density and the proportion of lodgepole pine within a stand at the time of the outbreak (influenced by productivity), the proportion of lodgepole pine in larger diameter classes, and time since previous mortality events (Roe and Amman 1970; Klutsch et al. 2011; Hicke et al. 2012; Jenkins et al. 2014). The period of elevated MPB activity may last from a couple of years to a decade in a given stand (Cole and Amman 1980; Hansen 2014). During epidemics, up to 90% of the largest trees can be killed, leaving primarily intermediate and suppressed trees (Cole and Amman

1980). Throughout many of the lodgepole pine systems previously studied, changes in species composition and structure post outbreak are driven by presence or absence of non-host species such as subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), mountain hemlock (*Tsuga mertensiana* [Bong.] Carrière) or Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) (Collins et al. 2011; Diskin et al. 2011; Kayes and Tinker 2012; Pelz and Smith 2012; Pelz et al. 2015).

In general, changes to the structure of crown fuels, surface loadings of fine fuels, and loadings of coarse woody material are the major effects of MPB epidemics on lodgepole pine forests (Jenkins et al. 2014). The various phases of structural changes through time have been previously referred to as "red," "gray," and "old" stages (Edburg et al. 2012; Hicke et al. 2012). The time necessary for a stand to progress through these stages varies across the species distribution (Jenkins et al. 2008; Hicke et al. 2012). During the red stage, a proportion of the tree crowns in the canopy have dead and dying foliage. Canopy bulk density drastically decreases through the red stage as dead foliage falls from trees (Simard et al. 2011; Hicke et al. 2012). This stage is relatively short-lived (2 to 4 yrs) and few other forest structural attributes change over this brief time period. Within a few years, the forest enters the gray stage and litter depths, fine fuel loadings, and herbaceous plant and shrub cover may increase (Page and Jenkins 2007; Collins et al. 2012). Coarse woody debris may also increase in the gray stage as branches and snags begin to fall (Mitchell and Preisler 1998; Hicke et al. 2012). The old stage is characterized by a shift in coarse woody fuel loadings as snags fall, generally 10 to 20 years following MPB attack. Growth of advanced regeneration may lead to increased canopy bulk density during this stage and decreased canopy base height. However, depending on stand structure and intensity of MPB-caused mortality, it may take decades for canopy (*i.e.,* canopy closure and canopy bulk density) to recover to pre-epidemic conditions (Hicke et al. 2012). The coarse fuel load on the forest floor may remain high for many decades while growth of shrubs and conifer regeneration create ladder fuels (Page and Jenkins 2007; Jenkins et al. 2008; Hicke et al. 2012).

In south-central Oregon, Aerial Detection Survey (ADS) data collected since 1980 (USDA Forest Service 2010) indicate the extent MPB-caused lodgepole pine (*Pinus contorta* var. *murrayana* [Greville & Balfour] Engelmann) mortality peaked in 1986 when more than 500 000 ha were detected with varying levels of MPB activity (Fig. 1). MPB activity peaked again in 2008, with over 160 000 ha of affected area detected. Although MPB epidemics are common in this region, research regarding changes in fuels and forest structure following MPB epidemics has focused on the seral lodgepole pine forests of the Intermountain West (*e.g.,* Page and Jenkins 2007; Klutsch et al. 2011; Pelz and Smith 2012). In contrast to most other lodgepole pine forests, the *Pinus contorta* var. *murrayana* zone of south-central Oregon is a unique setting because lodgepole pine is an edaphic and topoedaphic climax occurring on both well drained and poorly drained pumice soils, associated with broad depressions in the landscape where cold air pools (Franklin and Dyrness 1973).

Lodgepole pine forests in this region are often single species, low productivity, largely uneven-aged stands, and are best characterized as having a mixed-severity fire

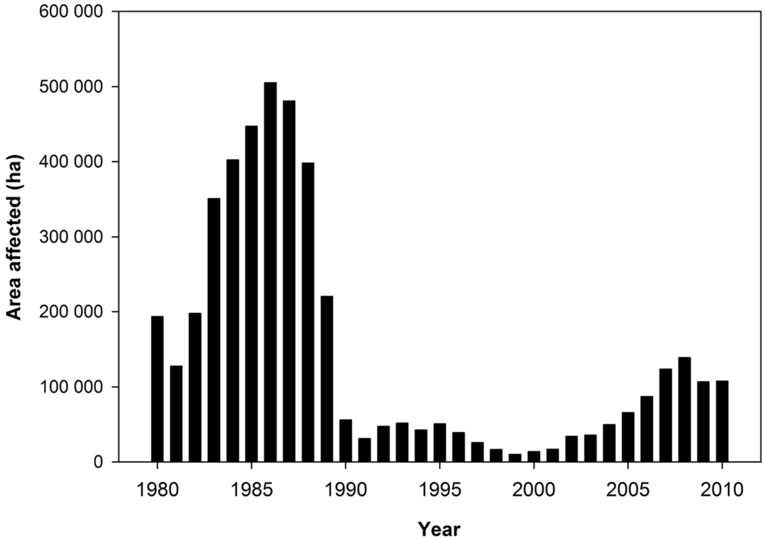

Fig. 1 Area affected by mountain pine beetle by year of mountain pine beetle epidemic initiation from 1980 to 2010 on the Deschutes and Fremont-Winema national forests, Oregon, USA, where climax lodgepole pine occurs, derived from ADS data (USDA Forest Service 2010)

regime, which may be fuel limited at various stages in forest development between fires (Geiszler et al. 1980, Gara et al. 1985, Agee 1993; Heyerdahl et al. 2014). In contrast, those of the Rocky Mountains, USA, often exist as single-aged stands that are characterized by a stand-replacing fire regime in which climate, rather than fuels, is limiting (Romme 1980; Schoennagel et al. 2004). Historical fire return intervals for the lodgepole pine forests of the Fremont-Winema National Forest, Oregon, have been estimated to range between 60 and 350 years (Stuart 1983). Agee (1981) estimated historical fire return intervals farther west in Crater Lake National Park, Oregon, at 60 years. Recent research by Heyerdahl et al. (2014) has corroborated the existence of a mixed-severity fire regime in dry lodgepole pine on an area of the Deschutes National Forest, Oregon, indicating historical fire return intervals of 26 to 82 years. Lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.) is prevalent in the lodgepole forest type in south-central Oregon and has been shown to strongly influence stand structure and fuels following an MPB epidemic (Agne et al. 2014; Shaw and Agne 2017). Cone serotiny is not common in lodgepole pine in south-central Oregon (Lotan and Critchfield 1990); therefore, the interaction of fire, bark beetles, and lodgepole pine seed reproduction may be significantly different than in areas of the Intermountain West where cone serotiny frequently occurs (Schoennagel et al. 2003). The lack of cone serotiny helps to define pre-MPB forest structure by providing consistent seed release without a need for fire to initiate regeneration. The lodgepole pine forests of south-central Oregon may be similar to other edaphic climax lodgepole pine forests including: lodgepole pine forests in the Bighorn Mountains in Wyoming, USA (Despain 1973); the Wind River Mountains, Wyoming (Reed 1976); as well as those found on obsidian sands near West Yellowstone, Montana, USA (Pfister et al. 1977). Little is known about the short- and long-term changes in fuels and forest structure following MPB epidemic in climax lodgepole pine forests.

To elucidate whether there were novel changes to fuels and forest structure in climax lodgepole pine types in this region compared with other lodgepole pine systems, we addressed the following two questions specifically for the lodgepole pine forests of south-central Oregon: 1) how do fuel profiles (ground, surface, ladder, and crown fuels) change over time in response to MPB epidemics? and 2) what are the key fuels and forest structure components that drive change over time? In order to reconstruct stand development and resultant ground, surface, ladder, and crown fuels following MPB epidemics and address these questions, we applied a retrospective approach using a space for time (chronosequence) study design.

Methods

Study area

The study area was located in the *Pinus contorta* zone (Franklin and Dyrness 1973) of central and south-central Oregon in the Eastern Cascades Slopes and Foothills ecoregion (Omernik 1987) on the Deschutes and Fremont-Winema national forests, Oregon, USA (Fig. 2). Stand structure varied from low density, open canopy conditions on drier, less productive sites to closed canopy conditions composed of larger trees with substantial regeneration on moist, higher productivity sites (Mowat 1960). Overstory tree species were dominated by lodgepole pine with other conifer species present in minor amounts (Fig. 3). Associated tree species also varied by elevation, and included ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.) at lower elevations, Engelmann spruce in moist cold flats, and subalpine fir, western white pine (*P. monticola* Douglas ex D. Don), and whitebark pine (*P. albicaulis* Engelm.) at higher elevations. Elevation within the study area ranged from approximately 1450 m to 2500 m and temperatures ranged from an average daily minimum of −3 °C to an average daily maximum of 27 °C. Annual precipitation, occurring mainly in the form of snow, ranged from 250 mm in the eastern portion of the study area to 2800 mm at the highest elevations (PRISM Climate Group 2013).

Understory vegetation varied with site productivity, but sites were generally characterized by persistent coarse woody debris; a significant bare ground component; and a mix of sedges, grasses, and shrubs. The most common shrubs included low-growing antelope bitterbrush (*Purshia tridentata* [Pursh] DC.), wax currant (*Ribes cereum* Douglas), yellow rabbitbrush (*Chrysothamnus viscidiflorus* [Hook.] Nutt.), and pinemat manzanita (*Arctostaphylos nevadensis* A. Gray). Herbs included Virginia strawberry (*Fragaria virginiana* Duchesne) and silvery lupine (*Lupinus argenteus* Pursh). Long-stolon sedge (*Carex inops* L.H. Bailey), Ross' sedge (*C. rossii* Boott), and grasses such as western needlegrass (*Achnatherum occidentale* [Thurb.] Barkworth) and Idaho fescue (*Festuca idahoensis* Elmer) were generally common.

Sampling design

We sampled from a 30-year post-MPB-attack chronosequence (1979 to 2008) in climax lodgepole pine forests of south-central Oregon based on previously developed plant associations (Hopkins 1979; Volland 1985; Simpson 2007) and ADS data, ultimately creating a 2- to 32-year chronosequence of time since beetle (TSB; see Additional file 1). Although there has been criticism of chronosequence approaches (Johnson and Miyanishi 2008; Jolly et al. 2012), these methods still hold value to study past disturbance effects and lend insights when

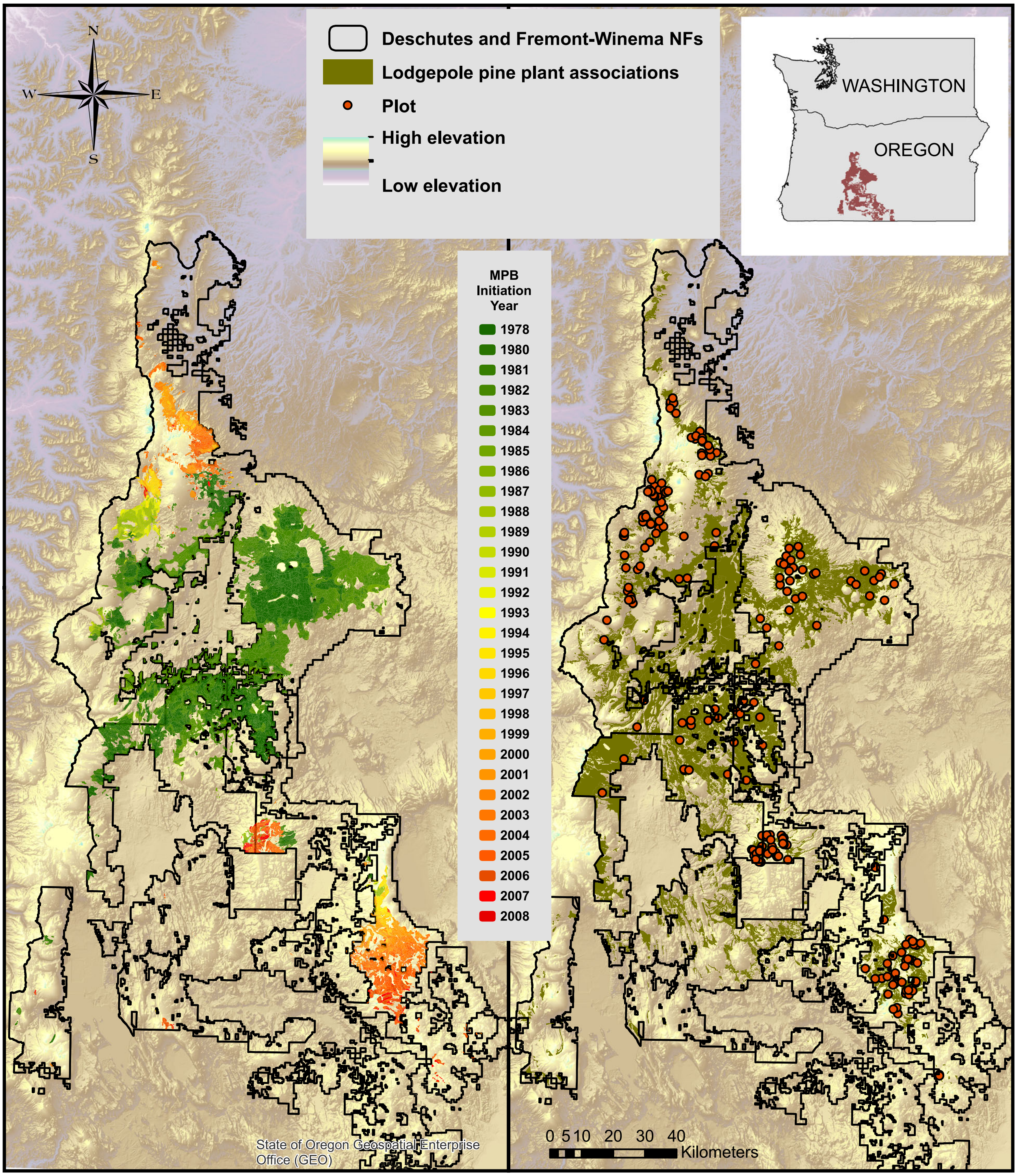

Fig. 2 Study area displaying climax lodgepole pine plant associations within the Deschutes and Fremont-Winema national forests (NFs), Oregon, USA, the year of outbreak initiation, and locations of randomly selected (spatially balanced) MPB epidemic chronosequence plot network

long-term studies are not feasible or data from them are not yet available. Using the local plant association groups, we identified areas of climax lodgepole pine forests across three categories of site productivity based on volume production (low: 0.4 to 0.85 m^{-3} yr^{-1}, moderate: 0.86 to 1.1 m^{-3} yr^{-1}, high: ≥1.2 m^{-3} yr^{-1}; Fig. 2; Hopkins 1979, Volland 1985, Simpson 2007). We then used ADS (USDA Forest Service 2010) cumulative mortality data (McConnell et al. 2000) to identify areas that had more than 12 dead trees ha^{-1} (minimum threshold), which is

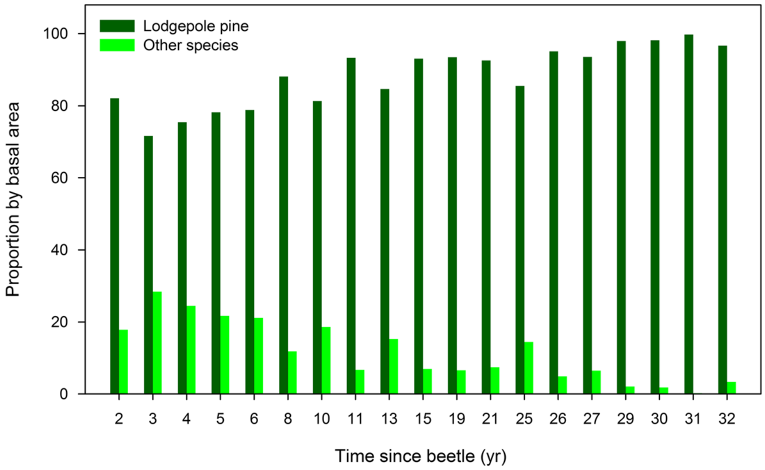

Fig. 3 Proportion by basal area of lodgepole pine and other species (>5 cm DBH) on plots across the 2- to 32-year chronosequence of post-MPB-epidemic stands in south-central Oregon, USA. Each bar represents the proportion of species on all plots in a year post-MPB outbreak

considered to be the point at which mortality levels become more epidemic in nature (A. Eglitis, Forest Health Protection, USDA Forest Service, Bend, Oregon, USA, unpublished data). Nineteen distinct years of epidemic initiation were identified within the 30 years of ADS data. Using this sampling frame we applied Generalized Random Tessellation Sampling (GRTS) methodology (Stevens and Olsen 2004) in an R statistical software environment (R Development Core Team 2009) to randomly sample four plot replicates within each productivity class for a total of 12 plots per epidemic year (Fig. 2), resulting in a 2- to 32-year chronosequence of time since beetle (TSB).

Field measurements

We sampled trees using an 8.92 m (0.025 ha) radius central tree plot. Measurements of individual trees ≥5 cm diameter at breast height included: DBH (diameter at breast height); tree height; crown class, and crown base height (height to lowest dead or live crown) of live trees and dead standing trees with >50% of needles remaining. We assigned all snags ≥5 cm DBH to a decay class based on five categories (Thomas 1979). In four 3.2 m radius subplots, located 25 m from plot center in the ordinal directions, we measured height and basal diameter and recorded species of all tree saplings and seedlings (<5 cm DBH). Within these subplots we also measured shrub cover and several characteristics to determine biomass, including basal diameter, height, crown width, and crown volume. A 2 m × 2 m quadrat was nested within each subplot for visual estimation of percent ground cover (*e.g.,* downed wood, mineral soil, rock, vegetation) and percent cover of herbaceous vegetation by species.

Surface fuels were measured along 25 m transects in the four cardinal directions using the methods of Brown et al. (1982). We tallied 1000-h fuels over the entire length of each transect. For each 1000-h piece, the diameter was measured and a decay classes was assigned based on five categories (Sollins 1982). We tallied 100-h fuels from 15 to 25 m, 10-h fuels from 20 to 25 m, and 1-h fuels from 23 to 25 m along each transect. We measured litter, duff, and surface fuel depths at 10 and 20 m along each transect. A convex densiometer was used to estimate canopy closure at the central tree plot center and each subplot center, following the methods of Strickler (1959). At the central tree plot center, we photographed the surface fuels in each cardinal direction (*i.e.,* along fuels transects), as well as the canopy directly above.

Data analysis

Data preparation

Field-derived counts of 1-h, 10-h, 100-h, and 1000-h fuels were converted to biomass (Mg ha^{-1}; Harmon and Sexton 1996, Harmon et al. 2008) using species-specific density values. We only used 1000 h fuels in decay classes 1 to 3 for further analyses, omitting the more decomposed decay classes, as extremely decayed material (decay classes 4 and 5) do not impede resistance to control efforts (*e.g.,* very difficult for hand crews; Brown et al. 2003). Seedling, sapling, and shrub counts were converted to biomass (Mg ha^{-1}) using relationships of height or basal diameter and mass (Brown 1976; Ross and Walstad 1986; Means et al. 1994). Herbaceous cover estimates were converted to Mg ha^{-1} using species-specific equations for the region in BIOPAK software (Means et al. 1994). For species with no available equations, we estimated mass based on equations for similar species. Biomass of duff and litter from depth measurements were calculated using conversion factors from FIREMON (Lutes et al. 2006). We determined canopy closure for each plot using the average of the five densiometer readings taken in the plot and subplots.

Canopy fuel parameters (canopy base height, canopy bulk density, and canopy height) were calculated using FuelCalc (Lutes 2014). FuelCalc defines canopy bulk density as the maximum of the 1.5 m running mean of increments 0.3 m in thickness, while canopy base height is defined as the lowest height at which canopy bulk density exceeds 0.012 kg m^{-3} (Scott and Reinhardt 2001, Lutes 2014). We used a novel approach to calculate canopy bulk density using live green trees as well as red (100% of needles remaining, recently attacked) and brown (<100% but >50% of needles remaining, not recently attacked) trees to account for changes in the density of foliage as attacked trees died (red) and began to lose their foliage (brown). These coarse estimates of remaining foliage were based on ocular estimates at the time of sampling. FuelCalc uses crown class adjustment factors to modify canopy fuel load based on trees' position in the canopy. Dominant and co-dominant trees with <100% but >50% of needles remaining were reclassified as intermediate crown class since the full complement of needles was not present.

TSB stage development

We constructed four post-MPB-epidemic initiation stages based on examining the 75th percentile fuel values (25th percentile for canopy base height) and assessing where natural breaks in the fuel loadings occurred over time (Figs. 4 and 5). We chose to use the 75th percentile for stage development because the upper end of fuel loading distributions is of particular interest and concern to managers due to the perceived connection between fuel load and higher levels of fire intensity, rate of spread, and resistance to control. Several surface and crown fuel parameters influenced the identification of stages. Canopy fuel parameters including canopy bulk density, dead basal area, and overstory canopy closure displayed large changes across the four stages. The surface fuels that exhibited substantial change through the stages included live woody, 100-h, and 1000-h fuel loads. Fuel bed depth, herbaceous fuel load, and 10-h fuel load changed to a lesser extent. All other fuels parameters measured were either highly variable or remained stable through all stages. The four stages (TSB1 to TSB4) served as the grouping variable for additional statistical analyses and are further described in detail in the Results section.

Statistical analysis

We used the four TSB stages and the fuels data from field plots associated with each stage in a MANOVA following the methods outlined by Grice and Iwasaki (2007) and subsequently applied an ANOVA to make comparisons of fuel variables that MANOVA indicated were most important. We analyzed the surface and crown fuel strata separately to account for the distinct contributions of crown fuels and surface fuels.

MANOVA We used multivariate analysis of variance (MANOVA; Grice and Iwasaki 2007) to determine which fuel and forest structure variables were most influential in changes over time. Given the multivariate nature of the fuels complex, a multivariate statistical approach allows greater understanding of which fuels parameters are changing over time while accounting for interacting factors. Surface fuel response variables examined included: 1-h, 10-h, 100-h, and 1000-h fuel loads; litter biomass; duff biomass; fuel bed depth; and herbaceous and live woody fuel loads (shrub, live seedling, and live sapling). Crown fuel response variables included: overstory canopy closure, basal area of live trees (live basal area), basal area of standing dead trees (dead basal area), canopy base height, canopy bulk density, and canopy height.

We derived two discriminant functions for each fuel strata. Each function is composed of coefficients that describe the relationship of the dependent fuel variables in that stratum. We then created two simplified multivariate composites for each strata. Simplification is the process by which the number of variables in a composite is reduced to those that have the largest effect on the response variable, thus the final variables included are the most informative and allow for ease of interpretation. Each simplified composite contains only the dependent variables that best discriminate between the stages of the post-MPB-epidemic environment. The final dependent variables were selected based on ranking their coefficient values, whereby larger coefficients (relative to the other coefficients) are retained and those closer to zero were removed. Only two composites were examined for each stratum because their effect sizes warranted their inclusion (Table 1). Effect size can be thought of as the amount of variance that the composite shares with the response variable. In both the crown and surface fuel strata, the effect size of the second composite was well above zero and, in all cases, nearly half the size of the values for the first composite. In addition, each set of composites had coefficients that differed, providing different and complimentary information.

ANOVA We then used these simplified composites (Grice and Iwasaki 2007) in analysis of variance (ANOVA) to identify covariates and significant changes in fuels composites over time. Covariates included the proportion of mountain pine beetle mortality (low: 20 to 37 trees ha^{-1}, moderate: 38 to 74 trees ha^{-1}, and high:

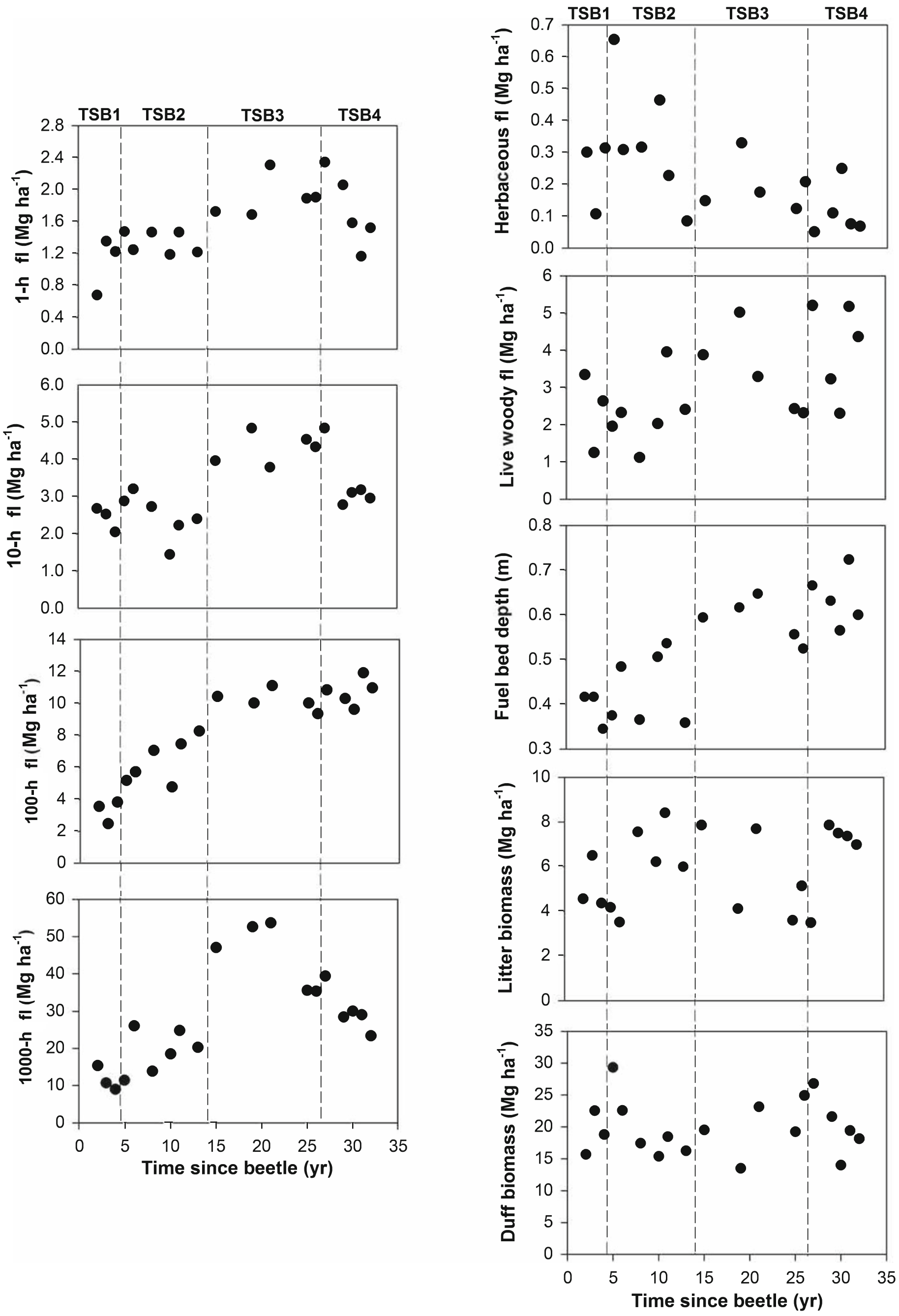

Fig. 4 Changes in surface fuel loads (fl) from 2 to 32 years following MPB infestation in south-central Oregon, USA. Each closed circle represents the 75th percentile value of all plots in that year

75 to 200 trees ha^{-1}) derived from ADS data and site productivity (low, moderate, high) derived from plant association data for climax lodgepole pine in the region. In addition, we performed univariate ANOVAs to obtain estimates of fuel parameters and standard errors for each of the fuel variables that drove the composites. We also performed pairwise comparisons for each of the four simplified composites between all combinations of TSB stages. We examined both univariate and multivariate assumptions and transformed the following variables to fit assumptions of normality and constant variance: canopy base height; canopy bulk density (CBD); and herbaceous, 1-h, 10-h, and 1000-h fuel loads. Bonferroni adjustments were applied, as recommended by Grice

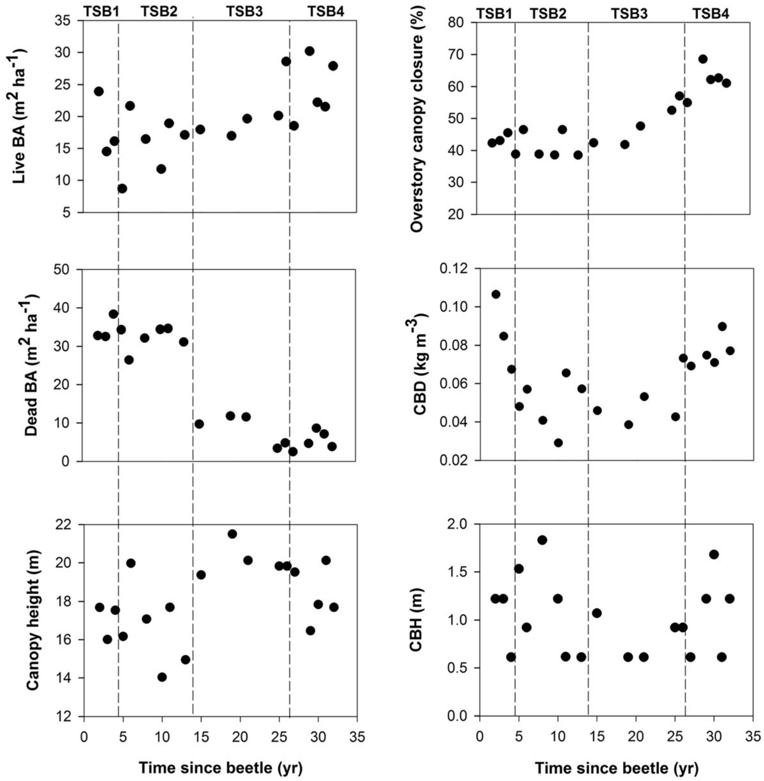

Fig. 5 Changes in canopy fuel loads (75th percentile) from 2 to 32 years following MPB infestation in south-central Oregon, USA. BA = basal area, CBD = canopy bulk density, CBH = canopy base height

and Iwasaki (2007). Median values were presented for transformed variables. We performed all statistical analyses using SAS Statistical Software v9.3 (SAS 2002).

Results

Fuels and forest structure: time since beetle (TSB) stages

Time since beetle 1 (TSB1): overstory mortality stage (2 to 4 years post-MPB-epidemic initiation)

Often referred to as the red stage, TSB1 is a mix of recently killed (red needled), dead (needleless), and living (green) trees (Fig. 6). The most apparent change that we noted was in canopy fuels, marked by a nearly 50% decrease in canopy bulk density during TSB1 due to needle loss following mortality (Fig. 5). Other fuel characteristics did not demonstrate a consistent trend during this stage. Overall TSB1 can be characterized by a change in canopy fuel characteristics, primarily driven by mortality, needle loss, and consequent changes in canopy bulk density.

Time since beetle 2 (TSB2): standing snag and snag fall stage (5 to 13 years post-MPB-epidemic initiation)

Often referred to as the gray stage, this period of time following MPB initiation was represented by gray standing snags intermixed with the green canopy. A large proportion of snag fall (>85% of basal area) occurred by the end of this stage (approximately 13 years TSB), although some standing snags remained in the regeneration stage (TSB3). The 100-h, 1000-h, and live woody fuel loads increased (Fig. 4), but these trends were not significant when all years were grouped for TSB2 (Fig. 7). In addition, overstory canopy closure and canopy bulk density were lower than in TSB1 (Fig. 8) and continued to decrease through TSB2 (Fig. 5). This stage can be characterized by increasing surface fuel loads and continued decrease in canopy fuels.

Time since beetle 3 (TSB3): regeneration stage (14 to 25 years post-MPB-epidemic initiation)

The most notable changes characterizing this stage were continued increases in 10-h, 100-h, and 1000-h fuel loads, resulting from continued snag fall (Fig. 4). Live woody fuel loads increased but were highly variable in this stage (Fig. 4), and both live woody fuel load and fuel bed depth increased compared to TSB2 (Fig. 7) due to an increase in lodgepole pine seedling and sapling density. Dead basal area drastically decreased (>90%), as most snags fell by the end of this stage (Figs. 5 and 8). Overall, this stage can be characterized by continued increases in surface fuel loads influenced by continued snag fall and initiation and advancement of tree regeneration.

Table 1 Discriminant function[a] coefficients from MANOVA analysis of surface and crown fuel variables from 2 to 32 years post-MPB epidemic initiation in lodgepole pine stands of south-central Oregon, USA. [a]Discriminant functions are represented as DF-1 surface, DF-2 surface, DF-1 crown, and DF-2 crown. [b]Larger values indicate stronger relationships. [c]Coefficient used in simplified multivariate composite to test significance using ANOVA

Variables for DF-1 surface	Standardized DF-1 surface coefficients[b]	Variables for DF-2 surface	Standardized DF-2 surface coefficients[b]
100-h fuel load	0.69[c]	10-h fuel load	−1.02[c]
Fuel bed depth	0.56[c]	100-h fuel load	0.69[c]
1000-h fuel load	0.46[c]	Fuel bed depth	0.56[c]
Herbaceous fuel load	−0.24	1000-h fuel load	0.46[c]
Duff biomass	−0.24	1-h fuel load	0.39
Litter biomass	−0.20	Duff biomass	−0.24
1-h fuel load	−0.04	Litter biomass	−0.20
10-h fuel load	0.03	Live woody biomass	−0.06
Live woody biomass	−0.06	Herbaceous fuel load	−0.02
Composite effect size	0.28	Composite effect size	0.13
Variables for DF-1 crown	**Standardized DF-1 crown coefficients[b]**	**Variables for DF-2 crown**	**Standardized DF-2 crown coefficients[b]**
Dead basal area	−1.28[c]	Canopy bulk density	1.50[c]
Overstory canopy closure	0.29[c]	Live basal area	−1.21[c]
Live basal area	0.28[c]	Canopy height	0.65[c]
Canopy base height	0.16	Overstory canopy closure	0.38
Canopy height	0.09	Canopy base height	−0.19
Canopy bulk density	0.01	Dead basal area	0.07
Composite effect size	0.46	Composite effect size	0.19

Time since beetle 4 (TSB4): overstory recovery stage (26 to 32 years post-MPB-epidemic initiation)

This stage was represented by an increase in canopy bulk density, overstory canopy closure, and live basal area compared to TSB2 and TSB3 (Fig. 8). By 32 years TSB, canopy bulk density values approached those seen at the beginning of TSB1 (Figs. 5 and 8), while canopy closure continued to increase and surpass TSB1 (Figs. 5 and 8). The 100-h and live woody fuel loads remained at levels similar to those of TSB3 (Figs. 4 and 7). However, the variability

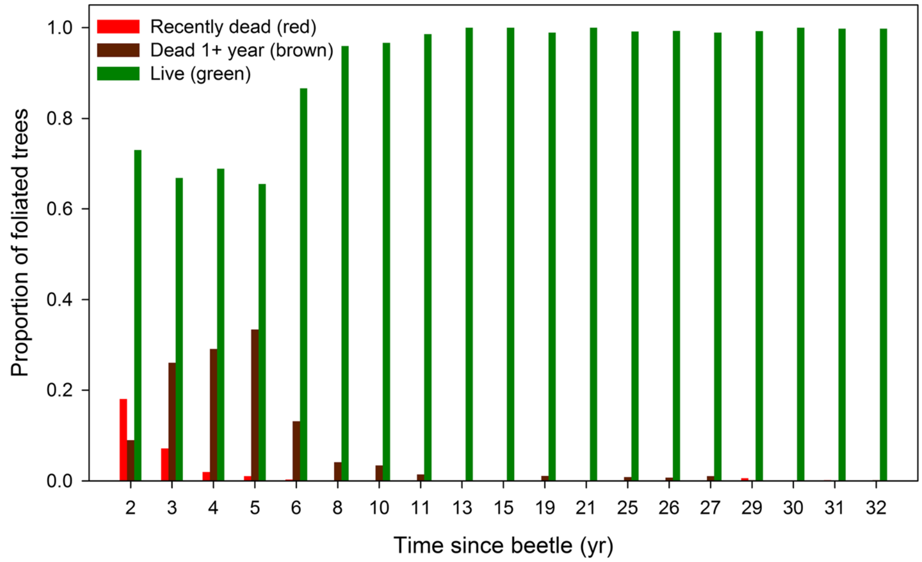

Fig. 6 Patterns in forest structure and fuels from 2 to 32 years post-MPB epidemic initiation (TSB) in south-central Oregon, USA, showing proportion of foliated trees in the red (recently dead), brown (dead one or more years with more than 50% of the needles remaining), and green (live at time of sampling; may or may not have been attacked). Each bar represents the proportion of species on all plots in a year post-MPB epidemic initiation

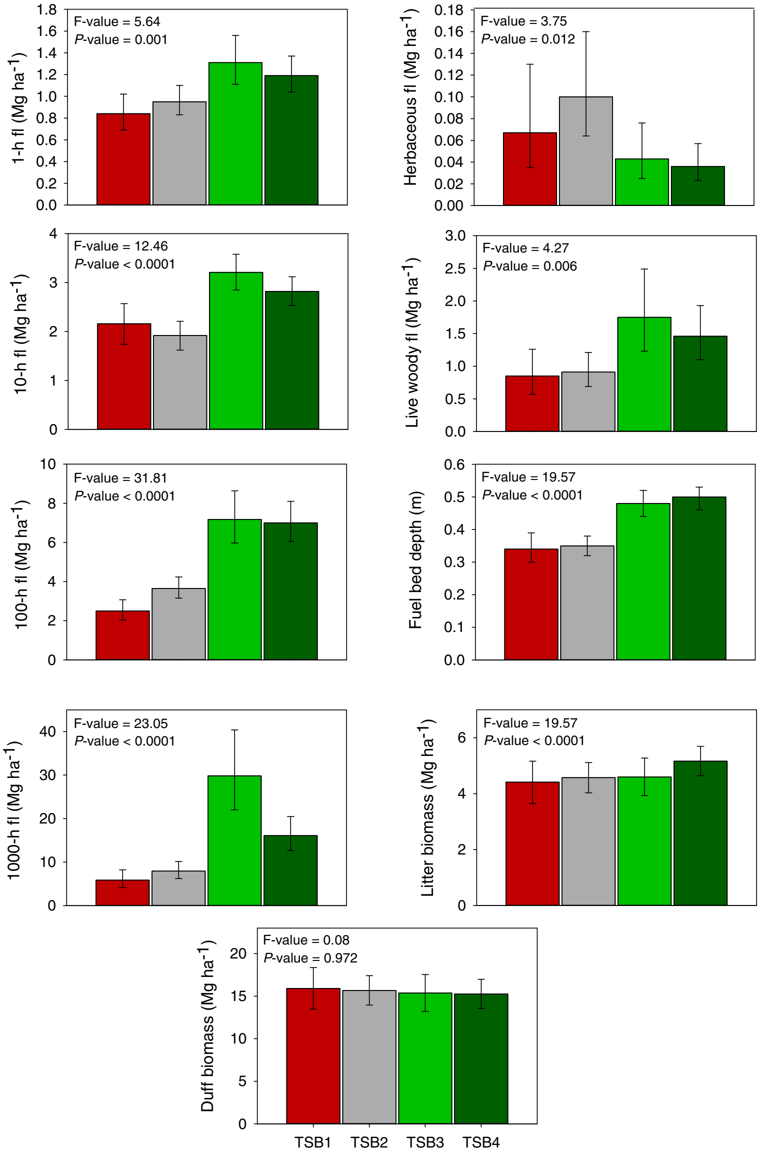

Fig. 7 Estimates of surface fuel loads (fl) for the four stages of time since beetle (TSB1 to TSB4) in south-central Oregon, USA. Bar color indicates post-epidemic stage (red = overstory mortality, gray = standing snag and snag fall, light green = regeneration stage, dark green = overstory recovery). Herbaceous, 1-h, 10-h, and 1000-h fuel values are median instead of mean values due to log transformations. Error bars represent 95% confidence intervals

in live woody fuels was quite high in this stage (Fig. 4), indicating different stand density trajectories within this stage of post-MPB development. Overall, this stage was characterized by a recovery of the overstory (CBD and canopy closure) as saplings and intermediate canopy trees (predominantly lodgepole pine) that survived the MPB epidemic became the new overstory.

Fuels and forest structure: MANOVA

MANOVA illustrated that changes in fuels 2 to 32 years TSB were driven by 3 to 4 fuel variables each for the surface and crown strata (Table 1). Larger values indicate a stronger relationship in the discriminant function analyses. Analysis of variance (ANOVA) performed on simplified composites indicated that all four simplified fuels composites (two surface and two crown) were significantly different (Bonferroni adjusted α = 0.008) between stages (Table 2). Notably, neither productivity nor level of mortality were significant covariates for the final composites.

The first multivariate composite for surface fuels was driven by 100-h fuel load, fuel bed depth, and 1000-h fuel load and could be described as a surrogate for changes in medium to coarse surface fuels and ladder fuels (Table 1). Pairwise comparisons among all combinations of TSB stages indicated that the simplified

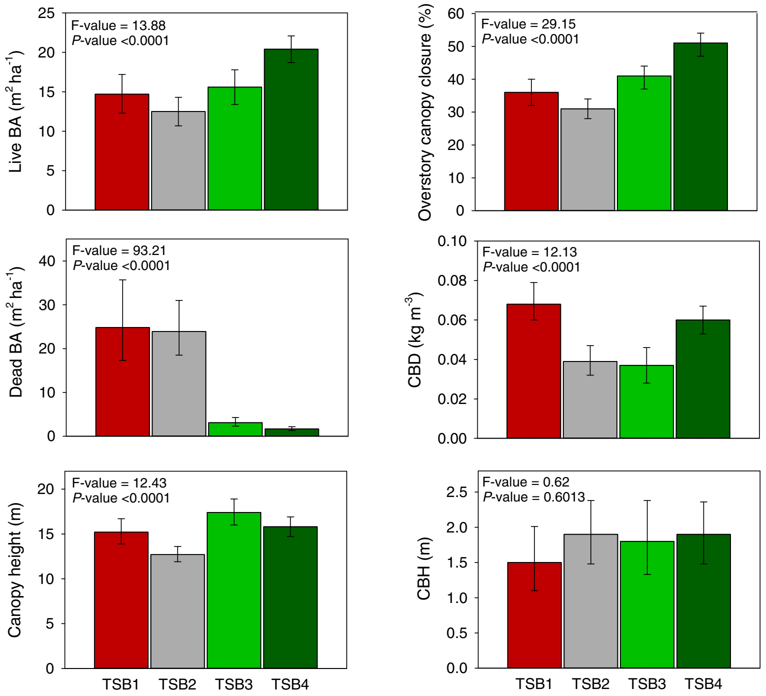

Fig. 8 Estimates of crown fuel loads for the four stages of time since beetle (TSB1 to TSB4) in south-central Oregon, USA. Bar color indicates post-epidemic stage (red = overstory mortality, gray = standing snag and snag fall, light green = regeneration stage, dark green = overstory recovery). BA = basal area, CBD = canopy bulk density, CBH = canopy base height. Canopy height and CBD values are median instead of mean values due to log transformations. Error bars represent 95% confidence intervals

version of the first composite was significantly different between TSB1 and TSB3, TSB1 and TSB4, and TSB2 and TSB3, but did not show a difference between TSB1 and TSB2 or TSB3 and TSB4 (Table 2). The second multivariate composite for surface fuels was similar to the first composite, but was strongly driven by 10-h fuel load that increased between TSB2 and TSB3. The 1-h fuel load played a marginal role in driving this pattern, while duff and litter biomass showed a trend of decreasing over time. This can be described as a composite representing change in fine to coarse surface fuels and fuel bed depth. However, the simplified version of this composite was only significantly different between TSB2 and TSB3 and did not show a difference between any other stages using pairwise comparisons (Table 2).

Fuels and forest structure: ANOVA

Crown fuel discriminant functions were dominated by dead basal area, live basal area, overstory canopy closure, canopy bulk density, canopy base height, and canopy height. The first multivariate crown fuels composite was driven by dead basal area, overstory canopy closure, and live basal area. This composite can be described as the proportion of live and dead trees and change in tree canopy closure over time. In pairwise comparison analyses, the simplified version of this composite was significantly different between all stages except TSB1 and TSB2 (Table 2). The second crown fuels composite was driven by changes in canopy bulk density, live basal area, and canopy height. This composite can be described as a combination of changing canopy bulk density and canopy height over time. Pairwise comparisons between stages indicated that the simplified version of this composite was significantly different between TSB2 and all other stages (TSB1, TSB3, and TSB4), while all other comparisons were not significant (Table 2).

Discussion

Forest fuels structure and composition changes over 32 years following MPB-caused mortality events in south-central Oregon lodgepole pine forests provided insights into fire regime characteristics and trajectories into the future compared to other lodgepole pine types. In contrast to both Simard et al. (2011) and Donato et al. (2013), who delineated only three post-MPB stages, our data from south-central Oregon climax lodgepole pine indicated four distinct stages (overstory mortality, standing snag and snag fall, regeneration, overstory recovery) of fuels changes over 32 years following MPB epidemic. Our key findings concerning changing fuels and forest structure following an MPB epidemic in these lodgepole pine forests include: little change in 1-h fuels

Table 2 Results from ANOVA for simplified composites derived from discriminant function/MANOVA analysis from 2 to 32 years post-MPB epidemic initiation in south-central Oregon, USA. PROD = productivity class; MORT = level of MPB mortality.[a]Surface fuels composite 1 is composed of the variables: 100-h fuel load, 1000-h fuel load, and fuel bed depth[b]Surface fuels composite 2 is composed of the variables: 10-h fuel load, 100-h fuel load, 1000-h fuel load, and fuel bed depth[*]Indicates a statistically significant difference between TSB stages or a statistically significant effect of a covariate (Bonferroni adjusted α = 0.008)[c]Crown fuels composite 1 is composed of the variables: dead basal area, live basal area, and overstory canopy closure[d]Crown fuels composite 2 is composed of the variables: live basal area, canopy bulk density, and canopy base height

Surface fuels composite 1[a]	**F-value**	***P*-value**	**Surface fuels composite 2[b]**	**F-value**	***P*-value**
Stage	40.46	≤0.001*	Stage	5.82	≤0.001*
PROD	1.48	0.230	PROD	0.11	0.895
MORT	2.07	0.129	MORT	0.09	0.914
TSB1 vs TSB2		0.189	TSB1 vs TSB2		0.011
TSB1 vs TSB3		≤0.001*	TSB1 vs TSB3		0.286
TSB1 vs TSB4		≤0.001*	TSB1 vs TSB4		0.440
TSB2 vs TSB3		≤0.001*	TSB2 vs TSB3		≤0.001*
TSB2 vs TSB4		≤0.001*	TSB2 vs TSB4		0.030
TSB3 vs TSB4		0.102	TSB3 vs TSB4		0.037
Crown fuels composite 1[c]	**F-value**	***P*-value**	**Crown fuels composite 2[d]**	**F-value**	***P*-value**
Stage	66.57	≤0.001*	Stage	23.35	≤0.001*
PROD	0.97	0.381	PROD	4.31	0.015
MORT	1.42	0.244	MORT	1.83	0.163
TSB1 vs TSB2		0.580	TSB1 vs TSB2		≤0.001*
TSB1 vs TSB3		≤0.001*	TSB1 vs TSB3		0.157
TSB1 vs TSB4		≤0.001*	TSB1 vs TSB4		0.466
TSB2 vs TSB3		≤0.001*	TSB2 vs TSB3		≤0.001*
TSB2 vs TSB4		≤0.001*	TSB2 vs TSB4		≤0.001*
TSB3 vs TSB4		≤0.001*	TSB3 vs TSB4		0.02

and litter over time, dramatic increases in surface fuel loads between TSB2 and TSB3, and continued dominance by lodgepole pine. These factors in combination with lower site productivity and low CBD density relative to other regions where lodgepole pine exists points to a perpetuation of a lodgepole pine-dominated system with a mixed-severity fire regime well into the future.

We found no distinction between TSB1 and TSB2 with respect to surface fuels. Slight increases in 100-h fuel load and herbaceous fuel load occurred, but other components of the fine fuel load, such as litter biomass, 1-h, and 10-h fuel loads, did not change between these stages (Fig. 7). Although this contradicts synthesized results by Hicke et al. (2012), Agee (1993) notes that litter is essentially non-existent in this forest type. Perhaps of more consequence, we found that surface fuel loadings changed dramatically between TSB2 and TSB3. Downed woody debris of all size classes increased (Fig. 7), concurrent with the majority of snagfall (Fig. 8). Furthermore, live woody fuels (representing shrubs and tree seedlings and saplings) also increased between these stages (Fig. 7) due to low incidence of cone serotiny, leading to seed dispersal at all phases of stand development, not just after a fire (Mowat 1960; Lotan and Critchfield 1990). This also indicates that combining long time spans of TSB into a single structural stage, as in some previous work (*e.g.,*Simard et al. 2011), or omitting stands representing the range of 15 to 25 years TSB (*e.g.,*Schoennagel et al. 2012) may miss critical changes in surface fuels following MPB epidemic. While Hicke et al. (2012) suggest that 100-h and 1000-h fuels slowly increase with time and continue on this trajectory for decades, our data support a transition between TSB2 and TSB3, with little change prior (*i.e.,* between TSB1 and TSB2) or after (*i.e.,* between TSB3 and TSB4). As previous research has discussed (Klutsch et al. 2011), dead fuels, combined with live intermediate and suppressed lodgepole pine cohort of trees that existed on the site prior to the outbreak, create a dynamic increase in fuels that is maintained through TSB4 and potentially longer periods of time. These fuels interactions may be extremely important for fire activity during phases when fuels, rather than climate, are the limiting factor for fire activity resulting in a mixed-severity fire regime (Heyerdahl et al. 2014).

The transition between the initial stage following MPB epidemic initiation (TSB1) and the following stage

(TSB2) was strongly driven by reduced canopy closure and canopy bulk density. However, the range of canopy bulk density values over the entire chronosequence was low compared to those observed in lodgepole pine forests in other regions. For example, in TSB1, mean canopy bulk density was approximately 0.07 kg m^{-3} (Fig. 8), while canopy bulk density in lodgepole pine stands in Idaho and Utah, USA, in this same stage ranged from 0.15 to 0.22 kg m^{-3} (Page and Jenkins 2007). We hypothesized that lodgepole pine forests in our study area experience mixed-severity fire regime (Agee 1993; Heyerdahl et al. 2014) in part because canopy bulk density is low and less likely to support active crown fire. Canopy bulk density continued to decline through TSB2 and TSB3, with some recovery during TSB4 (Figs. 5 and 8). Although this general pattern follows the conceptual framework outlined by Hicke et al. (2012), other chronosequence investigations of MPB and fuels succession have not indicated a significant recovery in canopy bulk density over time following the red stage (Simard et al. 2011; Schoennagel et al. 2012). However, the methods we used to calculate CBD differed from Simard et al. (2011), which makes comparisons difficult. Jolly et al. (2012) pointed out that the categorical reductions to crown biomass, which subsequently reduced their calculated CBD values, may have been inaccurately applied. Similar to the pattern we detected, but less pronounced, Schoennagel et al. (2012) reported increasing canopy bulk density by approximately 30 years post-MPB epidemic at sites in Colorado and Wyoming, USA. It is likely that the increase in canopy bulk density and canopy closure shown in our chronosequence will continue and approach or exceed pre-epidemic levels until self-thinning (via suppression mortality or endemic MPB mortality) or low- or moderate-intensity surface fire reduces tree density.

Most snags fall within 20 years TSB, as noted in other studies (Mitchell and Preisler 1998); therefore, significant increases in 1000-h fuels beyond this point are unlikely. However, we hypothesize that the decrease observed in 1000-h fuel load in TSB4 (Figs. 4 and 7) was an artifact of the chronosequence sampling method that we used, not using decay class 4 and 5 in our analysis, and large variations of coarse fuels due to MPB mortality, rather than different rates of decomposition. Previous work in our study area indicates that coarse wood remained relatively sound (decay classes 1 to 3) up to 27 years after snags had fallen (Busse 1994). If most snags fell between 10 and 20 years TSB, as indicated by our data (Fig. 4: 1000-h fuel load), we should not see transition into less sound coarse wood (decay classes 4 and 5) until 37 to 47 years following MPB initiation, based on decay rates described by Busse (1994). It is therefore unlikely that there was substantial decomposition of 1000-h fuels within the time since beetle covered by our chronosequence.

This climax lodgepole pine system is influenced by interacting disturbance agents (Kane et al. 2017), low site productivity, and dominance by a single tree species, manifesting in a mixed-severity fire regime (Agee 1993), as compared with the high-severity fire regimes of lodgepole pine forests in the Rocky Mountains (Romme 1980) where most previous research on MPB and fuels has been conducted. While fuels are unlikely to contribute substantially to fire activity under most circumstances in Rocky Mountain lodgepole pine forests, in which fire is primarily limited by climate (Schoennagel et al. 2004), changes in fuel loadings may have more of an influence on fire in south-central Oregon, where fire may be limited by fuels or climate at various times (Agee 1993, Heyerdahl et al. 2014). In addition to the low productivity and mixed-severity fire regime found in this lodgepole pine system, a major difference contrasting with those found in much of the Rocky Mountain region is that here lodgepole pine is a climax species, and spruce (*Picea*), fir (*Abies*), and other pine species do not become major components of the tree species composition following MPB epidemics. Our study supported this, and lodgepole pine remained the dominant tree species on the landscape throughout the chronosequence following the MPB epidemic (Fig. 3). This indicates that these lodgepole pine systems will maintain similar communities (resilience) following subsequent fire that seems likely to remain mixed in severity (*i.e.*, maintained intensity; Kane et al. 2017). When MPB selectively removes the dominant and co-dominant lodgepole pine from sites in the Rocky Mountain region, changes in composition and stand succession may be accelerated by releasing spruce and fir regeneration (Collins et al. 2011; Diskin et al. 2011; Kayes and Tinker 2012; Pelz and Smith 2012; Pelz et al. 2015). However, in the climax lodgepole pine system of south-central Oregon, the post-MPB succession is facilitated by existing cohorts of lodgepole pine, indicating a resilient ecosystem response to interacting disturbances (Kane et al. 2017). Although the difference among regions in the change in species composition over time likely has a minimal effect on fuels over the time covered by the chronosequence in this study, these compositional differences are likely to have considerable effects on the ecology of the forest over longer time scales. The effects of intermittent MPB-caused mortality, multiple interacting disturbance factors, and other unique characteristics of climax lodgepole pine communities (*e.g.*, low productivity, lack of cone serotiny) facilitate a mixed-severity fire regime and a mosaic of conditions on the landscape that distinguish this lodgepole pine type from previously studied lodgepole pine forests.

Conclusion

The findings of this study have important implications for several different management objectives. Our results inform fire and forest managers in the region by describing how fuels change with time following dominant and co-dominant cohort mortality caused by MPB in these multi-aged, single-species stands. Late TSB2 and TSB3 are likely the most difficult and dangerous settings in which to perform fire suppression activities as snagfall is active and coarse woody debris slows the pace of fire-line construction (Page et al. 2013). Using data from this study in conjunction with ADS data to map fuels for TSB stages may inform planning prior to fire season in conjunction with existing land management plans and provide the opportunity to manage fires in these areas to achieve resource benefits and reduce firefighters' exposure to hazard.

Ecologically focused management decisions may be heavily influenced by an MPB epidemic due to known influences of MPB on biodiversity (Koch et al. 2011; Treu et al. 2014), hydrology (Rex et al. 2013; Bradford et al. 2014), and carbon sequestration (Brown et al. 2010; Bright et al. 2012; Kasischke et al. 2013). In the lodgepole pine forests of south-central Oregon, the impacts may be more nuanced as there is typically no shift in tree species composition following MPB. However, the influence on fuels and forest structure may have implications for fire activity under moderate climate conditions, given the mixed-severity fire regime that characterizes this forest type. Using the data and results of this study, forest and fire managers in south-central Oregon can better understand future trajectories of forest structure and fuels conditions over key time periods (*e.g.,* TSB2 to TSB3) in areas affected by mountain pine beetle and therefore better determine the potential effects and risks to multiple resource values.

Additional file

Additional file 1: Figure S1. Photographs depicting examples of fuels conditions over time following MPB epidemics in south-central Oregon, USA. (PDF 843 kb)

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Availability of data and materials

The datasets generated or analyzed during the current study are available in the USDA Forest Service Data Archive, https://www.fs.usda.gov/rds/archive/Product/RDS-2014-0017.

Authors' contributions

TW developed study and sampling design and field data collection protocols, lead data collection, and developed and performed statistical data analysis, and lead drafting and revisions of the manuscript. DCS participated in discussions of study design and field data collection protocols, and assisted in drafting and revisions of the manuscript. LTH provided expertise in fuels data processing and assisted in drafting and revisions of the manuscript. MCA assisted in data collection, analysis, and in drafting and revisions of the manuscript. SF assisted in development of field data protocols, participated in discussions of study design, and assisted in drafting and revisions of the manuscript. AE provided expertise in mountain pine beetle ecology and use of aerial detection survey data in sampling design and data analysis, and assisted in drafting and revisions of the manuscript. LK assisted in development of field data collection protocols, and assisted in drafting and revisions of the manuscript. All authors read and approved the final manuscript.

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests.

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