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Bark beetles and dwarf mistletoe interact to alter downed woody material, canopy structure, and stand characteristics in northern Colorado ponderosa pine

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ABSTRACT

Due to the recent outbreaks of bark beetles in western U.S.A., research has focused on the effects of tree mortality on forest conditions, such as fuel complexes and stand structure. However, most studies have addressed outbreak populations of bark beetles only and there is a lack of information on the effect of multiple endemic, low level populations of biotic disturbance agents that could influence forest dynamics, fuel heterogeneity, and species composition. Downed woody material, fuel parameters and stand characteristics were assessed in areas of ponderosa pine (*Pinus ponderosa*) infested with southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum*), and in areas with endemic populations of mountain pine beetle (*Dendroctonus ponderosae*) and *Ips* spp. (Coleoptera: Curculionidae, Scolytinae) in northern Colorado. Both endemic bark beetles and dwarf mistletoe were associated with more dense stands than uninfested plots and resulted in reducing basal area of live trees. The amount of downed woody material was positively related to time since tree mortality and basal area of bark beetle-attacked trees. There was an increase of up to 10% for fine and coarse downed woody material for every increase of 1 m^2 ha^{-1} basal area of mortality from mountain pine beetle that was 4–15 years after death. The average intensity of dwarf mistletoe infections on live trees was positively related to amount of 10-h downed woody material and negatively associated with percent live ponderosa pine crown. Fuel bed and canopy characteristics were dependent on the presence of both dwarf mistletoe and mountain pine beetle-caused mortality. Together these endemic biotic disturbances have an effect on downed woody material biomass accumulation, fuel arrangements, stand densities and species composition.

1. Introduction

Recent studies have identified significant effects of bark beetle outbreaks on downed woody material and stand conditions (Kulakowski et al., 2003; Billings et al., 2004; Schulz, 2003; Lynch et al., 2006; Page and Jenkins, 2007a; Klutsch et al., 2009). However there is little information on the effect of endemic disturbances. Biotic disturbance agents at low population levels are characterized as endemic and tend to be restricted to a small number of trees scattered in the landscape. Information on the effects of multiple endemic disturbances is even more limited. This is despite the presence of multiple endemic biotic disturbances that occur throughout most forests. Due to the importance of low-level populations of biotic disturbances and their interactions, we examined the impact of three endemic disturbances on stand characteristics and downed woody material in ponderosa pine (*Pinus ponderosa* Laws.) forests in the Colorado Front Range.

There is increased interest in managing and understanding the factors that contribute to downed woody material in forests (Woodall et al., 2013). Downed woody material and other fuel complexes such as vegetation are part of the determination of fire hazard. Authors working in ponderosa pine forests (Alexander and Hawksworth, 1976; Lundquist, 2007; Hoffman et al., 2007; Stanton, 2009) and subalpine forests (McCullough et al., 1998; Kulakowski et al., 2003; Lynch et al., 2006; Page and Jenkins, 2007a,b; Jenkins et al., 2008; Klutsch et al., 2011) have identified relationships between fire hazard and bark beetle outbreaks and pathogens. Along with contributing to increased fire hazard, downed woody material plays a crucial role in providing habitat for wildlife and invertebrates, giving structure to the forest floor for retention of sediments and stream characteristics, and contributing to nutrient cycling and nitrogen fixation (Harmon et al., 1986; Vanderwel et al., 2006).

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Large disturbances, such as bark beetle epidemics, can lead to shifts in species composition and increased structural diversity post-infestation forests (Collins et al., 2011; Kayes and Tinker, 2012). Multiple disturbances can also alter forest composition, which can have consequences for forest successional trajectories and susceptibility to future disturbances (Kulakowski et al., 2013). However, it is not known if the impact of mortality of a limited number of widely dispersed trees due to endemic biotic disturbances has the same consequence for stand characteristics and species composition as epidemic disturbances.

Endemic populations of two bark beetles species and one pathogen were studied to identify changes in downed woody material and stand characteristics in ponderosa pine. At epidemic population levels, mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Coleoptera: Curculionidae, Scolytinae) infestations can cause extensive mortality in susceptible pine forests. However, tree susceptibility is not static and is dependent on beetle population size along with tree size and stand conditions. Populations of endemic mountain pine beetle are maintained on a low number of weak and low vigor trees, such as trees with root disease or damaged from lightning (Furniss and Carolin, 1977; Schmid and Amman, 1992; Schmid and Mata, 1996; Negrón and Popp, 2004). These trees are generally greater than 15–20 cm diameter at breast height (dbh, at height of 1.37 m) (Negrón and Popp, 2004; Smith et al., 2011). Stand conditions that contribute to the susceptibility of a ponderosa pine to infestation by eruptive populations of mountain pine beetle include: high stand stocking >17.1 m^2 ha^{-1} basal area, high stand density index (SDI), and high quadratic mean diameter (Negrón and Popp, 2004). Species of *Ips* (Coleoptera: Curculionidae, Scolytinae), such as *I. pini* (Say) and *I. knausi* Swaine, that infest ponderosa pine in the Rocky Mountains are secondary bark beetles that usually infest small diameter stressed trees, and generally cause limited mortality in ponderosa pine of northern Colorado (Furniss and Carolin, 1977).

Along with endemic populations of bark beetles, we examined the effect of the pathogen dwarf mistletoe on ponderosa pine forests. Dwarf mistletoes are obligate parasitic plants that infest conifer species in the Pinaceae family (Hawksworth and Wiens, 1996). In Colorado, southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum* [Engelm.] Hawksworth and Weins) infects ponderosa pine causing abnormal shoot growth, reduced radial growth, persistence of infested branches, and reduced tree vigor eventually leading to tree mortality. Dwarf mistletoe infestations can increase the amount of downed woody material on the forest floor and provide fire ladders that together can move surface fires into the crown by an increase in the amount and flammability of branches and foliage (witches' brooms) near the ground as compared to uninfested stands (Koonce and Roth, 1985; Hoffman et al., 2007; Stanton, 2009).

There may also be interactions between these disturbance agents that can result in changes in downed woody material and stand characteristics. Although the extent of dwarf mistletoe-induced susceptibility to bark beetle attack is unclear, studies have documented a predisposition of dwarf mistletoe infected trees to infestation by *Ips* spp. (Negrón and Wilson, 2003; Kenaley et al., 2006; Beam, 2009) and an association between dwarf mistletoe and mountain pine beetle (Johnson et al., 1976; McCambridge et al., 1982b; Smith et al., 2011). The compound effect of these two disturbance types (bark beetles and pathogen) that infest the same host species may lead to greater shifts to non-host species along with increases in downed woody material.

This study examined dynamics of downed woody material, canopy and fuel bed characteristics, along with stand structure during endemic bark beetle populations and dwarf mistletoe infestation in ponderosa pine in northern Colorado. The objectives were to: (1) identify changes in stand characteristics created by bark beetles or dwarf mistletoe or both; (2) quantify downed woody material and determine whether the biomass is a function of the amount of tree mortality, time since bark beetle-caused mortality, and dwarf mistletoe intensity; and (3) examine the effect of interactions between endemic bark beetle-caused mortality and dwarf mistletoe infestation on fuel bed and canopy fuel characteristics.

2. Materials and methods

2.1. Study site and plot selection

The study was conducted in the Canyon Lakes Ranger District, Arapaho-Roosevelt National Forest along the eastern slopes of the Front Range in the Rocky Mountains of northern Colorado (40°37′N, 105°28′W). The study area comprises approximately 2500 km^2 and ranges in elevation from 2060 to 2730 m. Populations of mountain pine beetle in northern Colorado have ranged from epidemic episodes (McCambridge et al., 1982b; Schmid and Mata, 1996) to endemic levels in ponderosa pine (Harris, 2005; USDA and CSFS, 1996–2006 Aerial Detection Surveys http://www.fs.fed.us/r2/resources/fhm/aerialsurvey/). Our study area contained endemic populations of mountain pine beetle and *Ips* spp. The number of killed trees was small (~2–20/patch), not substantially increasing over time, and reflected infestations from varying years, which suggested low-level chronic beetle populations. Southwestern dwarf mistletoe had a moderate occurrence where 19–27% of surveyed plots had infected trees in northern Colorado, which is the northern limit of southwestern dwarf mistletoe distribution (Merrill et al., 1987; Beam, 2009).

In 2005 and 2006, stand and fuel conditions were measured in 150 fixed radius plots (0.04 ha) within the ponderosa pine forest type. Plots were established to represent four disturbance types: uninfested (38 plots), those infested with only dwarf mistletoe (17 plots), only bark beetles (37 plots) and both disturbances together (58 plots). Areas with biotic disturbances were located using aerial survey maps for mountain pine beetle (USDA and CSFS, 1996–2006 Aerial Detection Surveys http://www.fs.fed.us/r2/resources/fhm/aerialsurvey/) and local knowledge of dwarf mistletoe infestation areas (Merrill et al., 1987; Beam, 2009). When infested trees were encountered within a stand, plot center was determined by choosing a random distance and direction from an approximate disturbance center, while ensuring that plots were a minimum of 100 m apart. Plots with uninfested trees were established within 500 m of infested plots.

2.2. Sampling methods

Site characteristics recorded in each plot included percent slope, aspect (degrees), and elevation (m). For all live and dead trees with a measurable diameter at breast height (1.37 m, dbh), we recorded tree species, tree height (m), dbh, live crown length as a percentage of tree height, and height to bottom of live crown. Average quadratic mean diameter, height, density (trees/ha), basal area (m^2 ha^{-1}), and stand density index (SDI) were calculated for ponderosa pine and for all tree species combined. Thirty year (1971–2000) average annual maximum and minimum temperatures were assigned to all plots from PRISM 800 m resolution (PRISM Group at Oregon State University, 2006).

The dwarf mistletoe infection intensity on a tree was assessed on all living ponderosa pine using the Hawksworth dwarf mistletoe rating with a scale of zero to six (Hawksworth, 1977). Plot average dwarf mistletoe rating for a plot was calculated by averaging the dwarf mistletoe rating of all susceptible trees (i.e., both uninfested and infested ponderosa pine trees). To estimate time since tree mortality, tree degradation status was assessed for all dead trees attacked by bark beetles. If trees exhibited external symptoms of bark beetle infestation, bark beetle species were identified from gallery size and patterns; the larger mountain pine beetle makes a single vertical maternal gallery per mating pair and the smaller *Ips* spp. makes multiple maternal galleries originating from a single nuptial chamber. In a bark beetle-attacked tree, mountain pine beetle was considered the mortality agent if its galleries were present, otherwise mortality would be attributed to *Ips* spp. if only *Ips* spp. were present. Based on the amount of tree degradation, the time after tree mortality was classified as recent (1–3 years) or older (4–15 years). Tree degradation assessments and fall rates of dead trees by Keen (1955) and Schmid et al. (1985) were used to develop the years after tree mortality classes used in this study. Recent tree mortality had a degradation status that ranged from all red needles present to <10% red needles still remaining with full retention of twigs and bark. Old tree mortality had a degradation status that ranged from no needles present but some small twigs still present to >75% of bark missing and only large branches present.

Within each plot, three modified Brown's planar transects were used to measure downed woody material, each radiating from plot center at 120 degrees from each other (Brown, 1974). Each 11.35 m transect represented a plane that vertically extended to 2 m in height, where the counts of downed wood that intersected the plane were recorded. Downed woody material was characterized by the size class that represents the amount of estimated time to reach 63% equilibrium moisture content, assuming constant temperature and relative humidity (Brown, 1978). The standard time-lag classes for the diameter of downed woody material were: 1-h (<0.6 cm), 10-h (0.6–2.5 cm), 100-h (2.6–7.6 cm), and 1000-h (>7.6 cm). The 1- and 10-h downed woody material were counted along the middle 1 m of the 11.35 m transect; 100-h along the middle 3 m of the transect; and 1000-h along the middle 9 m. The duff depth and fuel bed were measured at three points along each transect, where duff was the decomposing organic layer above the mineral soil, and fuel bed was the vertical continuous available fuels from woody components. The cover of shrubs, grasses, and forbs was recorded as a percent of the length of the entire transect intersected by the cover type. Within a 0.001 ha plot placed in the center of the transect, all live and dead trees shorter than 1.37 m were counted and assessed for species and dwarf mistletoe rating.

2.3. Data analysis

To compare the density of trees pre-infestation (initial tree density) by bark beetles to the density of current live trees, a paired *t*-test was used. The initial tree density included trees that were live and less than about 15 years after death as we felt we could not adequately attribute tree death to bark beetles beyond that. After determining normality, homogeneity of variance, and lack of outliers, an ANOVA and Tukey–Kramer method were used to evaluate differences in stand characteristics and fuel complexes between the four disturbance types. Chi-squared tests were used to determine differences in distribution of diameter classes infested by each disturbance. Although tree growth and regeneration establishment occurred, in our calculations determining initial stand conditions, we did not remove the amount of biomass that could have accumulated on living trees since mortality or the amount of basal area from ingrowth of trees reaching dbh in the last 1–15 years since it is negligible in this dry area (Meyer, 1934; Mogren, 1956; Schubert, 1974). The percent of basal area growth per year ranges from 0.5% to 1.8% (Woodhouse et al., 2006, USDA FIA data available at: http://www.fia.fs.fed.us/) and the amount of annual ingrowth ranges from 0 to 10 trees (Mast et al., 1998; Kaufmann et al., 2000; Woodhouse et al., 2006) in our study site. Furthermore, the amount of growth release in live trees resulting from endemic bark beetle-caused tree mortality in the stand is negligible due to the low amount of trees in the stand killed (4.5% of basal area was considered older mortality from bark beetles in bark beetle affected plots) and evidence of a lack of response due to outbreak mountain pine beetle attack in the same region (Kulakowski and Jarvis, 2011).

Downed woody material biomass and regeneration densities were modeled using a Generalized Linear Model (GLM) approach with a negative binomial distribution. For measures of fuel bed and canopy fuel characteristics, we also used a GLM approach with a lognormal distribution. The following site and stand characteristics from each plot were tested in all models as potential covariates: 30 year average annual mean, minimum and maximum temperatures, habitat type as defined by Peet (1981), aspect (categorized as north, south, east, and west), basal area, stems ha^{-1} and average tree height. Covariates that produced the lowest model Akaike's Information Criterion (AIC) score were kept in all models and included: 30 year average annual maximum temperature, basal area and tree height. AIC takes into account the number of covariates and model fit in determining relative model quality. These covariates were used to determine the relative influence of each disturbance agent while accounting for known factors that affect downed woody material biomass, fuel bed, and canopy characteristics.

We expressed results for analyses on count data (i.e. downed woody material) as incidence rate ratios, which are the exponentiated parameter estimates (β coefficients) and interpreted as the percent change in the dependent variable with a unit increase of the independent variable holding all other variables constant. An IRR value that is equal to one is interpreted as a one to one relationship between response and predictor variables, while values that are above one indicate that the rate of increase in the response variable is greater than the predictor variable. The reverse is true for IRR values that are below one. To interpret interactions, we used the simple slopes method, where one predictor variable (moderator) was recentered by one standard deviation above and below the mean. Then the slope of the independent variable from a regression with the transformed moderator variable was tested against zero. The data analysis for this paper was generated using SAS software, Version 9.3 (Copyright, SAS Institute Inc. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc., Cary, NC, USA).

3. Results

3.1. Infested stand characteristics

Although bark beetles and dwarf mistletoe both occurred in dense stands pre-disturbance, endemic bark beetles were associated with greater densities of ponderosa pine while stands with dwarf mistletoe had greater densities of all tree species as compared to uninfested plots (Table 1). In all plots, the most prevalent non-ponderosa pine species was Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) and made up on average 17% and 13% of stand density and basal area, respectively. The non-ponderosa pine species were a greater proportion of the small live and dead tree component (dbh < 15 cm) of the stand than ponderosa pine (chi-square = 47.3, df = 8, $p < 0.0001$). Stands with both bark beetles and dwarf mistletoe had characteristics of both individual disturbance types and had a greater density and basal area of all live and dead tree species and ponderosa pine, while also averaging smaller tree diameters compared to uninfested plots.

Bark beetle-infested trees made up an average of 26% of live and dead ponderosa pine density in bark beetle-affected plots, with

Table 1
Comparison of mean (standard error) stand characteristics in plots uninfested, with bark beetle-induced *Pinus ponderosa* mortality (*Dendroctonus ponderosae* and *Ips* spp.), with dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum*) infestation, and with both bark beetle and dwarf mistletoe infestations in northern Colorado, 2005–2006. Live and dead stand characteristics included trees that were live and less than about 15 years after death, while live trees were uninfested and live at time of sampling. Different letters denote significance at $P < 0.05$ between plot infestation types. The unit for basal area (BA) is $m^2\ ha^{-1}$, stand density index (SDI) is metric, and quadratic mean diameter (QMD) is in cm.

	Not infested ($n = 38$ plots)	Bark beetle ($n = 37$ plots)	Dwarf mistletoe ($n = 17$ plots)	Bark beetle and dwarf mistletoe ($n = 58$ plots)	P-value
Live and dead trees					
Total trees ha^{-1}	811.3 (111.4) a	1198.3 (112.0) ab	1399.5 (165.0) b	1226.5 (94.5) b	0.0063
P. ponderosa ha^{-1}	369.0 (79.1) a	700.7 (79.5) b	584.3 (117.1) ab	899.5 (67.1) b	<0.0001
Total BA	23.7(1.6) a	29.1 (1.6) ab	31.2 (2.3) b	29.7 (1.3) b	0.0083
P. ponderosa BA	17.8 (1.7) a	22.7 (1.7) ab	19.6 (2.5) ab	24.3 (1.4) b	0.0147
Total SDI	426.2 (28.7) a	495.7 (28.9) ab	577.1 (42.5) b	511.6 (24.3) ab	0.0186
Total QMD	23.0 (0.9) a	19.2 (0.9) b	19.2 (1.4) ab	18.8 (0.8) b	0.0027
P. ponderosa QMD	27.1 (1.2) a	22.7 (1.2) b	21.6 (1.8) ab	20.5 (1.0) b	0.0004
Live trees					
Total trees ha^{-1}	610.4 (64.8) a	789.2 (65.2) ab	908.2 (96.0) b	768.7 (55.0) ab	0.0475
P. ponderosa ha^{-1}	369.5 (60.0) a	586.1 (60.1) b	545.2 (88.5) ab	612.6 (50.7) b	0.0117
Total BA	20.6 (1.4)	17.1 (1.5)	22.9 (2.1)	18.5 (1.2)	0.0939
P. ponderosa BA	17.1 (1.6)	13.5 (1.6)	18.5 (2.3)	15.3 (1.3)	0.2367
Total SDI	393.0 (26.7)	356.3 (26.9)	457.8 (39.6)	383.4 (22.7)	0.2006
Total QMD	23.2 (1.0) a	18.7 (1.0) b	19.3 (1.5) ab	18.1 (0.9) b	0.0009
P. ponderosa QMD	27.2 (1.3) a	21.6 (1.3) b	21.8 (1.9) b	21.0 (1.1) b	0.0018

mountain pine beetle attributed to 67% of bark beetle-caused mortality and *Ips* spp. making up the rest. The size classes of trees infested by each species of bark beetle were different with mountain pine beetle proportionally infesting more trees in diameter class 17.5 cm and greater than *Ips* spp., while *Ips* spp. proportionally infested more trees in diameter classes 2.5 cm and 7.5 cm (chi-square = 490.0, df = 16, $P < 0.0001$) (Fig. 1). Dwarf mistletoe-infested trees made up 73% of trees in dwarf mistletoe-infested stands, and infections were found on all size classes equally (chi-square = 13.1, df = 8, $P = 0.1090$).

The composition of bark beetle species may have been related to presence of dwarf mistletoe. This is evidenced by more *Ips* spp.-infested trees found in plots with the two disturbance types than plots with only bark beetles (104.9 ± 22.2 stems ha^{-1} and 25.4 ± 24.8 stems ha^{-1} respectively; $P = 0.0074$). By comparison, the density of mountain pine beetle-caused mortality was not different in plots with the two disturbance types and plots with only bark beetles.

Bark beetles infestations altered stand characteristics by reducing live ponderosa pine and total stand densities and basal areas

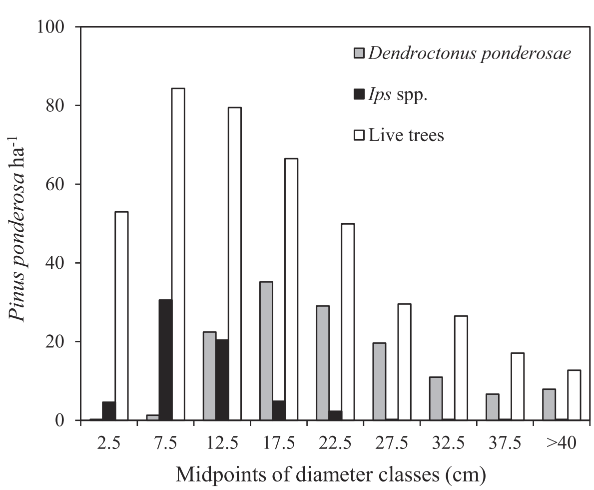

Fig. 1. Diameter distribution of live and uninfested, mountain pine beetle (*Dendroctonus ponderosae*)- and *Ips* spp.-infested *Pinus ponderosa* trees in plots with bark beetle-caused mortality ($n = 97$ plots, chi-square = 489.97, df = 16, $P < 0.0001$).

($P < 0.05$). While bark beetles and dwarf mistletoe initially infested stands with greater basal area than uninfested, tree mortality resulted in stands with the same live basal area as uninfested (Table 1). In comparison, there was not a change in stand conditions of plots with only dwarf mistletoe-infested trees between initial and current live trees. Additionally, there was mortality in the non-ponderosa pine species that was made up mainly of Douglas-fir in the smaller tree classes. The average height of live ponderosa pine (greater than 1.37 m in height) did not differ between disturbance types (data not shown).

Densities of live tree regeneration for all species and each species individually were not different between disturbance types (587 ± 123 seedlings ha^{-1}). The density of live Douglas-fir regeneration (260 ± 83 seedlings ha^{-1}) was twice that of live ponderosa pine, (127 ± 36 seedlings ha^{-1}) and together both species made up 66% of total live regeneration. On average, 5% of the regeneration was dead. In plots with dwarf mistletoe infested trees, 31% of live ponderosa pine regeneration had dwarf mistletoe infections.

3.2. Effects on downed woody material

The average amount of total downed woody material ranged from 12.3 Mg ha^{-1} to 29.5 Mg ha^{-1} between plots with different disturbance types (Table 2). The amount of biotic disturbance and the time since tree mortality were both important in describing the amount of downed woody material (Table 3). The analysis showed that there was an increase of up to 10% for the amount of downed woody debris in size classes 10-h to 1000-h for every increase of 1 $m^2\ ha^{-1}$ basal area of older mountain pine beetle-infested trees. In contrast, the basal area of recent mountain pine beetle-caused mortality was associated with a 9% decrease in 1000-h downed woody material. We did not find a relationship between *Ips* spp.-caused mortality and downed woody material, but did find that there was a 7% increase of 10-h downed woody material for every increase in dwarf mistletoe rating.

3.3. Effects on fuel bed and canopy characteristics

Individually, dwarf mistletoe and bark beetles did not explain the variability in fuel bed characteristics (Table 2). However, at high dwarf mistletoe ratings (DMR $\geqslant$ 4.6), the amount of mountain pine beetle-infested trees was positively related to fuel bed depth

Table 2
Summary statistics (mean [standard error]) for downed woody material biomass (Mg ha^{-1}), fuel bed and canopy characteristics in plots uninfested, with bark beetle-induced *Pinus ponderosa* mortality (*Dendroctonus ponderosae* and *Ips* spp.), with dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum*) infestation, and with both bark beetle and dwarf mistletoe infestations in northern Colorado, 2005–2006. Different letters denote significant differences at $P < 0.05$ between plot infestation types with a Tukey's adjustment.

	Not infested (n = 38 plots)	Bark beetle (n = 37 plots)	Dwarf mistletoe (n = 17 plots)	Bark beetle and dwarf mistletoe (n = 58 plots)	*P*-value
1-h (Mg ha^{-1})[a]	0.3 (0.1)	0.4 (0.1)	0.3 (0.04)	0.5 (0.05)	0.8892
10-h (Mg ha^{-1})[a]	1.3 (0.2) a	2.0 (0.3) ab	1.3 (0.4) a	2.5 (0.3) b	0.0111
100-h (Mg ha^{-1})[a]	2.1 (0.5)	1.9 (0.4)	1.4 (0.4)	3.2 (0.5)	0.0819
1000-h (Mg ha^{-1})[a]	8.6 (2.2) a	25.2 (5.6) b	10.7 (3.3) ab	20.7 (2.9) ab	0.0085
Duff depth (cm)[b]	1.8 (0.2)	2.6 (0.2)	2.2 (0.4)	2.0 (0.2)	0.0460
Fuel bed height (cm) (n = 149)[b]	13.1 (4.7)	8.0 (1.0)	7.7 (1.3)	10.7 (1.0)	0.6638
Understory vegetation percent cover[b]	32.3 (3.7)	28.1 (3.4)	23.1 (2.2)	30.6 (1.9)	0.7431
Total height to bottom of crown (m)[b]	1.5 (0.1)	1.6 (0.1)	1.5 (0.2)	1.5 (0.1)	0.4972
P. ponderosa height to bottom of crown (m)[b]	2.1 (0.2)	2.2 (0.2)	2.0 (0.2)	2.1 (0.2)	0.7295
Total percent live canopy[b]	77.9 (2.1)	61.8 (3.1)	69.5 (4.8)	71.9 (2.2)	0.0840
P. ponderosa percent live canopy[b]	75.1 (1.8)	58.3 (2.7)	69.5 (3.1)	63.5 (2.4)	0.1049

[a] Response variable fit to a negative binomial distribution.
[b] Response variable fit to a natural log distribution.

Table 3
Mean (standard error) downed woody debris and incidence rate ratios (standard errors) for main effects and covariates as explained by dwarf mistletoe rating (*Arceuthobium vaginatum* subsp. *cryptopodum*, DMR), basal area (m^2 ha^{-1}) of recent and older *Dendroctonus ponderosae* and *Ips* spp.-caused *Pinus ponderosa* mortality.

Downed woody material size classes	Average biomass (Mg ha^{-1})	DMR	Basal area of *D. ponderosae*-infested trees		Basal area of *Ips* spp.-infested trees	Canopy closure[a]	Total live tree basal area	Total live tree height (m)	30 year average annual maximum temperature (Celsius)
			1–3 years after infestation	4–15 years after infestation					
1-h	0.4 (0.03)	1.04 (0.06)	0.99 (0.04)	1.02 (0.03)	0.94 (0.09)	0.94 (0.33)	1.03 (0.01)	0.94 (0.06)	–[b]
10-h	1.9 (0.2)	**1.07 (0.03)**	0.99 (0.02)	**1.06 (0.02)**	1.03 (0.04)	1.04 (0.23)	1.01 (0.01)	1.02 (0.04)	0.97 (0.08)
100-h	2.4 (0.3)	1.09 (0.06)	0.94 (0.04)	**1.08 (0.03)**	0.99 (0.06)	1.12 (0.39)	1.00 (0.01)	0.93 (0.05)	1.02 (0.11)
1000-h	17.6 (2.0)	1.07 (0.05)	**0.91 (0.04)**	**1.10 (0.04)**	1.15 (0.09)	0.86 (0.32)	1.02 (0.02)	0.89 (0.05)	0.95 (0.11)

Note: Incidence rate ratios are from negative binomial regressions and are interpreted as ratios with values above one indicating a positive relationship and values below one indicating a negative relationship. Bolded values are significant at $p < 0.05$.
[a] Treatment effect for closed canopy.
[b] Removed covariate due to failure of model optimization.

and vegetation cover (Table 4). Site and stand conditions were also important in predicting fuel bed characteristics. Fuel bed characteristics were positively associated with average annual maximum temperature. Furthermore, total basal area was positively associated with duff depth, while negatively associated with vegetation cover.

Effects of disturbances were only evident on measures of canopy characteristics for ponderosa pine and these changes were not large enough to alter the total stand canopy characteristics (Table 4). Similar to fuel bed characteristics, the amount of bark beetle-caused mortality was not related to canopy characteristics. However, dwarf mistletoe infection affected the percent live ponderosa pine canopy with a 1% decrease for every increase of dwarf mistletoe rating. There was a significant interaction between dwarf mistletoe and mountain pine beetle in explaining ponderosa pine height to bottom of crown. Only at a low basal area of mountain pine beetle-infested trees was there a negative relationship between height to bottom of crown and dwarf mistletoe rating. As the basal area of mountain pine beetle increased, the relationship between height to bottom of crown and dwarf mistletoe rating became neutral. Stand conditions were also associated with changes in canopy characteristics with higher height to bottom of crowns and lower percent live canopy with greater total tree basal area. Furthermore, as the average stand height increased, so did the height to bottom of crown.

4. Discussion

4.1. Stand characteristics and regeneration

Endemic bark beetle-caused mortality and dwarf mistletoe occur in stands more dense than uninfested stands. Similar to Negrón and Popp (2004), mountain pine beetle occurred in stands with greater density of ponderosa pine ha^{-1} compared to uninfested stands. The trees that accounted for the high density in stands with dwarf mistletoe-infected trees consisted mainly of non-host species small diameter dead Douglas-fir. The dead Douglas-fir was mostly from a western spruce budworm (*Choristoneura occidentalis* Freeman) outbreak that ended in the mid-1980s (Swetnam and Lynch, 1989; Hadley and Veblen, 1993). Together mountain pine beetle, *Ips* spp., and dwarf mistletoe were infesting similarly dense stands with small diameter trees and the resulting mortality led to lower stand basal area and a potential shift in species composition. Structural diversity of infested stands was increased through the conversion of live trees to dead and selective host species mortality.

After severe mortality events that are selective to tree size and host species, such as mountain pine beetle outbreaks, it is the smaller size class trees and advanced regeneration that will determine forest successional trajectory (Collins et al., 2011; Kayes and Tinker, 2012). In the case of when all tree size classes are affected

Table 4
Relationship between measures of fuel bed and canopy fuel characteristics and dwarf mistletoe rating (*Arceuthobium vaginatum* subsp. *cryptopodum*, DMR), basal area (m^2 ha^{-1}) of *Dendroctonus ponderosae* and *Ips* spp.-infested *Pinus ponderosa*. Mean (standard error of the mean) of fuel bed and canopy fuel characteristic is presented. The regression coefficients (standard error) for the main effects, interactions, and covariates are presented for models fit to a log normal distribution.

	Mean	DMR	Basal area *D. ponderosae*-infested trees		Basal area of *Ips* spp.-infested trees	Canopy closure[a]	Total live tree basal area	Total live tree height (m)	30 year average annual maximum temperature (Celsius)
			Total infested trees	Interaction of DMR and total infested trees					
Duff depth (cm)	1.8 (0.2)	−0.03 (0.02)	0.01 (0.01)	ns	0.03 (0.03)	0.10 (0.13)	**0.02 (0.01)**	−0.01 (0.02)	**0.09 (0.04)**
Fuel bed height (cm) ($n = 149$)	13.1 (4.7)	−0.04 (0.04)	0.01 (0.02)	**0.01 (0.01)**	−0.02 (0.04)	−0.23 (0.20)	−0.01 (0.01)	0.03 (0.03)	**0.33 (0.07)**
Understory vegetation percent cover	32.3 (3.7)	−0.03 (0.03)	0.01 (0.01)	**0.01 (0.01)**	0.01 (0.03)	−0.14 (0.14)	**−0.01 (0.01)**	0.01 (0.02)	**0.18 (0.05)**
Total height to bottom of crown (m)	1.5 (0.1)	−0.02 (0.02)	0.01 (0.01)	ns	−0.03 (0.02)	**0.23 (0.11)**	**0.01 (0.01)**	**0.16 (0.02)**	−0.04 (0.04)
P. ponderosa height to bottom of crown (m)	2.1 (0.2)	**−0.07 (0.03)**	−0.01 (0.01)	**−0.01 (0.01)**	−0.03 (0.03)	0.02 (0.13)	**0.02 (0.01)**	**0.11 (0.02)**	0.04 (0.05)
Total percent live canopy	77.9 (2.1)	−0.01 (0.01)	−0.01 (0.01)	ns	−0.01 (0.01)	−0.05 (0.03)	**−0.01 (0.01)**	−0.01 (0.01)	0.01 (0.01)
P. ponderosa percent live canopy	75.1 (1.8)	**−0.01 (0.01)**	−0.01 (0.01)	ns	−0.01 (0.01)	−0.05 (0.03)	**−0.01 (0.01)**	0.01 (0.01)	0.02 (0.01)

Note: Bolded values are significant at $p < 0.05$.
[a] Treatment effect for closed canopy.

by host-specific disturbances, it will be the non-host species that may become the new dominant tree species. Therefore, endemic populations of bark beetles and dwarf mistletoe may cause small-scale shifts in species composition through mortality of host species of all size classes. The large component of non-host species of regeneration will contribute to an increase in the proportion of non-host species in small diameter classes with the potential of replacement of ponderosa pine as a dominant species (Keane et al., 1990). At a larger scale, fire suppression has also been a factor shifting this northern Colorado ponderosa pine forest towards non-host species, by fostering intensification of both dwarf mistletoe (Hawksworth, 1961) and less fire resistant non-host species during the longer modern fire return intervals (Kaufmann et al., 2000). It appears that the combination of endemic bark beetle and dwarf mistletoe infestations in small scattered patched throughout the forests may be contributing to a shift in dominance from ponderosa pine to non-host species, such as Douglas-fir, but at a smaller spatial scale than the effect of fire.

4.2. Effect of endemic disturbances on fuel complexes

The range of downed woody material in our study was similar to other forests where endemic bark beetles and other pathogens are present. Page and Jenkins (2007a) and Klutsch et al. (2009) reported that total downed woody material loads ranged from 20 to 40 Mg ha^{-1} in lodgepole pine not affected by epidemic mountain pine beetle. This range is comparable to the total downed woody material load for plots with endemic bark beetle infestation for our study area (29 mg ha^{-1}). Furthermore, the fine downed woody material load (1–100-h size classes) for ponderosa pine reported by Lundquist (2007) was higher (9 Mg ha^{-1}) than our study (5 Mg ha^{-1}). The differences in site conditions and stand history in the Lundquist (2007) study site may have influenced the difference in fine downed woody material amount. Battaglia et al. (2005) reported a range of 0–43 Mg ha^{-1} for total downed woody material in a Front Range ponderosa pine forest south of our study site. This range encompasses the downed woody material amounts found in our study area and also illustrates the high variability in downed woody material.

Unlike research on epidemic populations of bark beetles, few studies have compared stands with endemic bark beetle infestation to uninfested stands. Where we found greater downed woody material with increasing time since and amount of mountain pine beetle-caused mortality, Lundquist (2007) found the same downed woody material amount in stands with and without mountain pine beetle infested ponderosa pine. However, Lundquist (2007) did not report the amount of mortality and time since tree mortality by mountain pine beetle. The increase in downed woody material found in our study was also associated with timing of endemic mountain pine beetle. Older mountain pine beetle-caused tree mortality contributed more downed woody material found in infested plots than recent tree mortality. Studies in mountain pine beetle outbreaks also found that recent bark beetle-caused mortality were not associated with changes in downed woody debris (Page and Jenkins, 2007a; Klutsch et al., 2009). It was not until 15–20 years after initial infestation that downed woody debris loads increased due to tree fall in mountain pine beetle-infested lodgepole pine (Page and Jenkins, 2007a; Klutsch et al., 2009). The negative association between recent mountain pine beetle-caused mortality and 1000-h downed woody material may be due to stand characteristics, such as stand history, that we did not measure.

There have been a few studies that identified relationships between dwarf mistletoe and fuel load amounts. These studies identified greater downed woody material in most size classes in highly infested stands (Koonce and Roth, 1985; Hoffman et al., 2007; Stanton and Hadley, 2010). In our study, we found the amount of 10-h downed woody material was positively related to dwarf mistletoe rating. Interestingly, only plots with both dwarf mistletoe and bark beetle infested trees had greater 10-h downed woody material amounts than uninfested plots, which indicates that the accumulation of multiple disturbances can lead to changes in downed woody material. It may be expected that fine downed woody material classes (1–100-h) would increase in dwarf mistletoe infested stands due to the increase in branch growth and reduction in bole radial growth of infected trees (Hawksworth and Wiens, 1996; Hoffman et al., 2007). Furthermore, dwarf mistletoe-induced production of abnormal tree growth in the form of witches' brooms along with the decrease in percent live crown with increasing dwarf mistletoe rating may contribute to changes in canopy fuel characteristics. Although the decrease in percent live canopy for ponderosa pine due to dwarf mistletoe infestation was low (i.e. 1% for every increase in dwarf mistletoe rating) and may not effectively alter fuel complexes to the point of influencing fire hazard, it represents the potential for reduced tree vigor (Assmann, 1970) and photosynthetic capacity (Meinzer et al., 2004). In the mixed species stands that comprise northern Colorado, the total canopy fuel characteristics did not seem to be influenced by dwarf mistletoe infestation.

The temporally discrete disturbances of epidemic bark beetles can result in different impacts to downed woody debris than endemic disturbances that progress over decades. Not only are there greater increases in downed woody material due to epidemic mountain pine beetle (almost 700% increase in coarse woody material) (Page and Jenkins, 2007a) as compared to endemic (less than 200% increase in coarse woody material), but there are also differences in diversity of decomposition classes for downed woody material. A slow accumulation of dead trees from decades of endemic bark beetles and diseases results in trees of different time since mortality contributing to the overall downed woody material load (Sturtevant et al., 1997). This is compared to a bark beetle outbreak that is intense and concentrated during a few years where eventually trees of similar time since mortality will be contributing to the downed woody material load. The diversity of decomposition classes can be a more important positive factor for wildlife habitat and other biotic communities than the total amount of downed woody material (Harmon et al., 1986; Vanderwel et al., 2006). Endemic disturbances may be providing the benefits from downed woody material without significantly impacting fire hazard unlike epidemic disturbances such as mountain pine beetle outbreaks (Page and Jenkins, 2007b; Jenkins et al., 2008; Klutsch et al., 2011).

4.3. Interactions of endemic disturbances

The addition of *Ips* spp. to the mix of disturbance agents present in ponderosa pine forests influenced the quantity and size of coarse woody material contributed to infested stands. First, where both bark beetles are present, all size classes of trees were susceptible to infestation. Mountain pine beetle infestations selectively removed large diameter class trees (dbh > 15 cm), while *Ips* spp. selectively infested smaller diameter class trees. The small diameter trees infested by *Ips* spp. contribute less volume to total downed woody material than the relatively large diameter trees that mountain pine beetle selectively infest. Due to this, the impact of *Ips* spp. on downed woody material may have been obscured by other factors influencing downed woody material amounts and explain the lack of association between *Ips* spp.-infestation and changes in fuel complexes. The presence of dwarf mistletoe-infested ponderosa pine changed the composition of the bark beetle population and thus eventually downed woody material. There was four times more mortality due to *Ips* spp. in plots with dwarf mistletoe-infested trees than plots with only bark beetle-caused mortality. This relationship between *Ips* spp. and dwarf mistletoe also influences size classes of downed woody material. The size of downed woody material is important for fire hazard, with smaller sized wood contributing more to fire spread than larger wood. Furthermore, decomposition rates are influenced by downed woody debris size, which may impact the length of time the wood is on the forest floor and processes such as nutrient and carbon cycling.

Fuel bed and canopy characteristics were affected by interactions between dwarf mistletoe and mountain pine beetle-infested trees. Stands with high dwarf mistletoe ratings and mountain pine beetle-infested trees had greater fuel bed height and vegetation cover. Dwarf mistletoe infestation may be mediating the spatial arrangement of mountain pine beetle infestations within stands, which could lead to a greater response in understory vegetation. Dwarf mistletoe-infested trees tend occur in pockets with highly infested trees and dead trees toward the middle surrounded by trees with lower infection (Hawksworth and Wiens, 1996). This pattern is due to the dispersal mechanism of seeds as they are explosively discharged. When endemic mountain pine beetle infest these weakened trees, the pattern of tree mortality may be concentrated around dwarf mistletoe infestation centers. The interaction of mountain pine beetle infesting dwarf mistletoe centers may lead to larger areas of continuous canopy openings that could result in increased sun and moisture on the forest floor. When mountain pine beetles remove overstory trees the amount of sunlight and soil moisture change leading to increased percent cover of grasses, forbs, and shrubs (McCambridge et al., 1982a; Stone and Wolfe, 1996; McMillin et al., 2003). Additionally, the average annual maximum temperature was positively associated with understory characteristics. This pattern follows Peet's (1981) assessment of vegetation cover with greater vegetation cover at lower elevation ponderosa pine habitat types that would have higher temperatures as compared to north facing and higher elevation habitat types. In the absence of dwarf mistletoe infection, endemic mountain pine beetle that infest a single tree or a small group of trees may not lead to a large enough canopy gap for significant response by understory vegetation.

Furthermore, mountain pine beetle and dwarf mistletoe also interacted by altering height to bottom of live ponderosa pine crown. A lower height to bottom of ponderosa pine crown was associated with a combination of high dwarf mistletoe rating and low basal area of mountain pine beetle-infected trees. The infection of lower portions of tree crowns by dwarf mistletoe can result in the prevention of self-pruning of lower branches, which can lead to a lower height to bottom of live crown. The effect of dwarf mistletoe on height to bottom of crown may have been obscured in stands with high amount of dead trees from mountain pine beetle-infestation.

4.4. Management implications

Management of downed woody debris is becoming increasingly important as we understand more about its influence on ecosystem processes and fire hazard especially in the context of recent bark beetle outbreaks (Woodall et al., 2013). The input of coarse woody material in the spatially and temporally heterogeneous patches of endemic bark beetle and dwarf mistletoe-infested trees across the landscape can contribute to ecosystem processes such as regulating surface water runoff, increasing nutrient cycling and influencing soil and water chemistry (Harmon et al., 1986). Within the ponderosa pine forests of the Canyon Lakes Ranger District in northern Colorado, these disturbances are acting endemically and not contributing to changes in downed woody material outside the range found in similar ponderosa pine forests (Battaglia et al., 2005). Instead, these endemic disturbances are contributors to the high variability of downed woody material found in ponderosa pine forests.

The heterogeneity in forest composition, downed woody material, and fuel bed characteristics introduced into the forests with areas of endemic biotic disturbances may be a benefit for increased diversity in ecosystem services such as wildlife habitat and biodiversity among others (Harmon et al., 1986; Vanderwel et al., 2006). For instance, the increase in non-host species may not change the susceptibility of the entire forest to future bark beetle infestation (Amman and Baker, 1972; McCambridge et al., 1982b; Negrón et al., 2008), but will instead increase ecosystem resilience by fostering residual stands. Although forest management may be appropriate to mitigate the impact of epidemic bark beetle populations and dwarf mistletoe infestations, the heterogeneity in forest structure provided by endemic biotic disturbances should be maintained. Incorporating the changes induced by endemic bark beetle and dwarf mistletoe on stand and fuel characteristics in future forest management planning will be important especially in urban interface areas that are throughout the Front Range of Colorado. Together these endemic disturbances create compositional and structural heterogeneity, which can be translated into spatiotemporally dependent patterns of different forest structures and species compositions.

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