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Impacts of mountain pine beetle outbreaks on lodgepole pine forests in the Intermountain West, U.S., 2004–2019

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ABSTRACT

Mountain pine beetle, Dendroctonus ponderosae Hopkins (Coleoptera: Curculionidae), is the most important forest insect in western North America. We determined causes and rates of tree mortality and changes in forest structure and composition associated with D. ponderosae outbreaks in the Intermountain West, U.S. during 2004–2019 based on a network of 125 0.081-ha circular plots installed in Colorado, Idaho, Montana, Utah and Wyoming. Incipient populations of D. ponderosae began in 2004; peaked in 2007; and returned to endemic levels in 2011 in Idaho, Montana, Utah and Wyoming. In Colorado, incipient populations began in 2004; peaked in 2009; and returned to endemic levels in 2012. A total of 5107 trees died, 98.6% were lodgepole pine, Pinus contorta Dougl. ex Loud. Fifteen contributing factors were identified, including (in order of importance, highest to lowest) D. ponderosae, unknown causes, pine engraver, Ips pini (Say), wind, breakage and/or adjacent tree fall, Pityogenes knechteli Swaine/Pityopthorus confertus Swaine, suppression, spruce beetle, Dendroctonus rufipennis (Kirby), root disease, western balsam bark beetle, Dryocoetes confusus (Swain), lodgepole pine dwarf mistletoe, Arceuthobium americanum Nutt. ex. Engelm., stem diseases, woodborers, North American porcupine, Erethizon dorsatum (L.), mule deer, Odocoileus hemionus (Rafinesque), and lodgepole pine beetle, Dendroctonus murrayanae Hopkins. Most tree mortality (68.8%) was attributed solely to D. ponderosae, although D. ponderosae also occurred in association with other contributing factors. Overall, significant reductions in mean dbh (by 5.3%), mean quadratic mean diameter (by 8.6%), mean tree height (by 15.9%), mean number of trees (by 40.8%), mean basal area (by 52.9%), and mean stand density index (SDI) (by 51.8%) were observed. Significant reductions in tree density were observed in all diameter classes, except the smallest (midpoint = 10 cm, 5-cm classes). Significant increases in the mean number of snags (by 1324.7%) were observed, and most snags remain standing (71.3%). Pinus contorta remains the dominant tree species, and while significant increases in the number of subalpine fir, Abies lasiocarpa (Hooker) Nuttall, seedlings and saplings were observed, a long-term shift in tree composition is unlikely. Tree mortality (number of trees killed) was positively correlated with the initial number of live trees, basal area of live trees, SDI, and aspect, but not slope or elevation. The implications of these and other results to recovery and management of P. contorta forests in the Intermountain West are discussed.

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1. Introduction

Mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), is the most important forest insect in western North America where it colonizes at least 15 *Pinus* species, most notably lodgepole pine, *Pinus contorta* Dougl. ex Loud. (Negrón and Fettig, 2014). The geographic distribution of *D. ponderosae* generally reflects the range of its primary hosts, although *P. contorta* extends further northward and other *Pinus* further southward than where *D. ponderosae* populations currently exist (Bentz et al., 2010). *Pinus contorta* grows throughout the Rocky Mountain and Pacific Coast regions, and has four geographically-distinct varieties: shore pine, *P. contorta* var. *contorta,* found in coastal areas of western North America; Bolander pine, *P. contorta* var. *bolanderi,* found in northwestern California, U.S.; Sierra lodgepole pine, *P. contorta* var. *murrayana,* found throughout much of California, and Rocky Mountain lodgepole pine, *P. contorta* var. *latifolia,* found from interior Alaska, U.S. (rare) and the Northwest Territories, Canada east to the Black Hills of South Dakota, U.S. and throughout much of the Rocky Mountains. Forests dominated by *P. contorta* cover nearly 26 million ha in western North America (Burns and Honkala, 1990). Outbreaks of *D. ponderosae* are most substantial in *P. contorta* var. *latifolia* (hereafter *P. contorta*) (Fettig et al., 2020). A century of research has produced a wealth of knowledge on *D. ponderosae*, much of which is captured in two recent syntheses (Safranyik and Wilson, 2006; Negrón and Fettig, 2014).

Dendroctonus ponderosae females initiate colonization of *P. contorta* in a behavioral sequence mediated by aggregation pheromones (Pitman et al., 1968, 1969; Ryker and Libbey, 1982) and host kairomones (Renwick and Vité, 1970; Borden et al., 1987; Miller and Lindgren, 2000). Once a host tree is selected, successful colonization requires overcoming tree defenses that consist of anatomical and chemical components that are both constitutive and inducible (Franceschi et al.,

2005). This can only be accomplished by recruitment of a critical minimum number of beetles to "mass attack" the tree and overwhelm tree defenses. Most hosts of *D. ponderosae* have well-defined resin duct systems, which are capable of mobilizing large amounts of oleoresin following wounding, and are considered the primary defense against bark beetle attack (Vité and Wood, 1961; Reid et al., 1967). There is some evidence that *D. ponderosae* orients to *Pinus* that are injured (Lerch et al., 2016) or diseased (Gara et al., 1984), particularly at endemic population levels (Boone et al., 2011), but this is not well substantiated. The killing of *Pinus* in groups is fundamental to the success of *D. ponderosae*, as the process of switching from an infested tree to an adjacent uninfested tree results in expansion of the infested area for the duration of an outbreak.

Since 2000, > 27 million ha have been impacted by *D. ponderosae* in western North America, with ~10.3 million ha occurring in the western U.S. (Fettig et al., 2020). The latter represents almost half of the total area impacted by all bark beetles combined during this period in the western U.S. *Dendroctonus ponderosae* is ranked as the most damaging forest insect on the National (U.S.) Insect and Disease Forest Risk Assessment (Krist et al., 2014), with a projected loss of ~65.8 million m^2 of basal area between 2013 and 2027. Some recent *D. ponderosae* outbreaks have occurred in areas where outbreaks were once uncommon, and *D. ponderosae* was detected for the first time in Nebraska, U.S. in 2009 (Costello and Schaupp, 2011), in Alberta, Canada in 2003 (Cudmore et al., 2010) and in the Northwest Territories in 2012 (Natural Resources Canada, 2013).

The extent and severity of recent *D. ponderosae* outbreaks have triggered concerns about short- and long-term impacts to forests and the many ecological goods and services they provide. Despite this, limited information is available that quantifies these impacts, and much of what we have learned comes from retrospective, short-term studies. The primary objective of our study was to determine the causes and
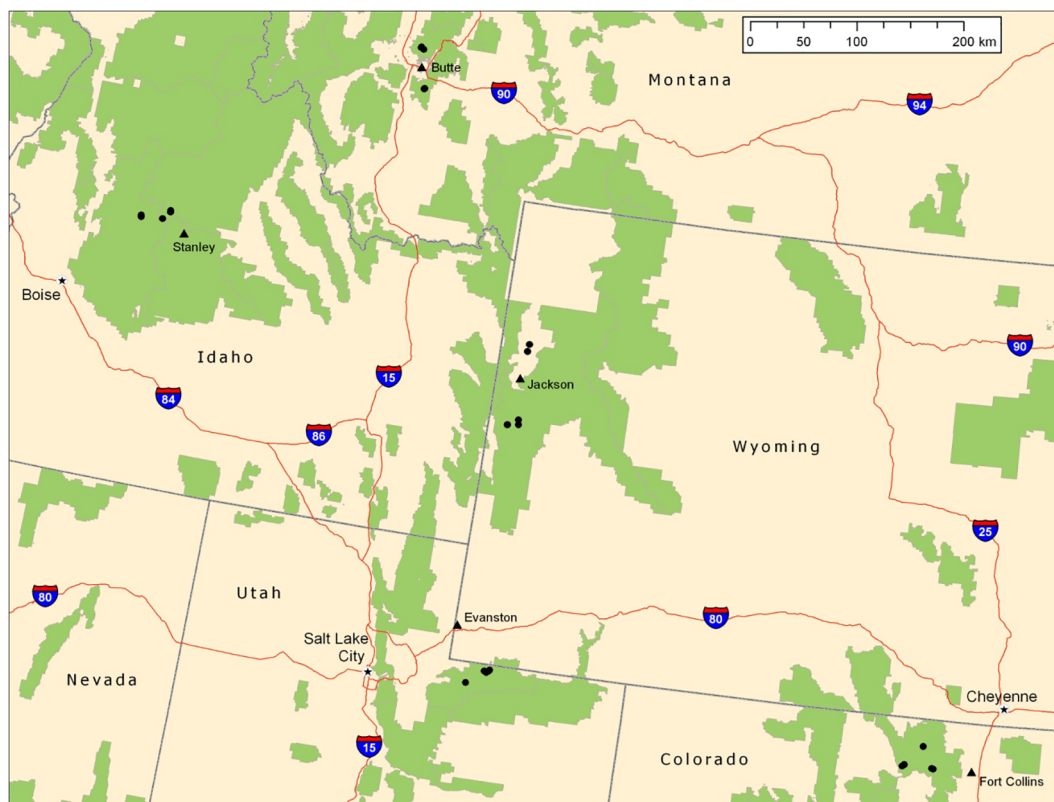

Fig. 1. Locations of experimental plots (filled circles, *n* = 25/state, but some overlapped due to scale) in Colorado, Idaho, Montana, Utah and Wyoming, U.S. Fifteen plots in Idaho were lost to wildfire and three plots in Wyoming were lost to tree cutting. Green depicts National Forest System lands administered by the USDA Forest Service. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

rates of tree mortality during and after *D. ponderosae* outbreaks based on a network of plots in five U.S. states (Colorado, Idaho, Montana, Utah and Wyoming), and to describe changes in forest conditions over time. The scope of our work encompasses areas where most of the tree mortality attributed to *D. ponderosae* has occurred in the western U.S. (Fettig et al., 2020). Herein, we concentrate on impacts to forest structure and composition based on responses of seedlings, saplings and trees.

2. Materials and methods

2.1. Study area and plot selection

A network of 125 0.081-ha circular plots was established in Colorado, Idaho, Montana, Utah and Wyoming (n = 25 per state) in 2010 (Fig. 1). For inclusion in the network, plots were required to be >50% *P. contorta* by basal area, and to contain a minimum of 10 *P. contorta* >13.9 cm dbh with evidence of at least two of these trees being colonized and/or killed by *D. ponderosae* within the last three years (as determined by crown condition, *see* 2.2). Plots meeting these criteria were randomly selected in groups of five, with plots within groups separated by ≥100 m. Within states, groups were separated by >1.6 km (mean distance ± SEM = 23.4 ± 3.0 km). Climate data for each group of plots were obtained for 2001–2010 and 2011–2019 from the Center for Forest Conservation Genetics, University of British Columbia (climatewna.com/). Fifteen plots were lost to high-severity wildfires in Idaho, and three plots were lost to tree cutting in Wyoming. These plots were excluded from our analyses. We refer to data from a single state by state, but caution the reader that the spatial scale of our network of plots is insufficient to capture the full diversity of impacts within each state.

2.2. Data collection and analyses

After plot establishment, all trees ≥7.62 cm dbh were tagged and the species, dbh, total height, height to the base of the live crown, status (live or dead), causal agent of mortality (when applicable), and year of death (when applicable) were recorded. For trees that died prior to plot establishment in 2010, year of death was estimated based on the color of faded needles in the crown and degree of needle and twig retention based on Klutsch et al. (2009) (i.e., 1 year prior, >90% retention of yellow and/or red needles; 2 years prior, ≥50–90% retention of red needles; 3 years prior, <50% retention of red needles; 4 years prior, no needle retention but small and large (5–7.62 cm diameter) twigs remain; 5 years prior, only large twigs remain; 6 years prior, both small and large twigs no longer remain). Trees that died prior to 2004 were ignored and excluded from our analyses.

For dead trees, a section of bark ~625 cm^2 was removed with a hatchet at ~1.7 m in height to determine if bark beetle galleries were present. The shape, distribution and orientation of galleries are commonly used to distinguish among bark beetle species (Furniss and Carolin, 1977). In some cases, the presence of entrance holes, boring dust, pitch tubes and deceased bark beetles were used to supplement identifications based on galleries. We attributed tree mortality to colonization by bark beetles only when these diagnostic characteristics were observed. The predominant bark beetle species causing tree mortality within our study was *D. ponderosae*, however, other bark beetle species were observed and are known to cause tree mortality (Furniss and Carolin, 1977). As such, we employed a conservative approach when attributing tree mortality to *D. ponderosae* in that only trees to which death was attributed solely to *D. ponderosae* were recorded as killed by *D. ponderosae*.

Three 16.1-m Brown's transects (Brown, 1974) were established at 0°, 120° and 240° from the plot center in order to measure fuels (data not shown). At the end of each transect, a 1-m^2 subplot was established in order to estimate forest floor composition, and beginning in 2012 a

complete census of each plot was conducted for invasive weeds (data not shown). A 3.6-m radius (0.004-ha) subplot was established at each plot center to estimate tree regeneration. All seedlings and saplings within the 0.004-ha subplot were identified to species and designated as seedlings (≤0.3 m tall) or saplings (>0.3 m tall and <7.6 cm dbh). Tree mortality and snag fall occurrences were recorded each year (2010–2019) while all other metrics were re-measured every fourth year (2010, 2014, 2018).

Several common stand measurements were calculated for live trees using data collected in 2010, 2014 and 2018 including dbh, quadratic mean diameter (QMD), height, basal area and stand density index (SDI). Percent composition by tree species was determined based on the number of live trees. Trees were partitioned into 5-cm dbh classes with mid-points of 10, 15, 20, 25, 30, and >32.5 cm in order to analyze tree density and tree mortality by causal agent within dbh class. The non-parametric, Kruskal-Wallis rank sum test (kruskal.test) was conducted to determine differences in means. When appropriate, a *post hoc* Dunn's multiple comparisons test (dunnTest) with a Bonferroni correction was used to identify which means differed. Linear regression (lm) was used to identify relationships between the number of trees killed and several variables. All analyses were conducted using R statistical software (3.6.3) in RStudio (1.2.5033) using the *stats*, FSA, MASS, and ggplot2 packages (R Core Team, 2020).

3. Results and discussion

Plots within our network ranged in elevation from 1919 m in Wyoming to 2991 m in Utah. Slopes ranged from 1% (several plots) to 40% in Colorado and Wyoming, with aspects of 0° (several plots) to 355° in Montana. Mean values (±SEM) are provided in Table 1. Mean annual temperature and precipitation increased slightly from 2001 to 2010 to 2011–2019 in all states except Utah where precipitation was unchanged (Table 1). Mean climatic water deficit, a measure of evaporative demand that exceeds available water computed as potential evapotranspiration minus actual evapotranspiration (Stephenson, 1998), declined slightly in all states except Idaho (Table 1).

3.1. General trends and causes of tree mortality

Across our network of plots, tree mortality attributed to *D. ponderosae* peaked on an annual basis in 2007 in all states except Colorado (2009) (Fig. 2). Nationally, *D. ponderosae* activity peaked in 2009 when nearly 3.6 million ha were impacted that year based on aerial detection surveys (Fettig et al., 2020). The highest annual rates of tree mortality were observed in Montana and Utah (22 and 23%, respectively). Idaho and Wyoming experienced lower rates of peak mortality with Colorado exhibiting intermediate levels (Fig. 2). While peak annual rates of tree mortality attributed to *D. ponderosae* are rarely reported in the literature, our data are similar to those observed for ponderosa pine, *P. ponderosa* Dougl. ex Laws., in South Dakota, U.S. (Schmid and Mata, 2005). As estimated from their data (Schmid and Mata, 2005), annual mortality peaked at 32.8%. We observed a slight increase in tree mortality in 2017 (Fig. 2), during which 60% of tree deaths (55 of 93 trees) were attributed to wind events.

A total of 5107 trees died across our network of plots, 98.6% were *P. contorta*. We identified 15 mortality agents with the five most prevalent (Fig. 3) responsible for 97% of the observed tree mortality. On occasion more than one agent was identified for the same tree, and therefore the total below (among agents) exceeds the total number of trees killed. In order of relative importance (number of trees and predominate tree species affected), tree mortality was attributed to *D. ponderosae* (3,512 trees, *P. contorta*, Fig. 3B), unknown causes (944 trees, *P. contorta*), pine engraver, *Ips pini* (Say) (265 trees, *P. contorta*), wind, breakage and/or adjacent tree fall (258 trees, *P. contorta*), *Pityogenes knechteli* Swain/ *Pityopthorus confertus* Swaine (239 trees, *P. contorta*), suppression (53 trees, *P. contorta*), spruce beetle, *Dendroctonus rufipennis* (Kirby) (32

Table 1

Topographic, climatic and structure and composition variables during and after *Dendroctonus ponderosae* outbreaks in *Pinus contorta* forests in the Intermountain West, U.S.

	Colorado	Idaho	Montana	Utah	Wyoming	All
Elevation (m)	2814 ± 20	2094 ± 17	2018 ± 18	2841 ± 15	2059 ± 15	2434 ± 37
Aspect (°)	169 ± 20	239 ± 33	152 ± 18	163 ± 22	119 ± 24	160 ± 10
Slope (%)	20 ± 2	16 ± 3	19 ± 2	13 ± 1	11 ± 3	16 ± 1
Annual temperature (°C, 2001–2010)	3.1 ± 0.4	3.9 ± 0.1	3.5 ± 0.2	2.2 ± 0.1	3.7 ± 0.2	3.3 ± 0.3
Annual temperature (°C, 2011–2019)	3.5 ± 0.4	4.1 ± 0.1	3.6 ± 0.3	2.5 ± 0.1	3.8 ± 0.2	3.5 ± 0.3
Annual precip.[1] (cm, 2001–2010)	62.3 ± 6.1	98.7 ± 2.2	57.9 ± 1.8	66.0 ± 3.1	68.1 ± 2.9	70.6 ± 7.2
Annual precip. (cm, 2011–2019)	68.5 ± 6.1	103.8 ± 2.6	65.1 ± 2.0	65.6 ± 2.6	75.7 ± 2.3	75.7 ± 7.3
Hargreaves CWD[2] (mm, 2001–2010)	310.4 ± 20.4	377.2 ± 16.1	240.4 ± 15.3	333.2 ± 9.8	405.2 ± 5.2	333.3 ± 28.5
Hargreaves CWD (mm, 2011–2019)	286.6 ± 14.7	392.4 ± 17.2	238.0 ± 14.1	310.4 ± 9.7	372.5 ± 11.7	320.0 ± 28.2
2004						
dbh (cm)	18.2 ± 0.2 a	17.8 ± 0.2 a	16.4 ± 0.1b	16.6 ± 0.1b	17.1 ± 0.3b	17.1 ± 0.1
Quadratic mean diameter (cm)	21.1 ± 0.5 a	19.9 ± 0.8 a	19.4 ± 1.0 a	21.7 ± 1.9 a	21.9 ± 0.9 a	20.9 ± 0.5
Tree height (m)	13.5 ± 0.1 d	17.2 ± 0.2b	18.0 ± 0.1 a	15.0 ± 0.1c	15.1 ± 0.2c	15.7 ± 0.1
Trees per ha	1169.8 ± 87.4 ab	1364.0 ± 96.1 a	1390.2 ± 112.1 a	1493.0 ± 181.1 a	772.2 ± 68.6b	1233.2 ± 63.3
Snags per ha	11.4 ± 1.7b	71.7 ± 21.9 a	32.1 ± 7.9 ab	44.5 ± 9.9 a	16.8 ± 3.5 ab	30.7 ± 4.2
Basal area (m² per ha)	38.4 ± 1.8 a	41.1 ± 2.3 a	36.1 ± 1.8 a	40.1 ± 2.5 a	26.8 ± 1.2b	36.1 ± 1.0
Stand density index	822.9 ± 41.7 a	895.7 ± 46.2 a	802.7 ± 39.4 a	854.3 ± 41.5 a	561.9 ± 21.5b	778.7 ± 20.4
% *Pinus contorta*	84.7 ± 3.0 bc	81.6 ± 3.5c	98.2 ± 0.5 a	89.8 ± 2.9 abc	94.5 ± 1.6 ab	90.8 ± 1.2
% *Pinus ponderosa*	0.7 ± 0.5 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.2 ± 0.1
% *Pinus flexilis*	5.1 ± 2.2 a	0.0 ± 0.0b	0.0 ± 0.0b	0.0 ± 0.0b	0.3 ± 0.3b	1.3 ± 0.5
% *Abies lasiocarpa*	3.4 ± 1.0b	16.7 ± 3.2 a	0.3 ± 0.9c	4.9 ± 1.7b	3.7 ± 1.3 bc	4.3 ± 0.7
% *Populus tremuloides*	1.4 ± 0.8 a	0.0 ± 0.0 ab	0.0 ± 0.0b	3.4 ± 2.4 ab	0.5 ± 0.5 ab	1.2 ± 0.6
% *Pseudotsuga menziesii*	0.3 ± 0.2 a	0.1 ± 0.1 a	0.7 ± 0.3 a	0.0 ± 0.0 a	0.5 ± 0.3 a	0.4 ± 0.1
% *Picea engelmannii*	4.5 ± 1.5 a	1.6 ± 0.6 a	0.8 ± 0.3 a	1.8 ± 1.0 a	0.4 ± 0.2 a	1.9 ± 0.4
2010						
dbh (cm)	15.3 ± 0.2b	16.8 ± 0.3 a	13.4 ± 0.2c	14.4 ± 0.1 d	14.3 ± 0.2 d	14.7 ± 0.1
Quadratic mean diameter (cm)	16.9 ± 0.4 a	18.7 ± 0.8 a	17.5 ± 1.7 a	20.3 ± 2.7 a	19.0 ± 1.3 a	18.4 ± 0.8
Tree height (m)	11.2 ± 0.1 d	14.6 ± 0.2 a	14.3 ± 0.1 a	12.5 ± 0.1b	12.1 ± 0.2c	12.8 ± 0.1
Trees per ha	813.0 ± 71.3 a	952.5 ± 60.8 a	717.1 ± 88.7 a	988.4 ± 144.7 a	586.3 ± 72.7 a	798.0 ± 48.0
Snags per ha	363.2 ± 30.8b	464.5 ± 53.3 ab	680.5 ± 50.3 a	563.9 ± 54.8 ab	199.9 ± 18.6c	460.1 ± 25.9
Basal area (m² per ha)	18.1 ± 1.6 ab	25.7 ± 1.4 a	13.5 ± 1.7b	18.4 ± 2.2 ab	14.1 ± 1.3b	17.0 ± 0.9
Stand density index	419.7 ± 37.0 ab	570.9 ± 28.2 a	309.1 ± 35.0b	396.3 ± 40.6b	312.6 ± 25.0b	380.5 ± 17.6
% *Pinus contorta*	81.8 ± 3.9b	78.7 ± 4.4 ab	95.9 ± 1.2 a	84.1 ± 3.9 ab	91.6 ± 2.2 ab	86.8 ± 1.6
% *Pinus ponderosa*	0.6 ± 0.6 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.1 ± 0.1
% *Pinus flexilis*	4.9 ± 2.3 a	0.0 ± 0.0 ab	0.0 ± 0.0b	0.0 ± 0.0b	1.1 ± 1.1b	1.7 ± 0.7
% *Abies lasiocarpa*	4.9 ± 1.6b	18.9 ± 4.0 a	0.6 ± 0.5c	8.3 ± 2.6b	5.1 ± 1.7 bc	6.1 ± 1.0
% *Populus tremuloides*	0.9 ± 0.5 a	0.0 ± 0.0 a	0.0 ± 0.1 a	4.1 ± 2.8 a	0.8 ± 0.8 a	1.5 ± 0.7
% *Pseudotsuga menziesii*	0.5 ± 0.3 a	0.0 ± 0.0 a	2.2 ± 1.1 a	0.0 ± 0.0 a	0.8 ± 0.4 a	0.8 ± 0.3
% *Picea engelmannii*	6.4 ± 2.4 a	2.3 ± 0.8 a	1.4 ± 0.6 a	3.6 ± 1.8 a	0.6 ± 0.3 a	3.1 ± 0.7
2014						
dbh (cm)	15.5 ± 0.2b	17.3 ± 0.3 a	14.4 ± 0.2 d	14.9 ± 0.1 cd	15.3 ± 0.2 bc	15.3 ± 0.1
Quadratic mean diameter (cm)	17.6 ± 0.4 a	19.0 ± 0.8 a	18.4 ± 2.0 a	20.8 ± 2.8 a	19.3 ± 1.4 a	19.0 ± 0.8
Tree height (m)	11.4 ± 0.1 d	14.9 ± 0.2 a	14.5 ± 0.1 a	12.8 ± 0.1b	12.2 ± 0.2c	13.0 ± 0.1
Trees per ha	696.3 ± 77.8 a	879.7 ± 59.6 a	718.6 ± 88.6 a	934.0 ± 135.6 a	567.2 ± 71.0 a	747.7 ± 46.6
Snags per ha	435.9 ± 29.1b	481.8 ± 49.0 ab	695.3 ± 50.4 a	620.7 ± 61.4 ab	211.2 ± 16.6c	497.8 ± 26.6
Basal area (m² per ha)	16.3 ± 1.7 ab	24.3 ± 1.4 a	14.3 ± 1.7b	18.2 ± 2.1 ab	14.1 ± 1.3b	16.6 ± 0.8
Stand density index	373.4 ± 39.2b	537.8 ± 27.7 a	323.2 ± 35.2b	390.0 ± 37.3 ab	309.9 ± 27.1b	367.8 ± 17.1
% *Pinus contorta*	79.6 ± 4.2b	75.5 ± 4.2b	94.9 ± 1.4 a	84.8 ± 3.9 ab	88.3 ± 3.1 ab	85.8 ± 1.7
% *Pinus ponderosa*	0.3 ± 0.3 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.1 ± 0.1
% *Pinus flexilis*	6.7 ± 2.9 a	0.0 ± 0.0b	0.0 ± 0.0b	0.0 ± 0.0b	1.3 ± 1.3b	1.8 ± 0.8
% *Abies lasiocarpa*	5.4 ± 1.8 bc	21.8 ± 3.8 a	0.7 ± 0.4c	7.5 ± 2.5b	7.1 ± 2.2 bc	6.7 ± 1.1
% *Populus tremuloides*	1.2 ± 0.8 a	0.0 ± 0.0 a	0.0 ± 0.1 a	4.0 ± 2.7 a	1.2 ± 1.2 a	1.5 ± 0.7
% *Pseudotsuga menziesii*	0.5 ± 0.3 a	0.1 ± 0.1 a	2.7 ± 1.4 a	0.0 ± 0.0 a	0.9 ± 0.4 a	0.9 ± 0.3
% *Picea engelmannii*	6.2 ± 2.2 a	2.6 ± 0.9 a	1.7 ± 0.7 a	3.7 ± 1.8 a	1.3 ± 0.7 a	3.2 ± 0.7
2018						
dbh (cm)	16.5 ± 0.2b	17.8 ± 0.3 a	15.6 ± 0.1c	15.5 ± 0.1c	16.8 ± 0.2b	16.2 ± 0.1
Quadratic mean diameter (cm)	17.9 ± 0.4 a	19.1 ± 0.7 a	18.7 ± 1.7 a	20.7 ± 2.6 a	19.4 ± 1.3 a	19.1 ± 0.8
Tree height (m)	11.4 ± 0.1 d	15.0 ± 0.2 a	14.5 ± 0.1 a	13.2 ± 0.1b	12.4 ± 0.2c	13.2 ± 0.1
Trees per ha	699.3 ± 81.2 a	842.6 ± 51.1 a	716.6 ± 85.7 a	861.9 ± 121.3 a	577.9 ± 67.4 a	729.8 ± 43.3
Snags per ha	389.9 ± 29.1 a	453.4 ± 35.5 a	547.6 ± 50.3 a	606.9 ± 66.7 a	166.2 ± 15.7b	437.4 ± 26.2
Basal area (m² per ha)	16.6 ± 1.8 ab	23.8 ± 1.5 a	15.4 ± 1.7 ab	17.9 ± 2.0 ab	15.0 ± 1.4b	17.0 ± 0.8
Stand density index	379.4 ± 41.7 ab	524.6 ± 29.4 a	344.7 ± 35.7b	383.7 ± 36.0 ab	326.7 ± 27.5b	375.0 ± 17.0
% *Pinus contorta*	78.2 ± 4.3b	73.4 ± 4.5b	93.1 ± 2.0 a	85.2 ± 3.7 ab	85.7 ± 3.6 ab	84.4 ± 1.7
% *Pinus ponderosa*	1.0 ± 0.7 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.2 ± 0.2
% *Pinus flexilis*	6.5 ± 2.8 a	0.0 ± 0.0b	0.0 ± 0.0b	0.0 ± 0.0b	2.3 ± 2.3b	2.0 ± 0.8
% *Abies lasiocarpa*	5.9 ± 1.9b	23.4 ± 3.7 a	0.9 ± 0.6c	7.9 ± 2.6b	8.5 ± 2.6b	7.4 ± 1.1
% *Populus tremuloides*	1.6 ± 1.2 a	0.0 ± 0.0 a	0.0 ± 0.0 a	4.0 ± 2.8 a	1.6 ± 1.4 a	1.6 ± 0.8
% *Pseudotsuga menziesii*	0.5 ± 0.3 a	0.5 ± 0.4 a	2.9 ± 1.5 a	0.0 ± 0.0 a	0.8 ± 0.4 a	1.0 ± 0.4
% *Picea engelmannii*	6.2 ± 2.2 a	2.7 ± 0.9 a	3.1 ± 1.1 a	2.9 ± 1.3 a	1.1 ± 0.5 a	3.3 ± 0.7

Values are mean ± SEM based on 0.081-ha circular plots (*n* = 25 plots per state, except for Idaho and Wyoming; all trees ≥7.6 cm dbh, diameter at 1.37 m in height). Means ± SEMs followed by the same letter within rows are not significantly different (*P* > 0.05).

[1] Precipitation.

[2] Climatic water deficit.

trees, Engelmann spruce, *Picea engelmannii* Parry ex Engelm.), root disease (22 trees, *P. contorta*), western balsam bark beetle, *Dryocoetes confusus* (Swain) [10 trees, subalpine fir, *Abies lasiocarpa* (Hooker) Nuttall], lodgepole pine dwarf mistletoe, *Arceuthobium americanum* Nutt. ex. Engelm. (9 trees, *P. contorta*), stem diseases (6 trees, quaking aspen, *Populus tremuloides* Michx.), woodborers (5 trees, *Po. tremuloides*), North American porcupine, *Erethizon dorsatum* (L.) (4 trees, *P. contorta*), mule deer, *Odocoileus hemionus* (Rafinesque) (2 trees, *P. contorta*), and lodgepole pine beetle, *Dendroctonus murrayanae* Hopkins (1 tree, *P. contorta*). *Pityogenes knechteli* and *Pity. confertus* are common associates of *D. ponderosae* (Bartos and Schmitz, 1998) and often co-occur in the same host. Their galleries were difficult to distinguish under field conditions, and as such we considered *Pit. knechteli/Pity. confertus* as one mortality factor. Suppression was assigned as the cause of death when evidence of other contributing factors (e.g., bark beetles, pathogens, and mechanical damage) was absent, and if little or no direct sunlight was received from above or on the sides of the crown (USDA Forest Service, 2018).

Most tree mortality was attributed solely to *D. ponderosae* (68.8%). We were unable to confidently identify a mortality agent (unknown causes) for 18.4% of trees, but presumably *D. ponderosae* was a contributing factor in some of these deaths as sampling for bark beetle galleries was limited to the lower bole. Of note, seven *Pi. engelmannii* (25.1 ± 3.2 cm dbh) were colonized by *D. ponderosae* on six plots in Colorado. While rare, *D. ponderosae* is known to colonize non-*Pinus* members of Pinaceae (e.g., including Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, *Abies* spp., *Larix* spp. and *Picea* spp.) especially when located near *Pinus* colonized by *D. ponderosae* (Gibson et al., 2009). However, successful brood production usually does not occur (Gibson et al., 2009). Interestingly, Huber et al. (2009) observed reproduction of *D. ponderosae* in interior hybrid spruce, *Picea engelmannii × glauca*, in British Columbia, Canada, and reported reproductive performance (i.e., offspring produced per mating pair of *D. ponderosae*) was higher in *Pi. engelmannii × glauca* than in nearby *P. contorta*. Wind was responsible for 5.1% of tree deaths in 80.4% of plots (86/107), with the majority (96.5%) occurring in 2010 or later. Average tree density decreased by 567 trees per ha (56%) prior to the occurrence of tree mortality due to wind. Given well-established increases in wind velocities within stands impacted by *D. ponderosae* (e.g., Hoffman et al., 2015), it follows that much of the tree mortality attributed to wind is an indirect consequence of *D. ponderosae*. Two other bark beetles, *I. pini* and *Pit. knechteli,* were the second and third leading biological agents of tree mortality. We attributed mortality of one *P. contorta* to *D. murrayanae* (16.5 cm dbh) in Wyoming given the density of entrance holes observed at the base of the tree. While *D. murrayanae* has received little study, it is not regarded as an important tree killer (Furniss and Kegley, 2008).

3.2. Forest conditions in 2004

Across our network of plots, mean dbh for all tree species was 17.1 ± 0.1 cm in 2004 (Table 1). Trees in Colorado and Idaho had significantly larger dbh than trees in Montana, Utah and Wyoming ($\chi^2 = 104.0$, $df = 4$, $P < 0.001$) (Table 1). No other significant differences in dbh or in QMD were observed ($\chi^2 = 7.4$, $df = 4$, $P = 0.11$; Table 1). Trees in Montana were significantly taller than in any other state, and significantly shorter in Colorado than in any other state ($\chi^2 = 1089.7$, $df = 4$, $P < 0.001$) (Table 1). Mean number of trees per ha across all plots was 1233.2 ± 63.3 (Table 1). Number of trees per ha was significantly greater in Idaho, Montana and Utah than in Wyoming ($\chi^2 = 19.5$, $df = 4$, $P < 0.001$). Basal area ($\chi^2 = 27.8$, $df = 4$, $P < 0.001$) and SDI ($\chi^2 = 34.2$, $df = 4$, $P < 0.001$) were significantly lower in Wyoming than in the other four states (Table 1).

Based on numbers of live trees, all plots were dominated by *P. contorta* ranging from 81.6 ± 3.5% in Idaho to 98.2 ± 0.5% in Montana (Table 1). Significantly higher percentages of *P. contorta* occurred in Montana than Colorado and Idaho ($\chi^2 = 27.8$, $df = 4$, $P < 0.001$). *Abies lasiocarpa* was the second most abundant tree species in all states except Colorado (limber pine, *Pinus flexilis* James, 5.1 ± 2.2%) and Montana (*Pi. engelmannii*, 0.8 ± 0.3%). Significantly higher percentages of *A. lasiocarpa* occurred in Idaho than in any other state ($\chi^2 = 32.7$, $df = 4$, $P < 0.001$). Significantly higher percentages of *P. flexilis* occurred in Colorado than in any other state ($\chi^2 = 20.3$, $df = 4$, $P < 0.001$), and the species was absent from our plots in Idaho, Montana and Utah. Significantly higher percentages of *Po. tremuloides* occurred in Colorado than Montana ($\chi^2 = 10.8$, $df = 4$, $P = 0.03$) (Table 1). *Populus tremuloides* was the only deciduous tree species observed in our study. *Pinus contorta*, *P. ponderosa*, and *P. flexilis* are regarded as primary hosts of *D. ponderosae* (Negrón and Fettig, 2014); *A. lasiocarpa* is the primary host of *Dr. confusus* (McMillin et al., 2017); and *Pi. engelmannii* is the primary host of *D. rufipennis* in the Intermountain West (Jenkins et al., 2014a).

3.3. Comparisons between 2004 and 2018

Data describing forest conditions in 2010, 2014 and 2018, and comparisons among states are provided in Table 1. In this section, we focus on changes in forest condition between 2004 and 2018, the latter the most recent year that all variables were re-measured across our network of plots. Data from 2018 represent growth of all surviving trees since 2004 as well as ingrowth by saplings ≥7.62 cm dbh. Overall, mean dbh was significantly lower in 2018 than in 2004 ($\chi^2 = 72.8$, $df = 1$, $P < 0.001$), decreasing by ~1 cm (5.3%). Mean dbh decreased significantly from 2004 to 2010 ($\chi^2 = 411.2$, $df = 1$, $P < 0.001$), but
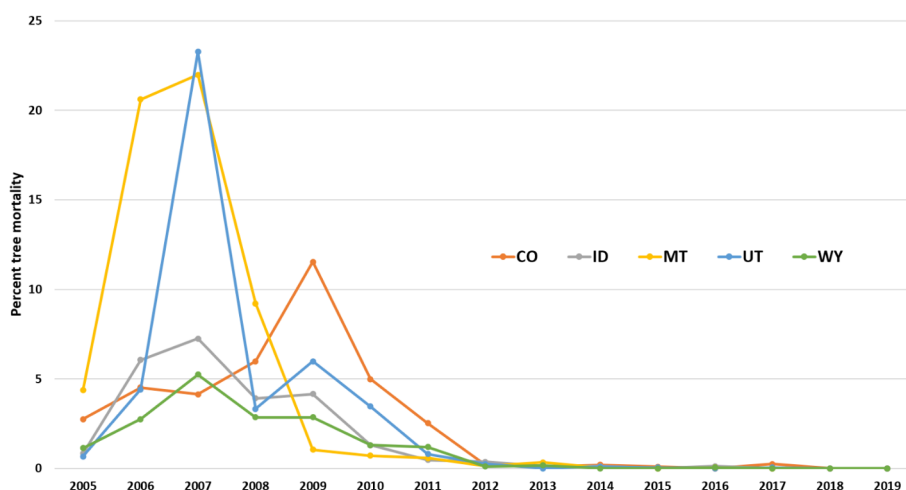

Fig. 2. Mean percent of *Pinus* killed during and after *Dendroctonus ponderosae* outbreaks in Colorado, Idaho, Montana, Utah and Wyoming, U.S., 2005–2019.
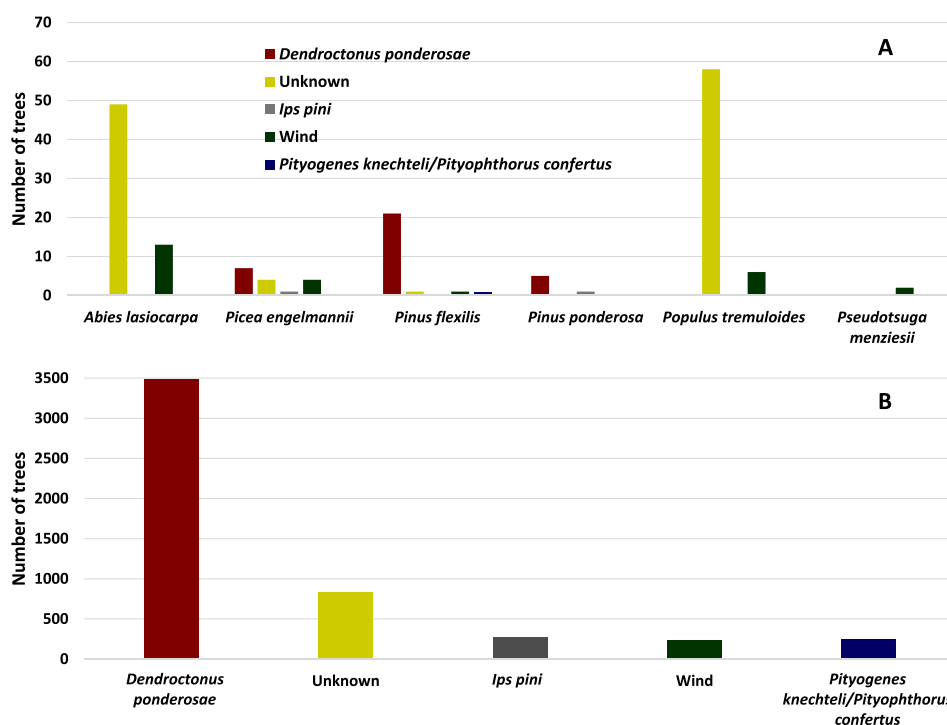
Fig. 3. Numbers of trees killed by the five most prevalent mortality agents for (A) *Abies lasiocarpa, Picea engelmannii, Pinus flexilis, Pinus ponderosa, Populus tremuloides* and *Pseudotsuga menziesii*, and (B) *Pinus contorta*, 2005–2019.

increased significantly from 2014 to 2018 ($\chi^2 = 42.5$, $df = 1$, $P < 0.001$). We attribute this increase in growth to increases in growing space due to the high levels of tree mortality observed (Oliver and Larson, 1996) (Table 1, Fig. 2). Interestingly, no differences in mean dbh were observed between 2004 and 2018 for Idaho ($\chi^2 = 0.003$, $df = 1$, $P = 0.96$) and Wyoming ($\chi^2 = 0.09$, $df = 1$, $P = 0.77$). Overall, mean QMD was significantly lower in 2018 than in 2004 ($\chi^2 = 10.4$, $df = 1$, $P = 0.001$), decreasing by ~0.8 cm (8.6%). Similar responses have been documented following other *D. ponderosae* outbreaks in the western U.S. and Canada (Romme et al., 1986; Dordel et al., 2008). Mean tree height was significantly lower in 2018 than in 2004 ($\chi^2 = 873.1$, $df = 1$, $P < 0.001$), decreasing by ~2.5 m (15.9%).

Overall, mean number of live trees per ha was significantly lower in 2018 than in 2004 ($\chi^2 = 37.3$, $df = 1$, $P < 0.001$), decreasing by ~500 trees per ha (40.8%) (Fig. 4). Despite incongruences in the mean number of live trees per ha among states in 2004, no differences were observed in 2018 ($\chi^2 = 6.1$, $df = 4$, $P = 0.19$) (Table 1). As in 2004, mean basal area differed among states in 2018, and again Idaho had the highest basal area and Wyoming the lowest (Table 1, Fig. 5). Overall, mean basal area was significantly lower in 2018 than in 2004 (Table 1; $\chi^2 = 114.5$, $df = 1$, $P < 0.001$), decreasing by ~19 m^2 per ha (52.9%). Colorado, Montana and Utah experienced basal area reductions of >55%. Basal area was significantly lower in 2010, 2014 and 2018 than in 2004 (Fig. 5; all $\chi^2 \geq 22.3$, all $df = 3$, all $P < 0.001$) (Fig. 5). Overall, mean SDI was significantly lower in 2018 than 2004 ($\chi^2 = 10.7$, $df = 1$, $P < 0.001$), decreasing by ~404 (51.8%). The observed reduction in mean SDI for each state from 2004 to 2018 was also highly significant for each pairwise comparison (all $\chi^2 \geq 14.3$, all $df = 1$, all $P < 0.001$). Reductions in the densities of *P. contorta* attributed to *D. ponderosae* were the biggest driver of these effects. Trends in *P. contorta* mortality are available from USDA Forest Service Forest Inventory and Analysis (FIA) data for the Intermountain West, and suggest our results are indicative of larger regional trends (Werstak et al., 2016; Thomson et al., 2017; DeRose et al., 2018; Witt et al., 2019a,b).

In Colorado, Klutsch et al. (2009) reported numbers of *P. contorta* and basal area of *P. contorta* declined by 62% and 71%, respectively, in plots infested by *D. ponderosae*. Pelz and Smith, (2012) reported that ~50% of *P. contorta* were killed by *D. ponderosae* during an outbreak in the late 1970s and early 1980s on the White River National Forest, Colorado, but that after 30 years stands recovered 91% of their original basal area. In our study, stands have only recaptured 47.1% of their original basal area, with a slight increase in basal areas observed between 2014 and 2018 (Table 1). Overall, mean number of snags was significantly greater in 2018 than 2004 ($\chi^2 = 149.2$, $df = 1$, $P < 0.001$), although much of this effect was attributed to increases occurring between 2004 and 2010 (Table 1). FIA data also corroborates these observations (Werstak et al., 2016; Thomson et al., 2017; DeRose et al., 2018; Witt et al., 2019a,b). Snags provide critical habitat for many fauna, and snags (and exposed dead wood in live trees) are required for roosting, feeding and nesting habitat by at least 85 species of birds in North America (Scott et al., 1977). Bollenbacher et al. (2008) provided estimates of snag densities in Montana forests as a supplement to regional protocols describing optimal densities for wildlife. They reported that on the Beaverhead-Deerlodge National Forest snags ≥25.4 cm dbh averaged 26.2 per ha in wilderness/roadless areas, and 7.2 per ha outside wilderness/roadless areas. In 2018, the mean number of snags across our network, which includes plots from the Beaverhead-Deerlodge National Forest, was nearly 17-fold higher (437.4 per ha). Presumably this is to the enrichment of snag-dependent species in the near-term. However, all snags will eventually fall to the forest floor increasing the amount of downed woody debris important to other wildlife species, perhaps resulting in a paucity of habitat for snag-dependent wildlife. Both snags and large accumulations of downed woody debris also represent important safety concerns. For example, increased difficulties in fireline construction and establishment of access, egress, and escape routes have been reported in forests heavily impacted by *D. ponderosae* in the Intermountain West (Jenkins et al., 2014b). Tree mortality (numbers of trees killed) was positively correlated with aspect ($F_{1,\ 105} = 4.85$, $P = 0.03$, $R^2 = 0.04$), but not slope ($F_{1,\ 105} = 3.77$,
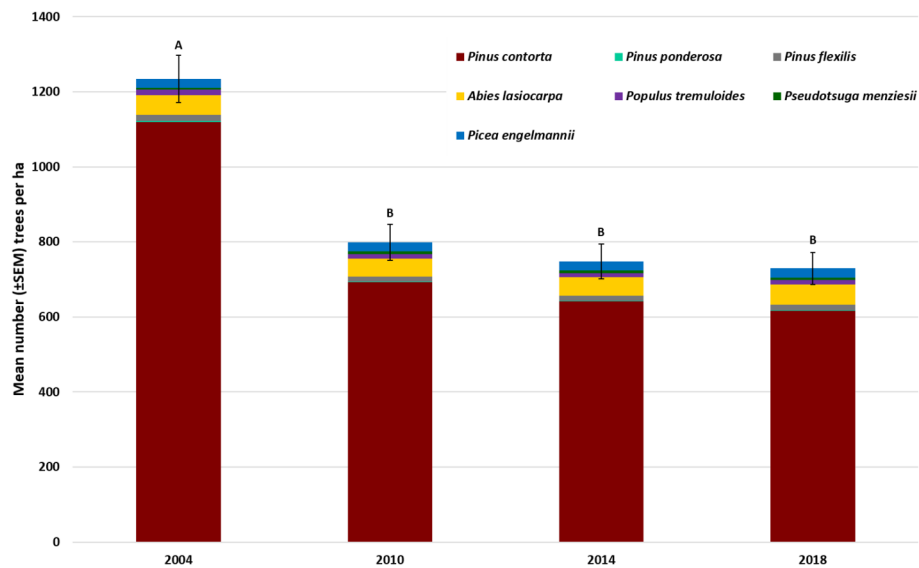
Fig. 4. Mean number of live trees per ha (±SEM) by year across five U.S. states (Colorado, Idaho, Montana, Utah and Wyoming) partitioned by species. Means (±SEMs) followed by the same number are not significantly different ($P > 0.05$).

$P = 0.06$) or elevation ($F_{1, 105} = 1.54$, $P = 0.22$). Kaiser et al. (2013) reported *D. ponderosae* infestations were more likely to occur on south-facing slopes and other areas of lower topographic wetness in Montana.

Despite the high levels of *P. contorta* mortality, *P. contorta* remains the dominant tree species (Table 1, Fig. 4), and no difference was observed in the overall percentage of *P. contorta* between 2004 and 2018 ($\chi^2 = 1.4$, $df = 1$, $P = 0.24$). Mean percentage of *P. contorta* was similar among states, except for in Montana where *P. contorta* represented a higher percentage of composition than in Colorado and Idaho ($\chi^2 = 17.2$, $df = 4$, $P = 0.002$) (Table 1). *Abies lasiocarpa* remained the second most dominant tree species in all states except for Colorado and Montana, where *P. flexilis* and *Pi. engelmannii* were well represented. Overall, *A. lasiocarpa* increased across our network of plots by ~72% ($\chi^2 = 6.2$, $df = 1$, $P = 0.01$).

3.4. Tree mortality by diameter class and density

Significant reductions in tree abundance were observed for all dbh classes except the smallest (10 cm dbh) ($\chi^2 = 1.2$, $df = 1$, $P = 0.28$; Fig. 6). The pattern observed in Fig. 6 was consistent in each state with the exception of a 4% increase in the number of trees from 2004 to 2019 in the 10-cm diameter class in Wyoming. Density was reduced the most for trees ≥17.5 cm dbh ($P < 0.001$, in all cases). When we examined percent mortality of all trees within each dbh class by mortality agent (*D. ponderosae* vs. other), differences were observed among dbh classes within each mortality agent, and between mortality agents within dbh class. *Dendroctonus ponderosae* killed a greater percentage of trees in the 25, 30, and ≥32.5-cm dbh classes than in the 10, 15 and 20-cm dbh classes ($\chi^2 = 323.6$, $df = 5$, $P < 0.001$) (Fig. 7). *Dendroctonus ponderosae* was responsible for relatively little tree mortality in the two
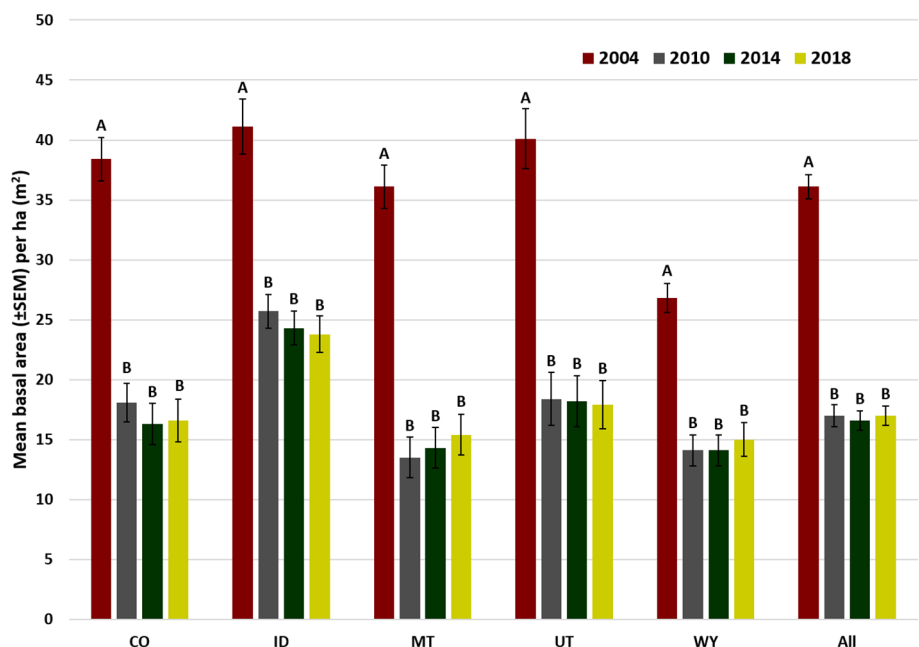

Fig. 5. Mean basal area of live trees (m² per ha ± SEM) by state (Colorado, Idaho, Montana, Utah and Wyoming) and for all states in 2004, 2010, 2014 and 2018. Means were compared within a given state and not among states. Means (±SEMs) followed by the same number are not significantly different ($P > 0.05$).
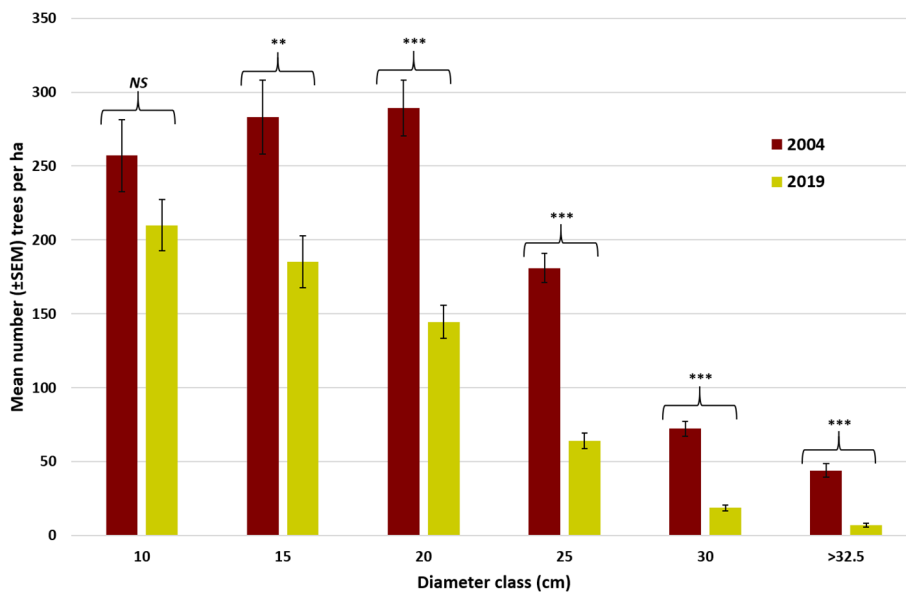
Fig. 6. Mean number of live *Pinus* per ha (±SEM) by diameter class (mid-point of 5-cm diameter classes, except for largest). 2019 values reflect the most recent assessment of mortality while assuming the same diameter classes as determined from sampling in 2018. Means were compared within each diameter class. Asterisks above brackets indicate significance levels: * = $P < 0.05$; ** = $P < 0.01$; and *** = $P < 0.001$.
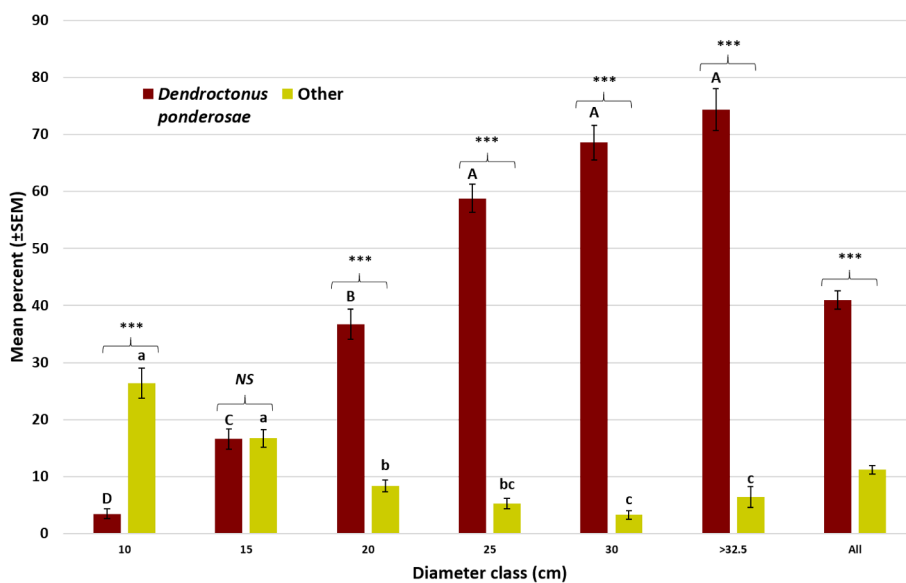

Fig. 7. Mean percent of trees killed (±SEM) by *Dendroctonus ponderosae* versus other mortality agents by diameter class (mid-point of 5-cm diameter classes, except for largest). Means were compared between mortality agents within each dbh class and are designated by brackets. Asterisks above brackets indicate significance levels: * = $P < 0.05$; ** = $P < 0.01$; and *** = $P < 0.001$. Means were also compared across diameter classes within each mortality agent. Means (±SEMs) followed by the same number are not significantly different (capital letters = *D. ponderosae*, lowercase letters = other agents; $P < 0.05$).

smallest dbh classes (Fig. 7). Thomson et al. (2017) reported similar trends among tree diameters following *D. ponderosae* outbreaks in Colorado. This is consistent with our understanding of host selection behavior in *D. ponderosae*. As an infestation develops, *D. ponderosae* initially colonizes the largest *P. contorta* (Shepherd, 1966; Rasmussen, 1972), with progressively smaller *P. contorta* being colonized over time (Klein et al., 1978) as the proportion of larger trees declines. For example, Mitchell and Preisler, (1991) reported in Oregon that small *P. contorta* were not colonized unless they were located near currently-infested larger trees (≥23 cm dbh). While larger-diameter trees typically have more pronounced defenses (Boone et al., 2011), they also generally provide for a higher reproductive potential and probability of survival for *D. ponderosae* (i.e., we refer to these trees as "beetle sources") (Amman 1969, 1975; Reid and Purcell 2011). This is due to the greater quantity of food (phloem) available on which larvae feed (Graf et al., 2012), and explains why *D. ponderosae* outbreaks are often associated with mature and overmature forest conditions (Fettig et al., 2007). Assuming favorable weather conditions (Bentz et al., 2010), outbreaks often subside when the remaining host trees are so nutrient poor (e.g., suppressed trees) that it takes more beetles to kill these trees than are produced within the trees ("beetle sinks"). An opposing trend

was observed for other causes of tree mortality (Fig. 7). More trees were killed by agents other than *D. ponderosae* in the 10 and 15-cm dbh classes than in the mid- and larger dbh classes ($\chi^2 = 175.8$, $df = 5$, $P < 0.001$). This is consistent with mortality attributed to *I. pini* (265 trees), which disproportionally affect smaller-diameter trees (Kegley et al., 1997), and suppression (53 trees).

Comparisons were also made between *D. ponderosae* and other causes of tree mortality within each dbh class (Fig. 7; brackets above paired bars). *Dendroctonus ponderosae* killed a significantly greater percentage of all trees (all diameter classes) and trees within the 20, 25, 30 and ≥32.5 cm dbh classes compared to other causes of mortality (Fig. 6; $\chi^2 \geq 86.2$, $df = 1$, $P < 0.001$ for all classes). Other mortality agents caused significantly higher levels of tree mortality in the smallest dbh class ($\chi^2 = 92.7$, $df = 1$, $P < 0.001$). Again, these observations are consistent with the beetle's propensity to colonize larger-diameter trees (Shepherd, 1966), and that of other tree mortality agents observed that disproportionally impact smaller-diameter trees (e.g., Kegley et al., 1997). They also indicate that the observed losses in basal area (Fig. 5), compared to number of trees, are explained by *D. ponderosae* host selection behavior.

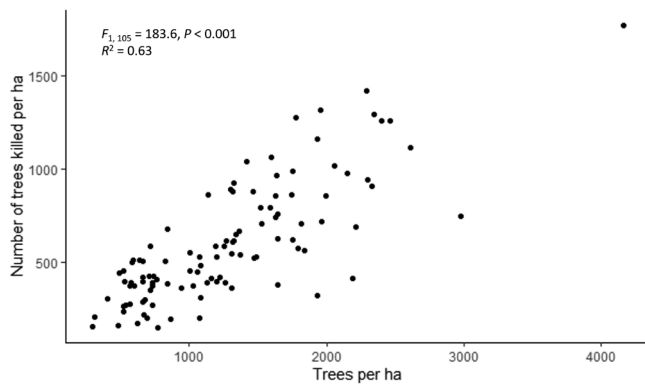Tree mortality was positively correlated with number of live trees,

Fig. 8. Relationship between the number of trees killed per ha (2005–2019) and the number of live trees per ha (2004) across five U.S. states (Colorado, Idaho, Montana, Utah and Wyoming).

basal area of live trees and SDI. For data pooled across states, the number of live trees per ha was strongly, positively correlated with the number of trees killed per ha ($F_{1, 105} = 183.6$, $P < 0.001$, $R^2 = 0.63$; Fig. 8). Basal area ($F_{1, 105} = 310.3$, $P = 0.006$, $R^2 = 0.07$) and SDI ($F_{1, 105} = 276.6$, $P < 0.001$, $R^2 = 0.26$) were correlated, but explained less variation. These relationships are not surprising given thinning has long been advocated as a measure to reduce stand susceptibility to *D. ponderosae* (Fettig et al., 2014a,b). Among other factors, thinning reduces host availability that supports beetle populations; reduces competition among trees for nutrients, water, and other resources thereby increasing growing space (Oliver and Larson, 1996), tree vigor and defensive mechanisms (Franceschi et al., 2005); and affects microclimate decreasing the effectiveness of chemical cues used in host finding, selection and colonization (Bartos and Amman, 1989; Thistle et al., 2004), all of which influence *D. ponderosae* survival and impacts.

3.5. Tree regeneration

Another objective of this study was to project what these forests might look like several decades following the outbreak. A good indication of future stand composition is relationships in tree regeneration. In 2018, *A. lasiocarpa* dominated seedling abundance in all states but Idaho and Montana (Table 2). In Idaho, *A. lasiocarpa* was second to *P. contorta* and these were the only species to produce seedlings. In Montana, *P. contorta* dominated seedling abundance followed by *Pi. engelmannii*, *P. flexilis* and *A. lasiocarpa*. Sapling abundance was dominated by *P. contorta* in every state except Utah where *A. lasiocarpa* abundance was twice that of *P. contorta* (Table 2). Montana was also an exception in that there was a similar abundance of *Ps. menziesii* and *P. contorta* saplings. Although FIA reports do not make a distinction between seedlings and saplings, *P. contorta* was reported by FIA as the most abundant tree species in the understory in the *P. contorta* type in Wyoming (DeRose et al., 2018) and Montana (Witt et al., 2019b).

Given the large amount of variation in seedling and sapling densities among plots, temporal trends in abundance are likely more revealing (Fig. 9). The abundance of saplings was significantly lower in 2010 than in 2014 or 2018 ($\chi^2 = 22.2$, $df = 2$, $P < 0.001$), however seedling abundance remained unchanged during this period. By 2018, the abundance of seedlings and saplings was nearly the same (Fig. 9), which suggests recruitment of seedlings into the sapling class but limited establishment of seedlings following the outbreak. This was despite somewhat favorable climatic conditions as, for example, most states experienced an increase in mean precipitation during 2011–2019 compared to the preceding 10 years (Table 1). Of note, we found no significant relationships between several climatic variables (e.g., temperature, precipitation, and CWD) and levels of tree regeneration. Carlson et al. (2020) examined the effects of a *D. rufipennis* outbreak

that began in 2004 on seedling abundance in subalpine forests in Colorado in 2017–2019. They reported lower abundances of recently established *Pi. engelmannii* seedlings in areas with higher levels of tree mortality, which appears attributable to increases in surface temperatures and forest litter. While *P. contorta* is a prolific seeder, germination occurs best in bare mineral soil or disturbed litter (Burns and Honkala, 1990). The amount of bare ground (but not specifically mineral soil) averaged <10% across all states and years (data not shown). Although germination and early survival of *A. lasiocarpa* is best on exposed mineral soil and moist humus, the species is less exacting in its seedbed requirements than *P. contorta* (Burns and Honkala, 1990). Taller seedlings are expected to have a competitive advantage, especially at higher light levels. For example, the height of *A. lasiocarpa* and *P. contorta* seedlings at the time of release have been shown to have positive effects on height growth, diameter growth and survival (Claveau et al., 2002). While we did not measure light intensity, crown cover (measured by densitometer at four points within each 0.081-ha plot) averaged <50% across all states and years. Overall, *A. lasiocarpa* comprised a greater proportion of regeneration (seedlings + saplings) than *P. contorta*, which deviates from the composition of trees (Fig. 4). Higher numbers of *A. lasiocarpa* seedlings ($\chi^2 = 9.5$, $df = 3$, $P = 0.02$) and saplings ($\chi^2 = 9.9$, $df = 3$, $P = 0.02$) occurred on western aspects (7.0 ± 4.6 and 7.1 ± 2.4, respectively) compared to southern aspects (1.6 ± 0.3 and 1.61 ± 0.71, respectively). Aspect has no effect on the number of *P. contorta* seedlings ($\chi^2 = 4.1$, $df = 3$, $P = 0.25$) and saplings ($\chi^2 = 1.2$, $df = 3$, $P = 0.76$). Carlson et al. (2020) reported higher densities of *Pi. engelmannii* seedlings occurred on northern aspects.

4. Conclusions

The recent *D. ponderosae* outbreak has significantly impacted conifer forests across western North America, with *P. contorta* forests in the Intermountain West and interior British Columbia most affected (USDA Forest Service, 2012; British Columbia Ministry of Forests, Lands, and Natural Resource Operations, 2013). Based on levels of tree mortality (see Carroll et al., 2006 for descriptions) observed in our network of plots, incipient populations of *D. ponderosae* began in 2004; peaked in 2007; and returned to endemic levels in 2011 in Idaho, Montana, Utah and Wyoming. In Colorado, incipient populations began in 2004; peaked in 2009; and returned to endemic levels in 2012 (Fig. 2). These observations tend to agree with published reports based on aerial detection surveys conducted at coarse scales (e.g., Jenkins et al., 2015) and FIA reports (Werstak et al., 2016; Thomson et al., 2017; DeRose et al., 2018; Witt et al., 2019a,b). Mean number of snags increased 1398.7% between 2004 and 2010 and declined 4.9% between 2010 and 2018 (Table 1). Snag retention was 71.3%. While published data are limited, the half-lives for *P. contorta* snags killed by *D. ponderosae* in Oregon were 8 and 9 years in thinned and unthinned stands, respectively (Mitchell and Preisler, 1998). In our study, most *P. contorta* killed during the peak of the outbreak remained standing in 2019 (72.7% in Colorado, 76.2% in Idaho, Montana, Utah and Wyoming). Rhoades et al. (2020) reported only 17% of snags fell between 2007 and 2018 following a *D. ponderosae* outbreak that peaked on the Fraser Experimental Forest, Colorado in 2006.

A common management strategy to reduce the probability and severity of future *D. ponderosae* infestations is to reduce stand density (Amman and Logan, 1998; Fettig et al., 2007). For example, Mata et al. (2003) suggested reducing the basal area of *P. contorta* stands to <27.5 m² per ha was effective for reducing stand susceptibility. Similarly, Bollenbacher and Gibson (1986) concluded that stands of high productivity, 60–125 years old, at <1829 m elevation and with basal areas >29.8 m² per ha were highly susceptible to *D. ponderosae*. In 2004, stand densities ranged from 26.8 m² of basal area per ha in Wyoming to 41.1 m² of basal area per ha in Idaho (Table 1, Fig. 5). In 2018, mean basal area ranged from 15.0 m² per ha in Wyoming to 23.8 m² per ha in Idaho (Table 1, Fig. 4). Given the substantial

Table 2

Tree regeneration after *Dendroctonus ponderosae* outbreaks in *Pinus contorta* forests in the Intermountain West, U.S., 2018.

	Colorado	Idaho	Montana	Utah	Wyoming	All
Seedlings[1] per ha						
Pinus contorta	217.4 ± 78.6b	3657.1 ± 1300.7 a	227.3 ± 129.1b	691.9 ± 186.6b	258.3 ± 107.2b	660.5 ± 160.6
Pinus ponderosa	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0
Pinus flexilis	19.8 ± 13.7 a	0.0 ± 0.0 a	69.2 ± 69.2 a	0.0 ± 0.0 a	0.0 ± 0.0 a	20.8 ± 16.4
Abies lasiocarpa	425.0 ± 121.5 bc	3014.6 ± 713.1 a	59.3 ± 25.8b	5100.1 ± 1675.5 ac	314.5 ± 186.2b	1651.2 ± 439.5
Populus tremuloides	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	59.3 ± 59.3 a	0.0 ± 0.0 a	13.9 ± 13.8
Pseudotsuga menziesii	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0
Picea engelmannii	69.2 ± 26.8 a	0.0 ± 0.0 a	158.1 ± 84.3 a	98.8 ± 62.2 a	0.0 ± 0.0 a	76.2 ± 25.4
Juniperus occidentalis	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0
Other spp.[3]	9.9 ± 9.9 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	22.5 ± 22.5 a	6.9 ± 5.1
All	741.3 ± 128.4b	6671.7 ± 1476.6 a	514.0 ± 160.1b	5950.2 ± 1647.4 a	595.3 ± 307.0b	2429.4 ± 478.4
Saplings[2] per ha						
Pinus contorta	652.3 ± 165.1 ab	6152.8 ± 3891.9 a	632.6 ± 202.3 ab	533.7 ± 184.2b	527.9 ± 203.9b	1108.5 ± 388.1
Pinus ponderosa	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0
Pinus flexilis	69.2 ± 41.6 a	0.0 ± 0.0 a	0.0 ± 0.0b	0.0 ± 0.0b	0.0 ± 0.0b	16.2 ± 9.9
Abies lasiocarpa	365.7 ± 135.4b	4546.6 ± 1241.1 a	247.1 ± 78.1b	1304.7 ± 379.7 a	292.0 ± 152.2b	933.0 ± 190.0
Populus tremuloides	217.4 ± 207.4 a	0.0 ± 0.0 a	0.0 ± 0.0b	108.7 ± 108.7 a	157.2 ± 100.9 a	108.5 ± 57.9
Pseudotsuga menziesii	0.0 ± 0.0b	0.0 ± 0.0 ab	642.5 ± 353.8 a	0.0 ± 0.0b	0.0 ± 0.0b	150.1 ± 85.1
Picea engelmannii	29.7 ± 16.4 ab	24.7 ± 24.7 ab	177.9 ± 76.2 a	0.0 ± 0.0b	0.0 ± 0.0b	50.8 ± 19.2
Juniperus occidentalis	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0 a	0.0 ± 0.0
Other spp.[3]	19.8 ± 19.8 a	49.4 ± 49.4 a	0.0 ± 0.0 a	0.0 ± 0.0 a	11.2 ± 11.2 a	11.5 ± 6.8
All	1354.1 ± 268.8 a	10773.6 ± 4989.0b	1700.0 ± 397.0 a	1947.1 ± 392.9 a	988.4 ± 298.0 a	2378.6 ± 537.0

Values are mean number of live seedlings and saplings ± SEM based on a 0.004-ha subplot within each 0.081-ha circular plot. Means ± SEMs followed by the same letter within rows are not significantly different ($P > 0.05$).

[1] Height ≤ 0.3 m.
[2] Height > 0.3 m and dbh (diameter at 1.37 m in height) <7.6 cm.
[3] Includes infrequently encountered species *Picea pungens* Englem., *Pinus albicaulis* Englem., and *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.

reductions in stand density (Table 1, Figs. 4–6), we conclude that the *D. ponderosae* outbreak has effectively thinned forests and shifted the age-class distributions of *P. contorta* in a manner sufficient to reduce susceptibility to future infestations for several decades (Anhold et al., 1996). This is not to suggest that trees killed by *D. ponderosae* were the same trees that would have been selected for removal during thinning (Fettig et al., 2014a); or to diminish the many ecological goods and services that have been negatively impacted by the outbreak (Morris et al., 2018). The extensive levels of tree mortality observed may impact timber and fiber production, water quality and quantity, fish and wildlife populations, fire risk and severity, recreation, grazing capacity, biodiversity, carbon storage, endangered species and cultural resources, among other factors, for decades (Morris et al., 2018). Of note, the large numbers of snags in these forests (Table 1) represent important safety

concerns to firefighters, other forest workers, and the public (Jenkins et al., 2014b). Many of these trees (now snags) would have been felled and removed during selective thinning operations. Furthermore, the size and spatial distribution of trees killed by *D. ponderosae* is likely to differ from those removed during thinning operations (Fettig et al., 2007).

We observed an increase in the relative abundance of *A. lasiocarpa* saplings (Fig. 9). Similar increases in the relative abundance of shade-tolerant conifers have been observed in Colorado and British Columbia following *D. ponderosae* outbreaks (Dordel et al., 2008; Klutsch et al., 2009), and suggest a shift towards greater representation in the overstory if suitable recruitment were to occur (Veblen et al., 1989; Nigh et al., 2008; Diskin, 2010). To that end, Collins et al. (2011) and Kayes and Tinker, (2012) suggested *D. ponderosae* outbreaks may
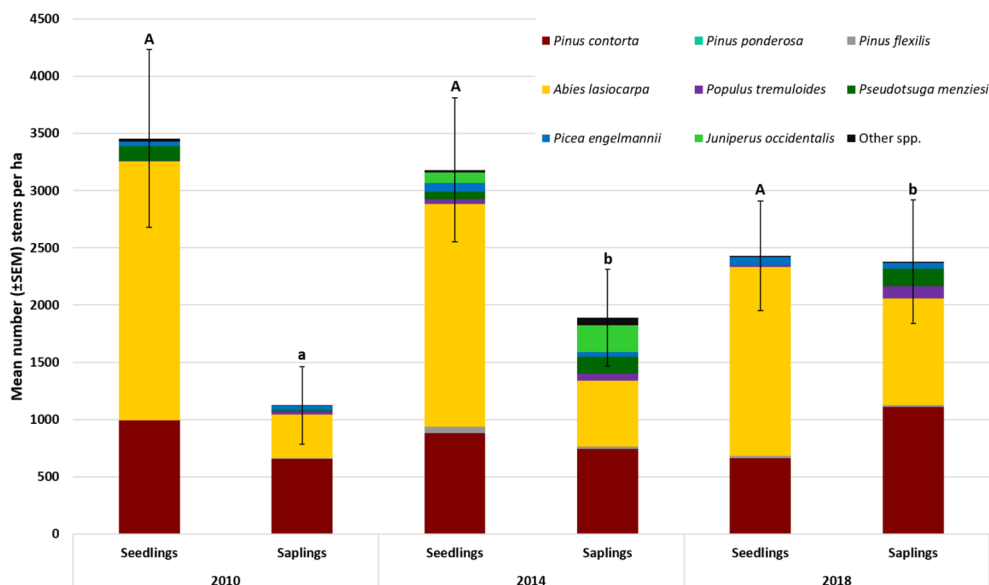

Fig. 9. Mean number (±SEM) of live seedlings (≤0.3 m tall) and saplings (>0.3 m tall and <7.6 cm dbh, diameter at 1.37 m in height) per ha partitioned by relative species abundance in 2010, 2014 and 2018. Mean number of seedlings (capital letters) and saplings (lowercase letters) were compared across years. Means (±SEMs) followed by the same letter are not significantly different ($P > 0.05$).

hasten a successional shift towards *Picea-Abies*, but we think this is unlikely. On the cold and dry sites that typify our network of plots, *P. contorta* is considered dominant seral or persistent with little evidence of replacement by shade-tolerant tree species (Burns and Honkala, 1990). In addition, balsam woolly adelgid, *Adelges piceae* (Ratzeburg), an invasive insect that colonizes *Abies* (Ragenovich and Mitchell, 2006), is now established in some areas of the Intermountain West (Fettig et al., 2020), and while not observed in our study *Ad. piceae* is likely to threaten populations of *A. lasiocarpa* in our study in the future. This would provide a competitive advantage to other tree species, such as *P. contorta*. In Oregon and Washington, where *Ad. piceae* has been established for decades, both grand fir, *A. grandis* (Douglas ex D. Don) Lindley, and *A. lasiocarpa* have been heavily impacted (Mitchell and Buffam, 2001). Furthermore, a shift towards *Picea-Abies* is likely only in the absence of wildfire (Brown, 1975). However, climate change is increasing the frequency of large fires and the cumulative area burned in the western U.S., and these trends are expected to continue throughout the 21st century (Vose et al., 2018). At the same time, experts are arguing for the increased use of managed wildfire (i.e., lightning-started fires that are allowed to burn under acceptable conditions) to increase the resilience of fire-prone landscapes at more meaningful scales (North et al., 2012).

This publication is the first of several that are planned describing the impacts of *D. ponderosae* outbreaks on forests across our network of plots. For example, determining the influence of *D. ponderosae* outbreaks on wildfires is another focus of this study. Although not yet fully understood, it is widely recognized that bark beetle outbreaks and wildfires influence one another (Jenkins et al., 2014b). To that end, today's rapid pace of environmental (and socioeconomic) change is likely to pose considerable challenges to managing forests in the future. In fact, a key finding of the latest National (U.S.) Climate Assessment is that "It is very likely that more frequent extreme weather events will increase the frequency and magnitude of severe ecological disturbances, driving rapid (months to years) and often persistent changes in forest structure and function across large landscapes" (Vose et al., 2018). As such, the ability of natural resource managers to act in a responsible manner to ensure the continued provision of ecological goods and services is increasingly important (Cottrell et al., 2020), and requires a better understanding of short and long-term constraints imposed by disturbances, such as *D. ponderosae* outbreaks.

CRediT authorship contribution statement

Jackson P. Audley: Formal analysis, Writing - original draft. **Christopher J. Fettig:** Conceptualization, Data curation, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing - original draft. **A. Steven Munson:** Conceptualization, Funding acquisition, Investigation, Project administration, Writing - review & editing. **Justin B. Runyon:** Data curation, Investigation, Methodology, Writing - review & editing. **Leif A. Mortenson:** Data curation, Investigation, Writing - review & editing. **Brytten E. Steed:** Investigation, Methodology, Project administration, Writing - review & editing. **Kenneth E. Gibson:** Investigation, Writing - review & editing. **Carl L. Jørgensen:** Investigation, Writing - review & editing. **Stephen R. McKelvey:** Conceptualization, Data curation, Investigation, Writing - review & editing. **Joel D. McMillin:** Investigation, Writing - review & editing. **Jose F. Negrón:** Conceptualization, Investigation, Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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