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Changes in understory vegetation including invasive weeds following mountain pine beetle outbreaks

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ABSTRACT

Bark beetle outbreaks alter forests in many ways including stand structure, fuels and fire behavior, wildlife habitat, and aesthetic value. Less understood are the effects outbreaks have on understory vegetation, despite the importance for overstory succession, nutrient cycling, water quality, soil erosion, and wildlife. Beetle outbreaks also change forests in ways that could promote invasion by nonnative weeds, but this is rarely studied. We assessed changes in cover of understory vegetation and presence/abundance of weeds in lodgepole pine forests in Colorado, Idaho, Montana, Utah and Wyoming, USA following recent mountain pine beetle outbreaks. Incipient beetle populations began in 2004, peaked around 2008, and returned to endemic levels by 2012. Understory vegetation was sampled in 2010, 2012, 2014 and 2018. Total understory cover and cover of shrubs and graminoids remained unchanged, while cover of forbs generally increased. Forb cover was negatively correlated with shrub and canopy cover. Approximately 20% of plots contained weeds and weed abundance increased over time. Presence of weeds was negatively correlated with graminoid cover and positively correlated with tree mortality and snag fall. By 2018, weed abundance was only positively correlated with snag fall. Localized soil disturbance created when snags uproot and fall appears to act as sites of weed invasion and proliferation. Lastly, we provide a global review of the effects of bark beetle outbreaks on understory vegetation which reveals a prevailing short-term increase following outbreaks, but the magnitude of response and cover type affected varies with beetle species/forest type and time since outbreak.

1. Introduction

Bark beetles (Curculionidae: Scolytinae) are among the most important disturbances in conifer forests. During attacks, adult beetles introduce symbiotic fungi and larvae construct galleries as they feed on the host's phloem which impede nutrient and water transport leading to tree death (Paine et al., 1997; Safranyik and Carroll, 2006; Hubbard et al., 2013). Endemic beetle populations infest relatively few and often weakened or injured trees, but during outbreaks beetles mass attack and overwhelm the defenses of healthy trees (Franceschi et al., 2005; Boone et al., 2011; Jenkins et al., 2014a). Recent bark beetle outbreaks have killed billions of trees across millions of hectares of forests in Europe and North America (Seidl et al., 2007; Meddens et al., 2012; Fettig et al., 2020). These outbreaks were in part driven by climate change, and the frequency and severity of outbreaks of some bark beetle species are predicted to further increase with increases in temperature and drought associated with climate change (Jönsson et al., 2009; Bentz et al., 2010; Kolb et al., 2016; Vose et al., 2018). The largest of recent outbreaks is mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in western North America, which since 2000 has affected greater than 27 million ha including more than 10 million ha in the U.S., primarily in lodgepole pine (*Pinus contorta* Dougl. ex Loud.) forests (Fettig et al., 2020). The extent, severity, and synchronicity of these *D. ponderosae* outbreaks have stimulated concerns and research regarding the short- and

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long-term changes to forests and the ecological goods and services that forests provide (Morris et al., 2018).

Among the myriad ways that *D. ponderosae* outbreaks change forests include stand structure and composition (Klutsch et al., 2009; Audley et al., 2020), quantity and quality of timber products (Lewis and Hartley, 2006), fuels and fire behavior (Klutsch et al., 2011; Jenkins et al., 2014b), habitat for wildlife (Chan-McLeod, 2006; Saab et al., 2014), carbon dynamics (Kurz et al., 2008; Hansen, 2014), and aesthetic and recreational values (Dhar et al., 2016). Less understood are the impacts outbreaks have on non-tree understory vegetation (hereafter understory vegetation). However, understanding how beetle outbreaks affect understory vegetation is important since the understory represents and supports much of the biodiversity in conifer forests and can drive fundamental ecosystem processes. For example, understory vegetation can affect rates of conifer regeneration (Mallik, 2003; Balandier et al., 2006), nutrient cycling and water quality (Nilsson and Wardle, 2005; Griffin et al., 2011) and soil erosion (Durán Zuazo and Rodríguez Pleguezuelo, 2008). Moreover, understory vegetation provides habitat and food for many mammal, bird, and insect species. The most obvious way beetle outbreaks could affect understory vegetation is by opening the canopy and increasing the amount of light reaching the forest floor (Barbier et al., 2008). The large-scale mortality of overstory trees caused by bark beetle outbreaks can also result in more extreme forest floor temperatures, decreased humidity and soil moisture, and accelerated nutrient fluxes in soil (Roberts, 2004; Swanson et al., 2011). Almost completely unstudied are the effects of bark beetle outbreaks on the abundance of nonnative invasive weeds (hereafter invasive weeds), which are a threat to the health, sustainability, and productivity of forests (Moser et al., 2009). Invasive weeds can reduce the abundance and diversity of native plants (Ortega and Pearson, 2005), change soil biota and chemistry (Weidenhamer and Callaway, 2010), reduce reproductive success of native wildlife (Ortega et al., 2006), and increase fire risk (D'Antonio and Vitousek, 1992). Bark beetle outbreaks could promote weed invasions as high-light environments (e.g., from canopy dieback of beetle-killed trees) are especially prone to invasion (Daehler, 2003). Moreover, the soil disturbance created when snags uproot and fall to the forest floor (Schaetzl et al., 1990) could promote the establishment and spread of invasive weeds.

In this study, we examined changes in cover of understory vegetation, including invasive weeds, across a network of plots in five U.S. states (Colorado, Idaho, Montana, Utah and Wyoming) from 2010 to 2018. The scope of our work encompasses areas where most of the tree mortality attributed to *D. ponderosae* has occurred in the Intermountain West, U.S. (Audley et al., 2020; Fettig et al., 2020). In addition, we provide a global literature review of the effects of bark beetle outbreaks on understory vegetation to put our findings into context, and to identify broad-scale patterns of how bark beetle outbreaks affect this critical component of forest ecosystems.

2. Materials and methods

2.1. Study sites

The experimental design is detailed in Audley et al. (2020). In brief, in 2010 a network of 0.081-ha circular plots was established in the northern Colorado Front Range, central Idaho, southwest Montana, northeast Utah, and western Wyoming (125 plots total, 25 per state) (Fig. 1 in Audley et al., 2020). For inclusion, plots were required to contain >50% *P. contorta* by basal area and a minimum of 10 *P contorta* >13.9 cm dbh (diameter at 1.37 m in height) with at least two of these trees being colonized and/or killed by *D. ponderosae* within the last three years. In each state, plots meeting these criteria were randomly selected in groups of five but separated by ≥100 m; groups within states were separated by >1.6 km (mean distance: 23.4 ± 3.0 km). Fifteen plots were lost to wildfires in Idaho and three plots were lost to unauthorized tree harvests in Wyoming. Data from these plots were excluded from analyses.

2.2. Data collection

Following 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 from 2010 to 2019. Tree mortality and snag fall were recorded annually. 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 (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) (Audley et al., 2020). In each plot, three transects were established radiating 0°, 120° and 240° from the plot center. Plot center and ends of each transect were permanently marked with rebar. Understory vegetation cover was described using 1-m^2 quadrats placed at the end of each transect (3 per plot, 375 total); the rebar stakes assured that the same 1-m^2 area was sampled through time. Understory vegetation and canopy cover were assessed once per year in 2010, 2012, 2014, and 2018 during the middle to late growing season (July and August). For each quadrat, understory vegetation was divided into three functional types: forbs, shrubs, and graminoids (grasses, rushes, sedges), and non-vegetated ground was classified as litter or bare ground (rock and mineral soil). The relative area covered within the quadrat by forbs, shrubs, graminoids, litter (including fine and coarse woody debris) and bare ground when viewed from directly above was visually estimated in 5% increments, except trace amounts recorded as 2.5%, with total relative cover summing to 100%. The presence of nonnative invasive weeds in quadrats was also recorded. In 2012, we noticed an increase in invasive weeds and that many plots contained weeds outside of quadrats. Therefore, in 2014 and 2018 we systematically surveyed all plots by walking linear transects (ca. 5 m apart) spanning each plot and recording the presence, identity, and abundance of invasive weeds. Abundance was determined by counting the number of aboveground stems. In 2010, 2014, and 2018, canopy cover was measured at plot center and at 4.5, 9, and 13.5 m from plot center along each transect, resulting in 10 measurements per plot. At each point, the proportion of the forest floor covered by the vertical projection of tree crowns in 10% increments was estimated (Jennings et al., 1999). The 10 measurements in each plot were averaged to determine mean canopy cover per plot.

For the literature review, we searched Google Scholar (http://scholar.google.com) and ISI Web of Knowledge (http://apps.webofknowledge.com) to generate a database of publications assessing the effects of bark beetle outbreaks on understory vegetation in April 2020. We used search terms: "bark beetle" or "beetle outbreak" or "pine beetle" or "Ips" or "Scolytinae" AND "vegetation" or "understory vegetation" or "understory plants" or "herbaceous vegetation". All publications meeting the search criteria were screened for additional articles on the effects of bark beetle outbreaks on understory vegetation cited within them. Publications were included in the database if they reported original data on changes to non-tree vegetation cover, height, biomass and/or species diversity related to outbreaks of any bark beetle species. Studies that only examined changes in a subset of plant species were excluded.

2.3. Statistical analyses

All statistical analyses were carried out with R statistical software version 3.6.3. (R Core Team, 2020). To test for changes in total cover of understory vegetation over time we used single-factor ANOVAs using the anova function in the stats package (R core Team, 2020) with

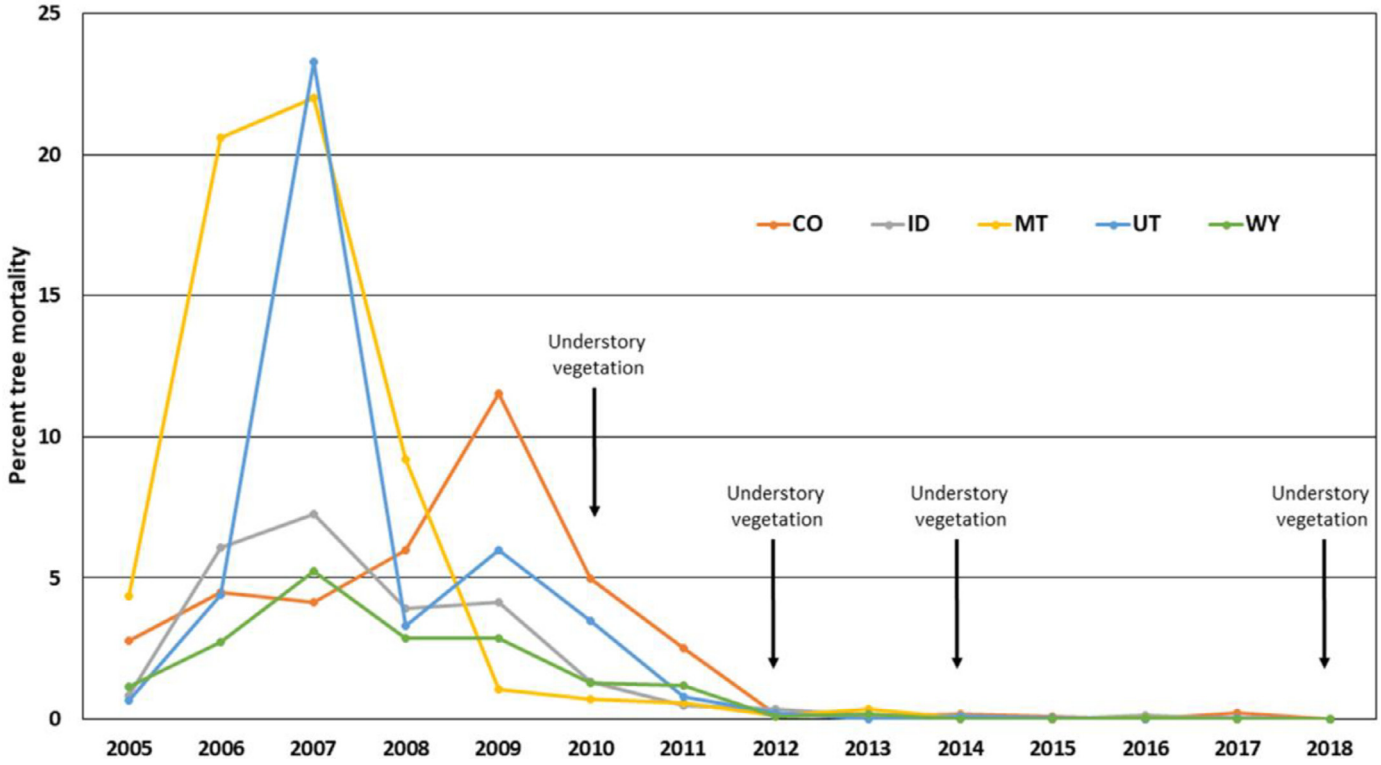

Fig. 1. Mean percentage of number of *Pinus* killed per year by year following *Dendroctonus ponderosae* outbreaks in Colorado, Idaho, Montana, Utah and Wyoming, 2005–2018. Arrows denote years when understory vegetation was sampled. Modified from Audley et al. (2020).

subsequent Tukey HSD tests using the emmeans package (Length, 2020) with state treated as a random effect. To test for changes in cover of understory vegetation among states over time we again used single factor ANOVAs using the stats package (R Core Team, 2020). Homogeneity of variance was checked for both analyses using Levene's test in the car package (Fox and Weisberg, 2019), and variables that failed this test were square-root transformed.

As forb cover was the only understory cover type to significantly change over time, we used linear modeling to further investigate forb cover in relation to other covers and tree metrics in 2018. A total of 10 explanatory variables were used: (1) shrub cover, (2) forb cover, (3) graminoid cover, (4) total understory vegetation cover (sum of forbs, shrubs, and graminoids), (5) litter cover, (6) bare ground cover, (7) percent tree mortality (dead trees), (8) percent fallen snags, (9) number of dead trees (snags), and (10) tree canopy cover. To reduce collinearity, the full models were reduced using the Variance Inflation Factor (VIF) until the highest VIF was ≤3 using the procedure outlined in Zuur et al. (2010).

We assessed relationships of the presence/absence of invasive weeds with understory vegetation and forest stand structure by Generalized Linear Mixed Modeling (GLMM) using a binomial distribution with a logit link function using the glmer function of the lme4 package (Bates et al., 2015). To achieve model convergence all explanatory variables were log transformed. To examine relationships among the abundance of invasive weeds (categorized as: 1–49 plants per plot = low, 50–124 = medium, >124 = high) we ran Linear Mixed-Effects Models (LMM) using the lmer function from lme4 package (Bates et al., 2015) and used the lmeTest package to determine *p* values (Kuznetsova et al., 2017). Abundance of weeds was categorized since it was highly skewed among plots and three seemingly natural levels of invasion were evident: most invaded plots had just a few weeds usually localized in a small area (e.g., at a tip up site), fewer plots had an intermediate number of weeds at multiple tip up sites and/or just expanding beyond these sites, and a small number of plots in which weeds had spread to cover most of the plot. The same explanatory variables and model selection procedure used in the linear modeling analysis above was used here. Both LMM and GLMM models were computed for 2014 and 2018 with tree metrics cumulative up to, but not including, the year of analysis (e.g., percent dead trees through 2013 were used in analysis of 2014 weeds). The present year's value was used for canopy cover (e.g., canopy cover in 2014 was used in analysis of 2014 weeds).

3. Results

3.1. Mountain pine beetle outbreak

Incipient populations of *D. ponderosae* began in 2004; peaked in 2007; and returned to endemic levels in 2011 in Idaho, Montana, Utah and Wyoming (Fig. 1). In Colorado, incipient populations began in 2004; peaked in 2009; and returned to endemic levels in 2012. Across our network of plots, annual mortality peaked in 2007 in Idaho, Montana, Utah and Wyoming with 23% of trees were killed that year in plots in Utah (Fig. 1). The percent of dead trees across plots varied from 16% to 88% with a mean ± SE of 46.8 ± 1.6%, whereas percent canopy cover varied from 0% to 100% with a mean ± SE of 41.6 ± 2%.

3.2. Changes in understory vegetation

Common shrubs in our plots included grouse whortleberry (*Vaccinium scoparium* Leiberg ex Coville), Kinnikinnick [*Arctostaphylos uva-ursi* (L.) Spreng.], Oregon grape [*Mahonia aquifolium* (Pursh) Nutt.], common juniper (*Juniperus communis* L.), and *Spirea* spp. Common forbs included *Lupinus* spp., *Arnica* spp., yarrow (*Achillea millefolium* L.), *Antennaria* spp., *Aquilegia* spp., *Fragaria* spp., sticky geranium (*Geranium viscosissimum* Fisch. & C.A. Mey.), and *Potentilla* spp. The most common graminoids included pinegrass (*Calamagrostis rubescens* Buckley) and *Carex* spp.

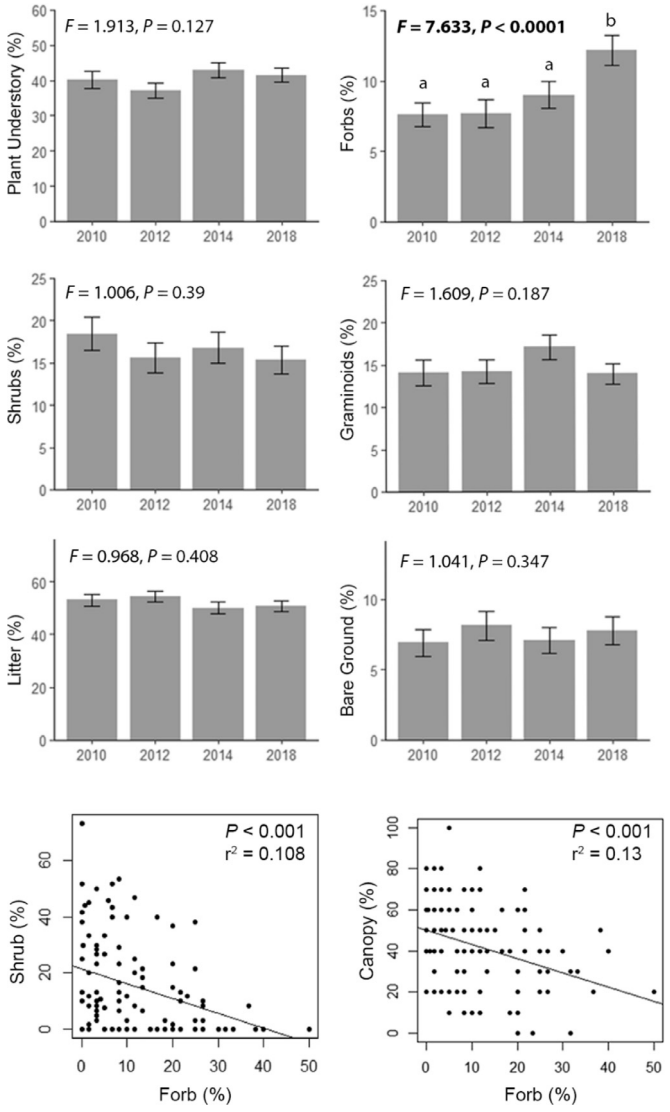

Fig. 2. Percent cover of total understory vegetation, forbs, shrubs, graminoids, litter and bare ground from 2010 to 2018 (ca. 2–10 years after peak levels of tree mortality due to *Dendroctonus ponderosae* outbreaks) across study plots in Colorado, Idaho, Montana, Utah and Wyoming, U.S. (df = 3, 428) and the relationship of forb cover with shrub and canopy cover in 2018.

Overall, percent cover of total understory vegetation, shrubs, graminoids, litter, and bare ground remained unchanged from 2010 to 2018 (Fig. 2). However, the cover of forbs significantly increased by about 60% from 7.6 ± 0.8% in 2010 to 12.2 ± 1.1% in 2018 (Fig. 2). In 2014 and 2018, the cover of forbs was negatively correlated with shrub cover (linear models, 2014, t-value −3.25, $P = 0.002$; 2018, t-value −4.21, $P < 0.001$) and canopy cover (linear models, 2014, t-value −3.72, $P < 0.001$; 2018, t-value −4.53, $P < 0.001$) (Fig. 2). No other correlations were statistically significant.

The mean percent cover of cover types varied among states (Fig. 3). Within years, every cover type significantly varied across states ($P < 0.05$) except for cover of bare ground in 2012 ($P = 0.07$). Changes in cover types over years also differed among states (Table 1). Forb cover significantly increased in Colorado and Montana and marginally increased in Utah ($P = 0.06$) (Fig. 3). Graminoid cover increased in Montana in 2014 but returned to pre-2014 levels by 2018 (Fig. 3). No other significant differences were observed within states over time (Table 1).

3.3. Changes in invasive weeds

Six invasive weeds were documented, including Canada thistle [*Cirsium arvense* (L.) Scop.], bull thistle [*C. vulgare* (Savi) Ten.], musk thistle (*Carduus nutans* L.), lamb's quarters (*Chenopodium album* L.), prickly lettuce (*Lactuca serriola* L.), and sulphur cinquefoil (*Potentilla recta* L.). *Cirsium arvense* was dominant representing about 95% of total weed abundance. *Cirsium arvense* was also most widely distributed, occurring on 20% of plots. *Cirsium vulgare* was the next most common invasive weed, and was present on 4% of plots. The remaining four weed species each occurred on 1–2% of plots.

In 2014 and 2018 approximately 20% and 21% of plots, respectively, contained at least one invasive weed. Colorado had the greatest percentage of plots with weeds (ca. 50%) followed by Montana, Utah, and Wyoming (Fig. 4A). No invasive weeds occurred on plots in Idaho. The percentage of plots with weeds decreased in Montana and increased in Wyoming from 2014 to 2018 (Fig. 4A). In 2014, the presence of weeds was negatively correlated with graminoid cover and positively correlated with levels of tree mortality (percentage of dead trees). In 2018, the presence of weeds was only positively correlated with snag fall (Table 2). In 2018, the number of fallen snags across plots ranged from 0 to 57 with a mean ± SE of 10 ± 1. The total number of invasive weeds across all plots increased about 31% from 7482 individual plants in 2014 to 9825 individual plants in 2018. The increase in forb cover (Fig. 2) is not explained by increases in invasive weeds since the distribution of weeds was patchy, and in 2018 just four quadrats (of 375, which were used to assess forb cover) contained weeds. The ranked abundance of weeds in 2014 was positively correlated with canopy cover, cover of shrubs, litter, bare ground, and percent dead trees (Table 3). By 2018, abundance of weeds was only positively correlated with snag fall (Table 3). The mean percent of fallen trees in plots with weeds was greater than twice that in plots without weeds in 2014 and 2018 (Fig. 4B).

3.4. Literature review

We compiled 23 papers assessing changes in understory vegetation following outbreaks of bark beetle species (Table 4). All studies were from North America ($n = 16$) and Europe ($n = 7$). Outbreaks of five bark beetle species were examined representing seven bark beetle/forest type combinations (Table 4). Most studied were outbreaks of *D. ponderosae* in *P. contorta* in western North America and European spruce beetle [*Ips typographus* (L.)] in Norway spruce [*Picea abies* (L.) H. Karst] in Europe ($n = 7$, both cases). Most papers examined short-term changes occurring within 10 years of outbreaks ($n = 16$) and the others assessed longer-term changes (10–30 years). No study evaluated vegetation >30 years after an outbreak. The most commonly reported metrics were vegetation cover (forbs, shrubs, graminoids and/or total, $n = 16$) and plant species diversity ($n = 10$), followed by vegetation height ($n = 6$) and aboveground biomass ($n = 6$). Surprisingly, only two of the 23 studies examined or discussed invasive weeds.

4. Discussion

4.1. Changes in understory vegetation

Overall, we observed no changes in understory vegetation types (shrubs, graminoids, litter and bare ground) aside from an increase in forb cover, which generally agrees with other studies on *D. ponderosae* outbreaks (Table 4). Understory plant growth in these forests is thought to be limited in part by light and nutrients (Barbier et al., 2008), both of which increase after *D. ponderosae* outbreaks (Griffin et al., 2011; Pec et al., 2015). Increased light and nutrients could explain the observed increase in forb cover, which was positively correlated in our plots with opening of the overstory canopy. Changes to available soil moisture were not measured in this study, but could also have affected

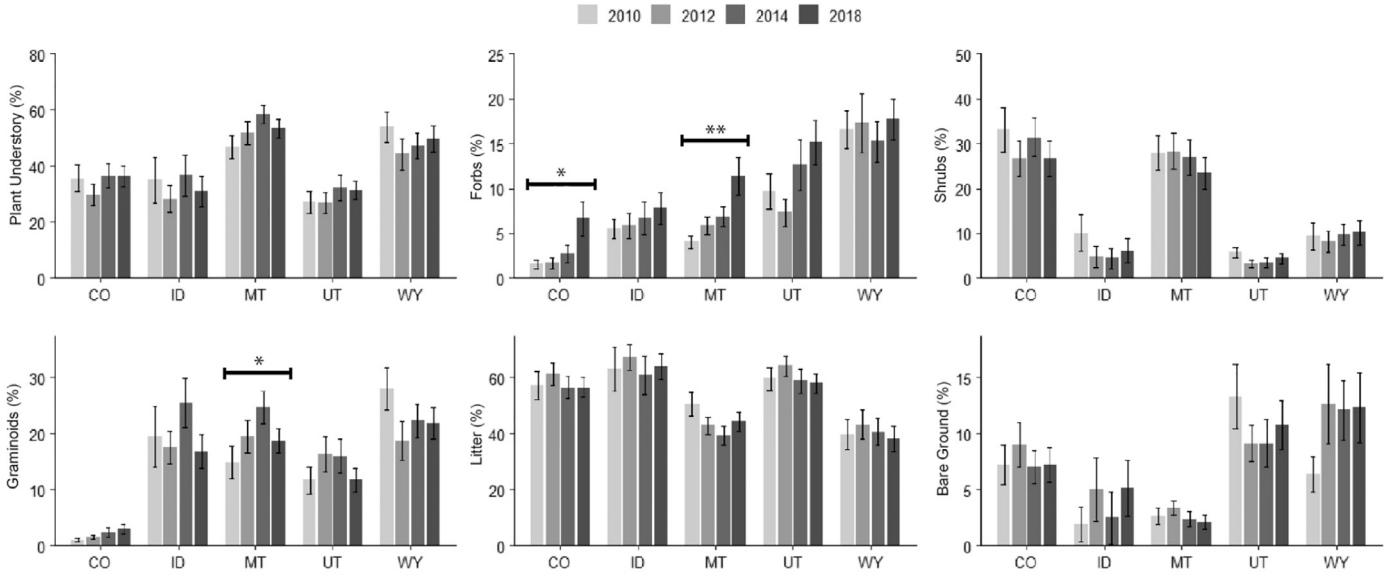

Fig. 3. Percent cover of total understory vegetation, forbs, shrubs, graminoids, litter and bare ground from 2010 to 2018 (ca. 2–10 years after peak levels of tree mortality due to *D. ponderosae* outbreaks) by year and state. Significant differences among years within states: $^{*}P < 0.05$, $^{**}P = 0.001$.

Table 1
ANOVA results testing for differences in mean percent cover of various understory cover types across years (2010–2018) for each state. Bold text indicates significant differences in means among years ($\alpha < 0.05$).

Cover type	CO			ID			MT			UT			WY		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
Total Understory	3,96	0.58	0.63	3,36	0.23	0.88	3,96	1.48	0.23	3,96	0.62	0.60	3,88	0.67	0.58
Forbs	**3,96**	**3.48**	**0.02**	3,36	0.34	0.79	**3,96**	**5.88**	**0.001**	3,96	2.50	0.06	3,88	0.12	0.95
Shrubs	3,96	0.55	0.65	3,36	0.82	0.49	3,96	0.31	0.82	3,96	1.30	0.28	3,88	0.10	0.96
Graminoids	3,96	0.98	0.41	3,36	0.92	0.44	**3,96**	**2.80**	**0.04**	3,96	0.57	0.64	3,88	1.51	0.22
Litter	3,96	0.34	0.80	3,36	0.28	0.84	3,96	1.51	0.22	3,96	0.54	0.66	3,88	0.23	0.88
Bare Ground	3,96	0.24	0.87	3,36	1.92	0.14	3,96	1.16	0.33	3,96	0.40	0.75	3,88	0.78	0.51

Table 2
Results of GLMM analysis (binomial) of effects of understory cover and tree metrics on the presence of invasive weeds. Only significant results shown. Full model AIC for 2014 = 63.9, for 2018 = 84.8.

Year	Variable	Estimate	SE	*Z*	*P*
2014	(Intercept)	−17.85	6.28	−2.84	0.004
	Graminoids	−2.65	0.74	−3.55	<0.001
	Percent dead	−10.72	3.63	2.95	0.003
2018	(Intercept)	−6.09	1.49	−4.09	<0.001
	Percent fall	4.05	1.12	3.66	<0.001

Table 3
Results of LMM models examining effects of understory cover and tree metrics on the abundance of invasive weeds. Only significant results shown.

Year	Variable	Estimate	SE	*t*-	*P*
2014	(Intercept)	−1.67	0.318	−5.24	<0.001
	Canopy cover	0.01	0.003	2.95	0.004
	Shrubs	0.01	0.004	2.40	0.018
	Litter	0.01	0.003	2.21	0.030
	Bare ground	0.02	0.006	2.57	0.012
	Percent dead	0.02	0.004	5.71	<0.001
2018	(Intercept)	−0.06	0.176	−0.35	0.742
	Percent fall	0.03	0.006	5.93	<0.001

forb cover (Pec et al., 2015). However, changes to forb cover were delayed and not evident until 2018, nearly 10 years after peak levels of tree mortality were observed. This could be partly explained by the fact that beetle-killed *P. contorta* retain red needles in the canopy for several years (Klutsch et al., 2009), which would slow opening of the canopy and changes to the forest floor (i.e., increases in light and nutrients). However, we did not sample in 2015–2017 and there is indication that forbs began to increase as early as 2014 (Fig. 2). Nevertheless, *D. ponderosae*-induced changes in forb cover were delayed for at least five years after peak levels of tree mortality occurred and influenced by geographic location (i.e. state, likely due to local conditions). Moreover, the increase in forbs is almost certain to be short-term as trees regenerate and the canopy closes (e.g., within 30 years, Griffin et al., 2011).

The lack of changes in the cover of shrubs and graminoids, despite putative increases in light and presumably water and nutrient availability, suggests growth of these plants is limited by other factors. For example, in the region in which our study was conducted most precipitation is received as winter snow with summer being very dry (Knowles et al., 2006). As such, growth of shrubs and graminoids might be limited by soil moisture during the dry growing season (Berdanier and Klein, 2011). Alternatively, multiple *D. ponderosae* effects could interact but result in no net change to understory vegetation. For example, the benefits of increases in light availability could be offset by a reduction in soil moisture due to increased temperatures (via solarization) and airflow (Roberts, 2004). It is also possible that some species responded positively to *D. ponderosae* disturbance whereas others responded negatively with no net change in total cover of shrubs and graminoids. Regardless, the total cover of shrubs, especially the dominant shrub in our plots grouse whortleberry, and graminoids is resistant to short-term changes resulting from *D. ponderosae* outbreaks in the Intermountain West. However, we cannot rule out the possibility that the height or biomass of shrubs and/or graminoids changed, as was found

Table 4
Summary of literature examining effects of bark beetle outbreaks on understory vegetation. +, increase; –, decrease; 0, no change. If empty, variable not examined. Number of + or – symbols indicates estimated magnitude of change: one symbol for <10% change, two symbols for 10–25% change, and three symbols for >25% change.

Bark beetle species	Forest type	Country	Time since outbreak (years)	Cover				Vegetation height	Above-ground biomass	Plant species diversity[1]	References
				Forbs	Shrubs	Graminoids	Total				
Dendroctonus ponderosae	*Pinus contorta*	USA	4–7						+++	+	Stone and Wolfe (1996)
		USA	20	0	0	0		+++ (shubs)	+++ (shrubs)		Page and Jenkins (2007)
		USA	0–3, 4–7	0	0	0	0	0 (0–3 yrs) +++ (4–7 yrs, grasses and forbs)			Klutsch et al. (2009)
		USA	2, 4, 30	+++ (2, 4 yrs) 0 (30 yrs)	0	0	+++ (2, 4 yrs) 0 (30 yrs)				Griffin et al. (2011)
		USA	5				+++				Norton et al. (2014)
		USA	10	+++	0	0	0				this study
		Canada	1–2						+ (yr 1) 0 (yr 2)	+ (forbs) 0 (shrubs)	Pec et al. (2015)
		Canada	7–8				– – – [2]			0	Edwards et al. (2015)
Dendroctonus ponderosae	*Pinus ponderosa*	USA	1–5						+ ++ (forbs, grasses) – (shrubs)		McCambridge et al. (1982)
		USA	0–10						+++[3]		Kovacic et al. (1985)
		USA	4–11	+	++	++	+++			–	Crotteau et al. (2019)
Dendroctonus pseudotsugae	*Pseudotsuga menziesii*	USA	5–10	+++	++	++	+++	+++			McMillin and Allen (2003)
		USA	4–5	++	0	++	++				Griffin and Turner (2012)
Dendroctonus rufipennis	*Picea glauca*	USA	17	0	0	+	+			–	Holsten et al. (1995)
		USA	8–9	0[4]	+[4]	0[4]	+[4]				Matsuoka et al. (2001)
Dendroctonus rufipennis	*Picea engelmannii*	USA	5	+++	0			+++ (forbs)	+++ (forbs)		Jorgensen and Jenkins (2011)
Dryocoetes confusus	*Abies lasiocarpa*	USA	1–4	+	+	+	+	+++			McMillin et al. (2003)
Ips typographus	*Picea abies*	Czech Republic	2–10	+			0			+ (vascular) – (moss)	Jonášová and Matějková (2007); Jonášová and Prach (2008)
		Germany	15							+	Lehnert et al. (2013)
		Germany	<20							+	Beudert et al. (2014)
		Germany	3–15	+	+	+	+			0	Fischer et al. (2015)
		Germany	3, 17–25	+++	0 (3 yrs) +++ (17–25 yrs)		+++	+		0 (3 yrs) + (17–25 yrs)	Winter et al. (2015a; 2015b)

[1] Only increase (+) or decrease (–) reported, not magnitude of change since different measures of diversity were used and species lists usually not provided.
[2] Decrease in total plant cover driven almost completely by reduction in the moss, *Pleurozium schreberi* (Brid.) Mitt.
[3] Biomass peaked at 5 years.
[4] Counted stems and leaves rather than cover.

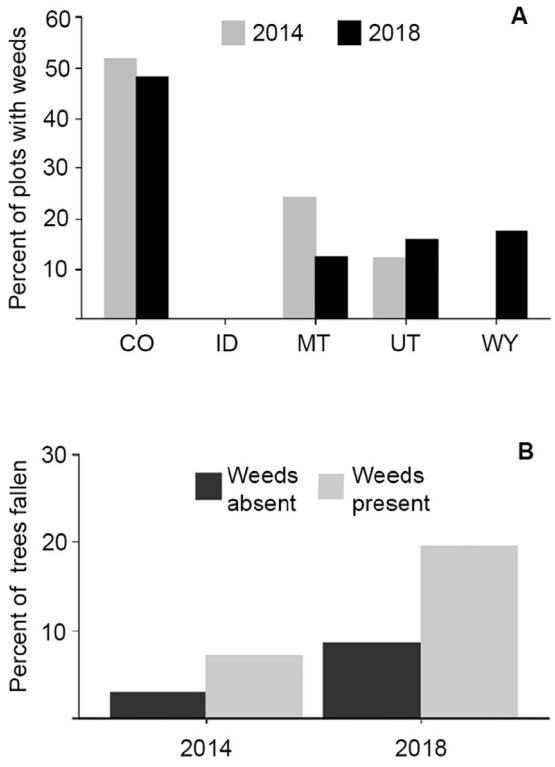

Fig. 4. (A) Percent of all plots with invasive weeds in each state in 2014 and 2018 (B) mean percent of snags fallen on plots with and without invasive weeds in 2014 and 2018.

in other studies (Stone and Wolfe, 1996; Klutsch et al., 2009; Pec et al., 2015).

4.2. Changes in invasive weeds

In 2014 and 2018, invasive weeds occurred on approximately 20% of our plots. In 2014, the presence of invasive weeds was negatively correlated with cover of graminoids and positively with percent dead trees, and by 2018 was only positively correlated with snag fall. There is evidence that grasses can inhibit invasion by weeds (e.g., Prober and Lunt, 2009). However, graminoid cover was generally low in our plots, and the state with the greatest number of weeds (Colorado) had by far the lowest cover of graminoids. This combined with the large amount of open, unvegetated ground in our plots suggests that the significance of graminoids could be an artifact. The strongest relationship was the positive effect fallen snags had on presence of invasive weeds in 2018. Some snags fell by tipping up in which the tree bole remains attached to exposed roots and a soil mound is produced (Schaetzl et al., 1990). This disturbance creates bare soil and these areas were frequently invaded by weeds (Fig. 5). In fact, these tip up sites were often the only place in which weeds occurred, but we also observed weeds spreading from tip up sites into nearby undisturbed areas. In Colorado, the effect appeared to be exacerbated by red squirrels [*Tamiasciurus hudsonicus* (Erxleben)] severing the heads of *C. arvense* and feeding upon them while perched on top of tip up mounds. The seeds are 4–5 mm long with a pappus that is readily dispersed by wind (Donald, 1994). Domestic and wild ungulates could also have facilitated the spread of weeds into our plots (Baltzinger et al., 2019). Thus, the disturbance created when snags uproot and fall seems to act as important sites for weed invasion by aerial or mammalian spread. Similar relationships have been observed in other systems. For example, in grasslands of the Carrizo Plain Natural Area in California soil disturbance by kangaroo rats [(*Dipodomys ingens* (Merriam)] promote weed invasions (Schiffman, 1994). Approximately 75% of trees killed by *D. ponderosae* activity during the outbreak remain standing and invasive weeds could worsen as more snags fall. Preliminary modelling of snag fall suggests most of the snags will remain standing for several more years. In fact, a significant number of snags will likely remain standing until 25–30 years after the *D. ponderosae* outbreak (Fettig et al., unpublished data). Monitoring invasive weeds at tip up sites could be a cost-effective and efficient tactic to limit invasions following *D. ponderosae* outbreaks in the Intermountain West.

We did not track the abundance of invasive weeds outside the quadrats on our plots until 2014, after we observed a noticeable increase in number from 2010 to 2012 in plots but outside of quadrats. The number of invasive weeds increased 31% from 2014 to 2018. Thus, the abundance of invasive weeds has likely increased since 2010. In 2014, the abundance of invasive weeds was correlated with five site characteristics (Table 3), however, by 2018 invasive weed abundance was only positively correlated with snag fall. Few snags had fallen by 2014 but by 2018, nearly three times as many snags had fallen. As more snags fell, the strong effect of fallen snags on weeds likely overwhelmed the influence of other site variables, further supporting the important role this disturbance can have in weed invasions in *P. contorta* forests.

Cirsium arvense was the dominant invasive weed on our plots. This species appears to be the primary weed of *P. contorta* forests in the Northern Rockies of the U.S., and can be problematic after disturbance events (Birdsall et al., 2012). Another trend observed was the increase in weeds in Wyoming plots between 2014 and 2018, driven entirely by the appearance of *Po. recta*. *Potentilla recta* is a plant of open habitats and is a strong invader in many systems (Pearson et al., 2016). A key factor promoting weed invasion is propagule pressure (Sutherland and Nelson, 2010), and many plots within our network that contained invasive weeds had nearby (within ~250 m) weed populations, usually along roadways, that could have acted as seed sources. Roads are known to be important sources of weed propagules that can influence invasion of nearby forests, especially if disturbed (Birdsall et al., 2012), suggesting that control of roadside weeds could reduce weed invasions into neighboring forests impacted by *D. ponderosae*.

4.3. Review of bark beetle outbreak effects on understory vegetation

Synthesis of the literature reveals an overwhelmingly positive short-term effect of bark beetle outbreaks on understory vegetation (Table 4). In fact, in just one instance did the cover of any vegetation type decrease following an outbreak, and this was a reduction of moss following a *D. ponderosae* outbreak in central British Colombia, Canada (Edwards et al., 2015). Moreover, all studies examining understory vegetation height and/or aboveground biomass reported short-term increases in both. The effects of bark beetle outbreaks on understory plant species diversity is more mixed, but six of 10 studies examining diversity reported an increase in diversity of at least one vegetation type. However, in some circumstances understory plant diversity can decrease following bark beetle outbreaks (e.g., Holsten et al., 1995; Crotteau et al., 2020).

The magnitude of understory vegetation changes generally varied with bark beetle species and forest type. For example, understory vegetation changes following *D. ponderosae* outbreaks in ponderosa pine (*P. ponderosa* Dougl. ex Laws.) and Douglas-fir beetle (*D. pseudotsugae* Hopkins) outbreaks in Douglas-fir [*Pseudotsuga menziesii* (Mirb.) Franco] consistently resulted in increases in cover of most plant types and plant height or biomass (McCambridge et al., 1982; Kovacic et al., 1985; McMillin and Allen, 2003; Griffin and Turner, 2012; Crotteau et al., 2020). Outbreaks of *I. typographus* in *Pi. abies* generally resulted in more subtle increases in most cover types and vegetation height with mixed effects on plant diversity (e.g., Jonášová and Matějková, 2007; Fischer et al., 2015; Winter et al., 2015a). The effects of spruce beetle [*D. rufipennis* (Kirby)] outbreaks seem to vary with forest type. *Dendroctonus rufipennis* outbreaks in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) in Utah resulted in large increases in the cover, height,

Fig. 5. The disturbance created when *D. ponderosae*-killed trees tip up and fall is prone to the establishment and spread of invasive weeds. Canada thistle (*Cirsium arvense*, shown here in a plot in Colorado, USA) frequently invaded these sites and spread to nearby less disturbed areas. Photo credit: J. Runyon, Rocky Mountain Research Station, USDA Forest Service.

and biomass of forbs, but not other plant types (Jorgensen and Jenkins, 2011) whereas outbreaks in white spruce [*Picea glauca* (Moench) Voss] in Alaska had relatively weak positive effects on vegetation, but no effect on forbs (Holsten et al. 1995; Matsuoka et al., 2001). The effect of *D. ponderosae* outbreaks on forb cover seems to vary by location. For example, we found that the cover of forbs, graminoids, and shrubs fundamentally differed among states as did the response of forbs to *D. ponderosae* outbreaks (Fig. 3). These disparities could be due to differences in local environmental conditions and stand histories. One obvious geographic difference is the abundance of moss in wetter, more northern *P. contorta* forests (e.g., in interior British Columbia), which was essentially absent in our plots, but when present can be severely negatively affected by *D. ponderosae* outbreaks (Edwards et al., 2015). Some of the variability in results among studies could be explained by year-to-year variation in weather, especially for studies assessing vegetation in only 1–2 years, since plant growth and competition among plants can vary by year depending on soil moisture levels (Pec et al., 2015).

Time since outbreak can have an important effect on understory vegetation. For example, the post-outbreak increase in forb cover found in our study was delayed by several years (Fig. 2), and other studies provide evidence suggesting that increases in forbs is temporary and wanes by 20 (Page and Jenkins, 2007) or 30 years (Griffin et al., 2011) after *D. ponderosae* outbreaks. Increases in plant height after *D. ponderosae* outbreaks in *P. contorta* also appear to be delayed by several years (Klutsch et al., 2009). Similarly, increases in shrub cover and plant species diversity following *I. typographus* outbreaks in *Pi. abies* is delayed by at least 3 years (Winter et al., 2015a). An experiment simulating *D. ponderosae* tree death in Alberta, Canada also found a delayed response with no changes to understory vegetation one year after treatment (McIntosh and Macdonald, 2013) but increases in plant richness and small changes to cover were found seven years after treatment and were related to treatment intensity (Steinke et al., 2020). Overall, the temporal effects of bark beetle outbreaks on vegetation are poorly understood since most studies are retrospective snapshots. Longer-term studies are needed to fully understand the dynamic effects of bark beetle outbreaks on understory vegetation through time.

Only two previous studies addressed the influence of bark beetle outbreaks on invasive weeds. McCambridge et al. (1982) noted a large increase in *C. nutans* about 5 years after a *D. ponderosae* outbreak in *P. ponderosa* in Colorado. Crotteau et al. (2020) monitored invasive weeds for about 11 years after a *D. ponderosae* outbreak in *P. ponderosa* in Montana but found very low cover of weeds and no change over time. In our study, weed invasions generally increased over time, but varied by state (Fig. 4A). Given the scarcity of studies, there is a clear need for more research on weed invasion following bark beetle outbreaks and on methods to best manage these invasions.

5. Conclusions

Natural resource managers are increasingly challenged to maintain resilient and productive forests during a period of rapid environmental change. Of note, a key finding of the latest National 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). Despite this, little is known of the effects of bark beetle outbreaks on understory vegetation. A review of the literature found a generally positive response of understory vegetation following outbreaks that varied with bark beetle species, forest type, and time since outbreak. In our study, understory vegetation remained relatively unchanged 14 years after *D. ponderosae* outbreaks began in Colorado, Idaho, Montana, Utah, and Wyoming. This is despite the high levels of tree mortality that occurred (Fig. 1). Of note, increases in the cover of forbs and invasive species were observed. Forbs are important resources for native insect pollinators and are likely increasingly important as populations of wild bees are in decline nationally (Koh et al., 2016). Relatedly, a recent study showed increases in the diversity and abundance of wild bees following a *D. pseudotsugae* outbreak in Idaho (Foote et al., 2020). Of concern is the increase in invasive weeds, which is likely to accelerate in the future as more snags fall. Furthermore, invasive weeds generally respond more favorably to elevated CO_2 than native plants (Bradley et al., 2010), whereas responses to changes in temperature and precipitation are variable and are influenced by the magnitude and direction of change (Dukes et al., 2009). As such, we feel these vegetation changes, and their consequences, warrant more long-term study which will allow land managers to predict and respond to changes following bark beetle outbreaks.

Declaration of Competing Interest

The authors have no competing interests to declare.

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