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Long-term forest understory recovery and tradeoffs in response to prescribed fire return interval

Becky K. Kerns[1*], Gregg M. Riegel[2], Nathan M. Wade[3,5], Deborah G. Nemens[4], Claire M. Tortorelli[1,5], Danielle H. Berger[3,6], Maureen C. Kennedy[7], G. L. Williams[3] and Susan Prichard[4]

Abstract

Background Prescribed fire is a critical tool for managers of dry fire-prone forests used to create more fire resilient forests, improve wildlife habitat and increase understory diversity. However, there are still knowledge gaps around how to apply fire to achieve and balance desired conditions, such as how the forest understory responds to frequency of burning. We leveraged a unique long-term prescribed burn experiment and evaluated the responses of different understory vegetation components to differing fire return intervals (5-, 10-, 20-year) including two common shrub species of interest in western forests, antelope bitterbrush (bitterbrush) and snowbrush ceanothus (snowbrush).

Results Five- and 10-year burn treatments suppressed bitterbrush cover throughout the study but after cessation of 5-year burning, cover rebounded substantially within a decade. Bitterbrush density demonstrated rapid recovery after burning later in the study and with 5-year burning. We found that all burn treatments increased snowbrush cover and density to some degree, although cover remained low with 5-year burning. In some areas, 10- and 20-year burning and associated substantial overstory loss catalyzed dominance of snowbrush. Burning increased total herbaceous cover and biomass, particularly for the latter part of the study and for longer fire return intervals. Richness was not impacted by the treatments. The positive herbaceous response was driven by the rhizomatous western brackenfern. Ordination results revealed differing plant communities in response to treatments, largely driven by the increase of snowbrush and western brackenfern.

Conclusions Wildland fire managers often face substantial tradeoffs as they plan to use prescribed fire to restore dry forests. Burning at 5-year intervals was the most successful at reducing surface litter and shrub cover but came with tradeoffs by reducing wildlife habitat values. Longer intervals (10- and 20-year) can sustain some bitterbrush cover but can also lead to dominance of snowbrush and western brackenfern in some areas. Designs that consider a matrix of unburned areas and a range of fire return intervals may be more likely to succeed in striking a balance. Although long-term studies of this nature are challenging to conduct, they remain critical to our understanding of how management activities affect ecosystem recovery and meet outcomes.

*Correspondence:
Becky K. Kerns
Becky.Kerns@usda.gov
Full list of author information is available at the end of the article

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Keywords Ponderosa pine, Repeat burning, Herbaceous response, Bitterbrush, Snowbrush, Wildlife habitat

Resumen

Antecedentes Las quemas prescriptas representan una herramienta crítica para gestores de bosques secos propensos a fuegos, para poder crear bosques más resilientes, mejorar el hábitat para la fauna e incrementar la diversidad del sotobosque. Sin embargo hay todavía vacíos en el conocimiento sobre cómo aplicar el fuego para obtener y balancear las condiciones deseables, tales como, la vegetación del sotobosque, responde a la frecuencia en las quemas. Aprovechamos un único experimento de quema prescripta a largo plazo y evaluamos las respuestas de diferentes componentes de la vegetación del sotobosque a quemas realizadas en distintos intervalos de tiempo (5-, 10-, y 20 años), incluyendo dos especies de arbustos de interés, comunes en bosques del oeste de los EEUU, bitterbrush (*Purshia tridentata*) y el arbusto de nieve (*Ceanothus velutinus*).

Resultados Cinco y 10- años luego de los tratamientos de quemas, suprimieron la cobertura del bitterbrush en todo el estudio, aunque luego de 5 años de la cesación de las quemas, la cobertura se recuperó substancialmente dentro de una década. La densidad del bitterbrush demostró una rápida recuperación luego del fuego en el estudio y dentro de los 5 años de quemado. Encontramos que todos los tratamientos de quemas incrementaron la cobertura del arbusto de nieve hasta cierto grado, aunque la cobertura fue baja dentro de los 5 años luego de las quemas. En algunas áreas, las quemas a 10- y 20 años y una pérdida substancial del dosel superior catalizó la dominancia del arbusto de nieve. La quema incrementó la cobertura total y la biomasa de herbáceas, particularmente en la última parte del estudio y en los períodos de intervalos de fuego más largos. La riqueza de especies no fue afectada por los tratamientos. La respuesta positiva de las herbáceas fue conducida por la especie rizomatosa helecho águila (*Pteridium aquilinum*). El ordenamiento de los resultados revela que las comunidades difieren en respuesta a los distintos tratamientos, condicionados grandemente por los incrementos en el arbusto de nieve y el helecho águila.

Conclusiones Los gestores de incendios forestales se enfrentan frecuentemente a sustanciales desafíos al planificar el uso de quemas prescriptas para restaurar bosques secos. Las quemas con intervalos de 5 años fueron las más efectivas para reducir la broza superficial y la cobertura de arbustos, pero tienen la desventaja de reducir los valores de hábitat para la fauna. Los intervalos de quema más largos (10- y 20 años) pueden sostener la cobertura del bitterbrush pero pueden también llevar hacia una dominancia del arbusto de nieve y del helecho águila en algunas áreas. Los diseños que consideran una matriz de áreas no quemadas y un rango de intervalo de quemas pueden ser exitosos en alcanzar un balance. Aunque los estudios de esta naturaleza a largo plazo son desafiantes para poder ser concretados, son extremadamente críticos para nuestro entendimiento sobre como las actividades de manejo afectan la recuperación de los ecosistemas y se alcanzan los objetivos deseados.

Background

Reintroducing fire in dry conifer forests through prescribed fire is a critical management strategy used to reduce fuels, protect human communities, create a more fire-resilient forest structure, improve ecological function, and mitigate future wildfire impacts (Fitzgerald 2005; Noss et al. 2006; Stephens et al. 2020; Prichard et al. 2021). Forests across much of western North America have been substantially altered in the past century following widespread fire suppression and exclusion, including the cessation of Indigenous cultural burning (Hessburg et al. 2005; Hagmann et al. 2021). Low-elevation ponderosa pine (*Pinus ponderosa*) forests have experienced some of the most dramatic changes following the disruption of historically low-severity frequent fire regimes (Steel et al. 2015; Haugo et al. 2019), such as increased tree densities, fuel accumulation, and shifts in species composition to more shade-tolerant and fire-intolerant tree species (Keeling et al. 2006; Noss et al. 2006).

Loss of frequent fire and changes in forest structure also impact forest understories, including many important browse and forage species that have been particularly impacted by fire exclusion and increased forest density (Hessburg et al. 2005). Without periodic fire, competition for light, water, and nutrients between understory species and overstory trees in ponderosa pine forests can result in reduced understory biomass and species diversity (McConnell and Smith 1970; Moore and Deiter 1992; Riegel et al. 1992; Naumburg and DeWald 1999). Forest biodiversity in temperate forests is largely a function of the understory community, and forest understories regulate many processes such as conifer regeneration, soil retention, nutrient cycling, and provide critical wildlife habitat (Biswell 1972; Alaback 1982; Allen et al. 2002; Gilliam 2007).

Despite the increased application of and calls for greater prescribed fire use, there are still knowledge gaps, uncertainties, and challenges around applying fire to achieve and balance desired conditions (Ryan et al. 2013; Hiers et al. 2020). Plants in dry western forests are generally considered adapted to frequent fire (fire-return intervals < 35 years) and possess fire-adapted traits such as resprout ability (Brown and Smith 2000; Keeley et al. 2011; Agee 2013; Pausas and Keeley 2014). These understories are often expected to be resilient—showing little change in cover or abundance—or to respond positively with increased richness or abundance following fire (Strahan et al. 2015; Strand et al. 2019; Springer et al. 2024). In addition, frequent burning has been found to favor herbaceous species over woody ones (Glitzenstein et al. 1995; Varner et al. 2007; Peterson and Reich 2008) and promote fast-growing annual or invasive species over native perennials (Keeley and McGinnis 2007; Bradley et al. 2018). However, after a century or more of fire exclusion and suppression in western forests and the introduction of new stressors (livestock grazing, drought, invasive plants), predicting successional trajectories of communities after fires is challenging. Multiple studies have examined the effects of prescribed fire and fire frequency on tree canopy structure and regeneration in the interior west, while far fewer studies pay attention to understory species responses, particularly outside the southwestern US (Metlen et al. 2004; Moore et al. 2006; Dodson et al. 2008; Scudieri et al. 2010). Using prescribed fire to reduce the severity of wildfires and simultaneously maintain diverse forest understories and critical wildlife habitat is a particular challenge for land managers (Pilliod 2006; Stevens et al. 2016; Kerns and Day 2018; Wright et al. 2023); there is often a lack of information needed to determine how often to conduct burns to achieve specific ecological, wildland fuel, and wildlife habitat related goals.

Two widely distributed ecologically important nitrogen-fixing shrubs that are of wildlife management and restoration interest in western forests include antelope bitterbrush (hereafter bitterbrush, *Purshia tridentata* (Pflug 1999)) and snowbrush ceanothus (hereafter snowbrush, *Ceanothus velutinus* Douglas ex Hook.). Both species provide important nitrogen contributions to soils and food and cover for wildlife; bitterbrush is one of the most important browse species in western North America, providing critical winter forage for mule deer (*Odocoileus hemionus* (Rafinesque)) (Zavitkovski and Newton 1968; Youngblood and Riegel 1999; Busse et al. 2000). Past studies have documented highly variable bitterbrush responses to fire, which likely reflect the species general intolerance to fire and inconsistent ability to resprout (Giunta et al. 1978; Busse and Riegel 2009). Snowbrush cover can increase after fire, particularly in open light environments, via resprouting and seeding, and can dominate post-disturbance landscapes and slow conifer regeneration (Conrad 1985; Erickson and Harrington 2006; Crotteau et al. 2013). Under low foliar moisture contents, both species can be highly flammable and serve as understory ladder fuels that can increase crown-fire risk in forests (Agee 1996; Heyerdahl et al. 2014; Kramer et al. 2014). Flammable ladder fuels such as shrubs are particularly concerning in the wildland urban interface (WUI), where they can increase wildfire risk to people and property (Kramer et al. 2014; Taccaliti et al. 2023). Management of these fuels is aided by understanding the appropriate prescribed fire regimes to balance tradeoffs between desired habitat conditions and reducing fire hazard, particularly in areas where wildfire can be a serious threat to communities (Guo et al. 2024).

Understanding how vegetation recovers from burning after a period of extensive fire exclusion, and how the understory responds to frequency of burning is critical for understanding the extent to which forest treatments meet fuel management and restoration goals. In this study, we leverage a unique long-term prescribed fire experiment located at the Metolius Research Natural Area (MRNA) in central Oregon within a dry ponderosa pine forest and WUI area. This long-term prescribed fire study was designed to evaluate understory vegetation response to differing fire return intervals (5-, 10-, and 20-years) over more than two decades, beginning in 1992 in a long-time fire excluded forest. The study was guided by the management goals of restoring historic stand structure and understory diversity, reducing fuel loads, and maintaining key habitat elements such as bitterbrush. Therefore, an important goal of our work here was to provide practical and scientifically robust information to land managers by working collaboratively to produce “actionable science” (Meadow et al. 2015; Beier et al. 2017).

Our co-developed research questions included the following: (1) How did bitterbrush, snowbrush, herbaceous plant groups, species richness and composition respond to different intervals of burning? (2) Did treatment responses differ at different points in time? We hypothesized the following: (1) plant responses would differ based on burn frequency, number of burns, and plant traits. (2) Frequent burning would favor resprouting or rhizomatous species generally and reduce woody species. (3) Frequent burning would increase species richness. (4) Different burn frequencies would create distinctly different plant communities by the end of the study. This study provides timely information on prescribed fire effects and management relevant outcomes in ponderosa pine forests given major investments to increase application of forest treatments to reduce woody fuel loads, wildfire impacts, and threats to people and communities (USDA Forest Service 2022).

Methods

Study area

We conducted our study within the Metolius Research Natural Area (MRNA), a 581-ha preserve established in 1931 that is administered by the Deschutes National Forest in central Oregon and adjacent to the small community of Camp Sherman, USA (Fig. 1). The site lies on a mostly level pumice bench at the base of a steep escarpment to the east (slopes 0–26%). Soils are very well-drained and formed in basalt and andesite residuum overlain with dacite pumice and basaltic ash; stonier; thinner soils and basaltic outcrops punctuate the bench and provide localized topo-edaphic heterogeneity (data on file with author; Youngblood et al. 2004; Youngblood and Riegel 1999). The climate is continental, with warm dry summers and cool winters during which most of the precipitation falls as snow (mean annual precipitation about 365 mm per year,Youngblood and Riegel 1999; Appendix 1 Fig. S1). Forest overstories are dominated by ponderosa pine, with commonly occurring Douglas-fir *(Pseudotsuga menziesii* Dougl. ex Laws.), grand fir (*Abies grandis* (Douglas ex D. Don) Lindl.) and occasional incense cedar (*Calocedrus decurrens* (Torr.) Florin) and western larch (*Larix occidentalis* Nutt.). Prior to burning the area was characterized by a mix of three plant associations related to localized topo-edaphic variability, an important driver of forest composition in central Oregon (Volland 1985; Merschel et al. 2018). Ponderosa pine/bitterbrush/western needlegrass (*Achnatherum occidentale)* and Ponderosa pine/bitterbrush/Idaho fescue (*Festuca idahoensis*) associations were reportedly common in areas with minimal to no relief while the Ponderosa pine/bitterbrush-greenleaf manzanita (*Arctostaphylos patula*)/western needlegrass association was more common in areas with more relief, thinner soils, and exposed bedrock (Volland 1985; data on file with author). Current understory vegetation is dominated by bitterbrush, snowbrush, and western brackenfern (Table 1).

Treatments

The study area was delineated into 3 blocks based on the initial burn year. Each block was divided into 4 units and randomly assigned a treatment including control (unburned), 5-year, 10-year, and 20-year fire return intervals, resulting in 12 experimental units ranging in size from 3.6 to 12.3 hectares, with an average size of 8.2 ha (Fig. 1). Initial burns were conducted in the spring of 1992 (Block 1), 1993 (Block 2), and 1994 (Block 3; Fig. 1). Hand-carried drip torches were used to ignite all burn treatment areas using strip head fires with the goal of maintaining a flame length less than 60 cm. Subsequent burns were conducted in the fall and maintained the staggered schedule based on block (Fig. 2). Fire behavior and effects were highly variable depending on fuel loads, moisture conditions, and weather at the time of burning (Gregg Riegel, personal observation). Temporal blocking for the fires was used to constrain the resources needed to conduct the burns and sampling and to compensate for the potential confounding effect of annual variability in weather that might occur.

Treatment intervals of 5, 10, and 20 years were selected to represent the historic range of variability of fire occurrence. Dendrochronological evidence from nearby sites suggested fire return intervals as low as 4 years, with an average of 9 to 11 years prior to fire suppression (Bork 1984; Morrow 1985) and a local study found that fire returned on average every 9.5 years (SD 3.96 years) from 1613 to 1898 (Johnston 2018). Fire history studies in similar ecosystems at broader scales suggest mean fire return intervals of about 15–32 years, with variable fire size and severity (Merschel et al. 2018; Heyerdahl et al. 2019).

Data collection

Initial sampling of understory vegetation for all blocks was conducted in 1995 following the first burns (Youngblood and Riegel 1999). Subsequent sampling was conducted every 2 years until 2015, and once again in 2023. Within each treatment unit, a 1-ha plot (100 m × 100 m) was randomly established. Three 100-m long permanent transects were systematically placed within each plot to capture understory variability. Transects were spaced 25 m apart oriented north–south. Both ends of each transect were marked with a metal fence post to ensure relocation.

Shrub cover was recorded by species along each transect using the line-intercept method. Shrub density was measured by species along a 2 m-wide belt transect centered on each transect. Herbaceous and ground cover were recorded using a modified 0.2 × 0.5 m Daubenmire frame (Daubenmire 1959; Coulloudon et al. 1999) placed every 10 m along each transect, for a total of 30 quadrats in each plot. Ocular cover was recorded by species and cover class: trace or 0.5%; 1–10%, to the nearest percent; and > 10% to the nearest multiple of 5. Ground cover included litter, bare ground, rock, moss, lichen and wood.

Herbaceous biomass data was collected at peak biomass. Ten regularly spaced microplots were clipped along each transect resulting in 30 samples per experimental treatment unit (plot). Samples alternated between the left

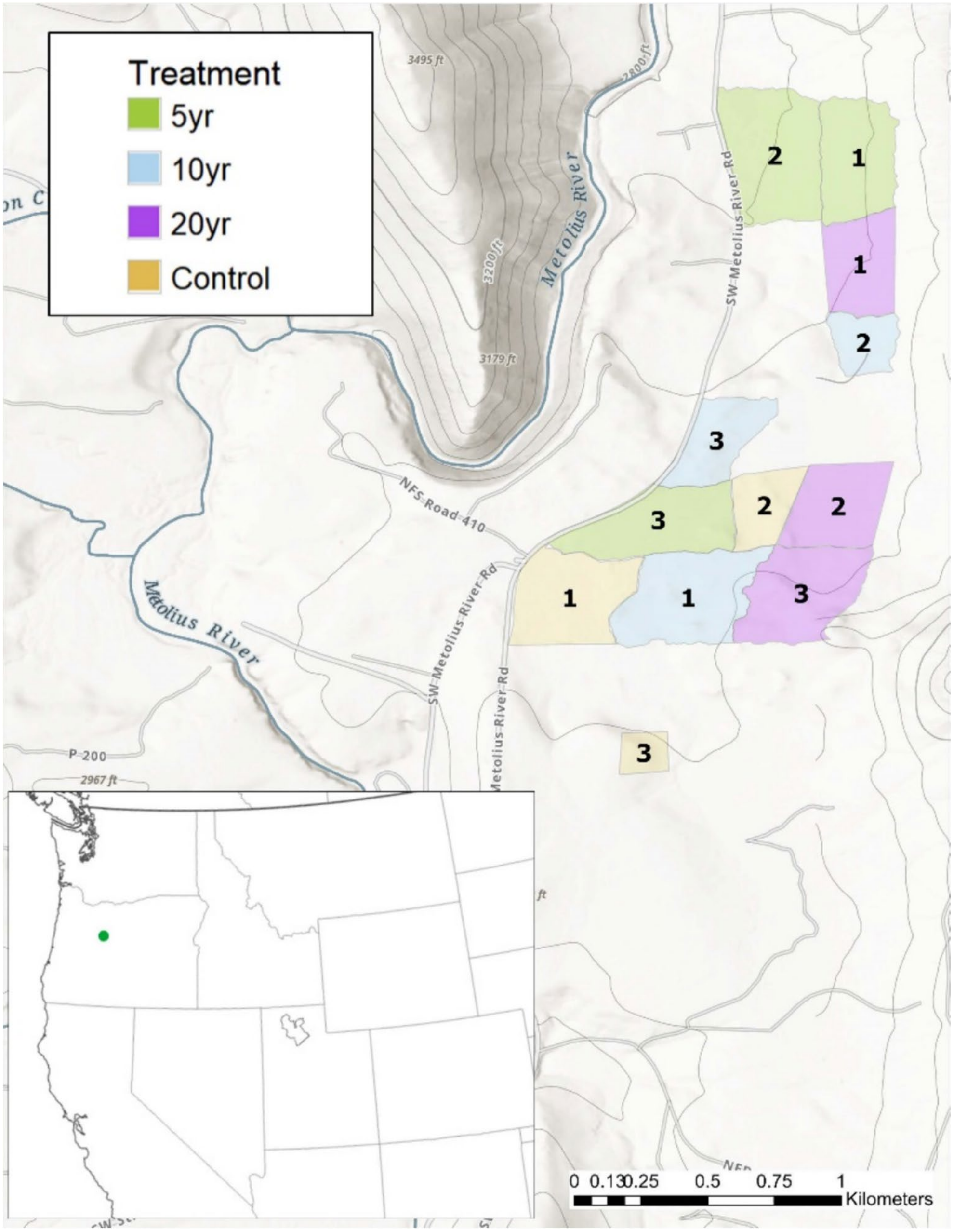

Fig. 1 Study site location and treatments in central Oregon, USA (Metolius Research Natural Area, Deschutes National Forest). Study plots are numbered by block and colored by treatment

and right side of the transect to avoid previously clipped areas. After harvest, samples were dried for 48 h at 60 °C and then weighed. Overstory metrics including tree density, percent sky visibility, and percent overstory canopy cover were also collected for some years; sampling methods and all results are detailed in Appendix 2.

Analysis

We evaluated the response to prescribed burn intervals through time for the following understory variables: bitterbrush and snowbrush cover and density; herbaceous plant group cover (Table 1); total additive cover; total herbaceous biomass; and species richness. For our herbaceous plant groups, we used a standard plant classification framework based on life-cycle (annual versus

Table 1 Dominant species for the herbaceous plant groups analyzed based on site-wide 2023 cover. All groups are native and perennial except as noted. A complete species list is presented in Appendix 1 Table S1

Species/group name	Dominant species	Common name
Rhizomatous forb/fern	*Pteridium aquilinum* (L.) Kuhn var. *pubescens* Underw	Western brackenfern
	Kelloggia galioides Torr	Milk kellogia
Non-rhizomatous forb	*Fragaria virginiana* Duchesne	Virginia strawberry
	Balsamorhiza sagittate (Pursh) Nutt	Arrowleaf balsamroot
Annual forb	*Microsteris gracilis* (Hook.) Greene var. *gracilis*	Slender phlox
	Gayophytum diffusum Torr. & A. Gray	Spreading groundsmoke
Perennial grass	*Festuca idahoensis* Elmer	Idaho fescue
	Elymus elymoides (Raf.) Swezey ssp. *elymoides*	Bottlebrush squirreltail

perennial) and reproduction characteristics linked to fire-resistant traits (seed versus vegetative reproduction) (Pyke et al. 2010; Agee 2013; Kerns and Day 2018; Ricci et al. 2024); finer-scale groups based on traits were not possible due to the relatively sparse understory. Plant groups with less than 1% mean cover for all years and treatments were not analyzed. This included shrubs other than bitterbrush and snowbrush (even when lumped), exotics, and sedges. Total species richness was generated from all the understory data for each plot. Although collated inconsistently through time, we also evaluated the overstory response variables to aid in interpretation (Appendix 2). Plot-level means for all response variables were used for all analyses except tree density, which was enumerated at the whole plot level.

The burn schedule and understory sampling were not always consistent throughout the entire 26-year sample period. To account for this, we selected sample years to include that reflected comparable and meaningful time since fire periods, generally 3–5 years since the last fire. In two cases, we combined 2 different years of data to create a consistent time since fire sample (2001/03, 2011/2013) (Fig. 2). We also included the 2015 observation as it was the only measurement after all treatments had been fully implemented (1–2 years post-fire), and our remeasurement in 2023 9–10 post-fire (Fig. 3). Cover data for our two species of management concern (bitterbrush and snowbrush) from all sample years are shown in Appendix 1 Fig. S2.

To evaluate the effects of burn interval on our response variables, we used generalized linear mixed models (GLMMs) and a log-linked Tweedie distribution, with the exception that percent sky visibility was modeled using a logit-linked Beta distribution (Gold et al. 2023) and density variables were modeled using a log-linked Poisson distribution (Brooks et al. 2019). The Tweedie distribution is suitable for a wide range of continuous response variables, is robust for non-normal zero-inflated data, and is commonly used for cover and biomass (Tweedie 1984; Rouge et al. 2022; Fajardo-Cantos 2026; Shrestha et al. 2026). Multi-year models were structured with year, treatment, and the year × treatment interaction as fixed effects and the random effect of plot nested within block. DHARMa plots were used to examine model fit and overdispersion. Due to our a priori interest in within-year treatment differences, multiple comparisons were conducted using Tukey's Honest Significant Difference test and unadjusted p-values are reported. For graphical representation and interpretation of effect sizes, back-transformed estimated marginal means (± SE) are presented. We emphasize differences among treatments within sample years and avoid quantitative comparisons between years to address our research questions and minimize potential bias based on annual variability in climate or changes in crews, particularly for ocular estimates of herbaceous cover. We discuss treatment mean differences using model-defined ratios for effect size when p-values are near to or less than 0.10 and avoid dichotomous statements around significance (Muff et al. 2022). Untransformed raw data means, p-values, and all effect sizes for contrasts are provided in Appendix 1 Tables S2 and S3.

Plant community patterns in relation to time and treatment were assessed using non-metric multi-dimensional scaling (NMDS) ordinations. Transects from the plots were ordinated to explore within-plot patterns. Herbaceous and shrub cover data from 1997, 2007, 2011/2013, and 2023 were combined into a single ordination with sampling period used as a grouping variable. Rare species were removed (< 5%), cover values were relativized by maximum cover, and the ordination was performed using a Bray–Curtis distance matrix. Patterns related to variables such as bare ground, litter, moss, lichen, coarse woody debris, and rock were examined using a permutation test to determine the correlation between each variable and the ordination axes.

All analyses and graphing were conducted using R statistical software version 4.4.1 (R Core Team 2024). Data summarization and graphing, GLMMs, model assessment, and post-hoc comparisons used the tidyverse,

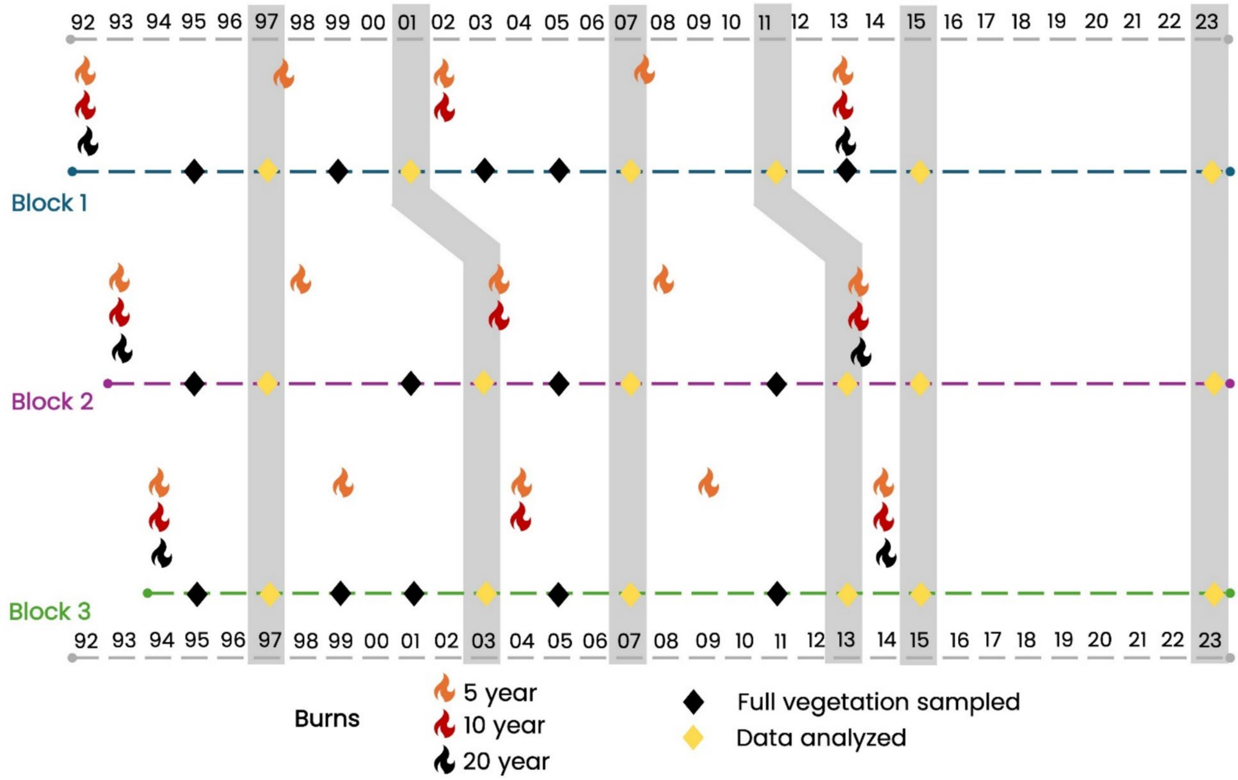

Fig. 2 Burn and sampling schedule by treatment and block. Sampling was always completed prior to burning in a given year. Blocking was based on year of initial burn, resulting in a staggered burn schedule. Years used in statistical analysis are shown in gray

glmmTMB, DHARMa, car, emmeans, and ggh4x packages (Pinheiro 2011; Hartig 2016; Brooks et al. 2017; Fox and Weisberg 2018; Wickham et al. 2019; Van Den Brand 2021; Lenth 2023). NMDS ordinations and testing of explanatory variables were conducted using the vegan package (Oksanen et al. 2013) and rare species were removed using the labdsv package (Roberts 2019).

Results

Bitterbrush and snowbrush response

In 1997 after the first burns, bitterbrush cover in the control was about four to ten times higher compared to the burn treatments (Fig. 4). Burning every 5 years maintained consistently low cover throughout most of the study, with cover four to more than seven times higher in the control. In 2023, with one missed burn interval, bitterbrush rebounded with similar cover as the control. Similarly, 10-year burning maintained consistently lower cover compared to the control, particularly after the second 10-year burn in 2007, and cover was consistently undifferentiated for the 5- and 10-year treatments, although the trend weakened in 2023 when the 5-year rebounded (5–10 $p=0.11$). Burning every 20 years allowed steady bitterbrush cover recovery compared to more frequent burning, until cover dropped in 2015 after all plots had been reburned. By 2023, the only treatment with lower cover than the control was the 10-year.

For bitterbrush density, burn treatments initially reduced density substantially, and in 2001/2003, the control had 5–6 times more shrubs compared to the burn treatments (Fig. 4). By 2007, differences among the treatments emerged and the recovering 20-year had 3–4 times more shrubs compared to the 5- and 10-year. In 2011/2013, density in the 5-year rebounded and was similar to the control, as was the recovering 20-year. At this time, the 5-year had about twice the estimated occurrence of shrubs compared to the 10-year. In 2015, with only 1–2 years since the fires, density in the 20-year was similar to the control and about 3 times higher than the 10-year. By 2023, the control still had about twice as many shrubs as the 10-year, but was similar to the 5- and 20-year.

In contrast to bitterbrush, snowbrush cover was essentially nonexistent at the time of the first measurement in 1997 and remained so within the controls throughout the study period (Fig. 4). This pattern led to issues with model convergence; therefore, the control treatment and 1997 were dropped from the model and only differences in burn treatments were assessed. Snowbrush established after burning in all the burn treatments, and like bitterbrush, burning every 5 years suppressed cover; by 2023,

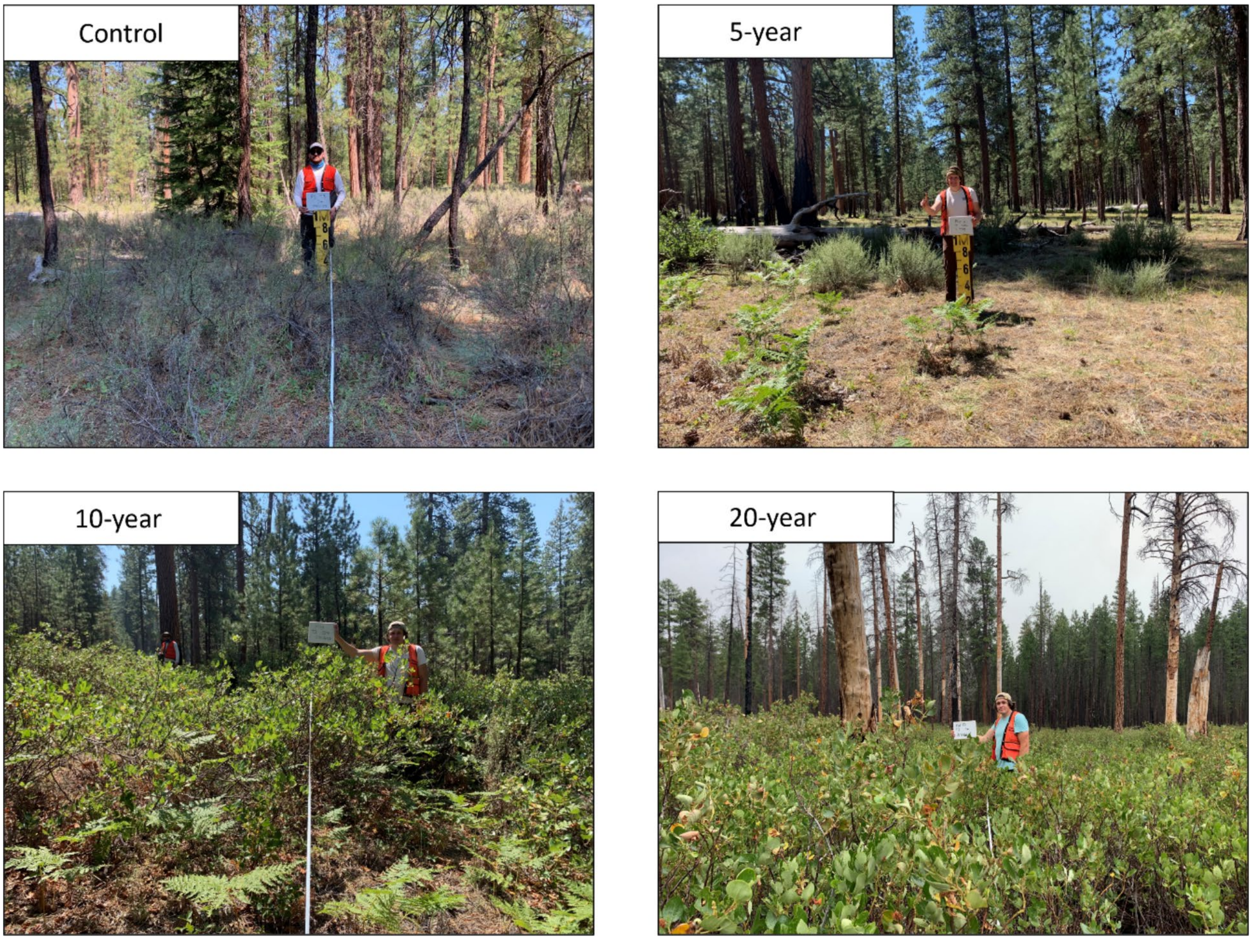

Fig. 3 Representative photos of each treatment in 2023 from one end of a transect. Control plots are characterized by bitterbrush and evidence of fire-sensitive tree species such as white fir. In the 5-year treatment photo patchy western brackenfern and smaller bitterbrush shrubs are evident, but shrub cover is relatively low. The 10- and 20-year treatment plots shown are dominated by snowbrush in 2023, and substantial overstory mortality is apparent in the 20-year treatment. Photo credits: control, Nathan Wade, others taken by Ursula Harwood

with the missed interval, cover did rise somewhat in the 5-year. Burning every 10 years initially suppressed cover until full recovery from the second burn in 2011/2013. At this time, cover in the 10-year was about 25 times higher compared to the 5-year. Cover also quickly rebounded after the third burn in 2015. By 2023, there was no evidence for treatment differences due to high variability. For 20-year burning, although cover increased through time, no differences were detected for this treatment. Cover did increase dramatically in some plots, leading to high variability in results later in the study. Patterns and high variability for the 10- and 20-year treatments were linked to two plots, one from the 10-year and another from the 20-year. Snowbrush cover in these plots exceeded 20% by 2011/2013 and 60% by 2023.

By 2001/2003, snowbrush density was about 33–100 times higher in the burn treatments in comparison to the control; all burn treatments were similar (Fig. 4). This pattern largely held throughout the experiment. Reflecting the patterns for snowbrush cover, density was highly variable and influenced by the same two plots, one in the 10- and one in the 20-year treatments. In 2015, one 20-year plot recorded over 100,000 shrubs/ha, although mean cover was still quite low in this plot immediately after the fires.

Herbaceous plant response

Total herbaceous cover was relatively low across the study area and there were few notable trends until the immediate post-fire response in 2015 (Fig. 5). At this time, the burn treatments had similar cover but the 10-year treatment had twice as much cover compared to the control. In 2023, cover was again about 2 times higher in both the 10- and 20-year treatments compared to the control. Patterns for biomass were similar, but differences among treatments were noted earlier in 2011/2013, and in 2015, biomass in all treatments was two to three times higher

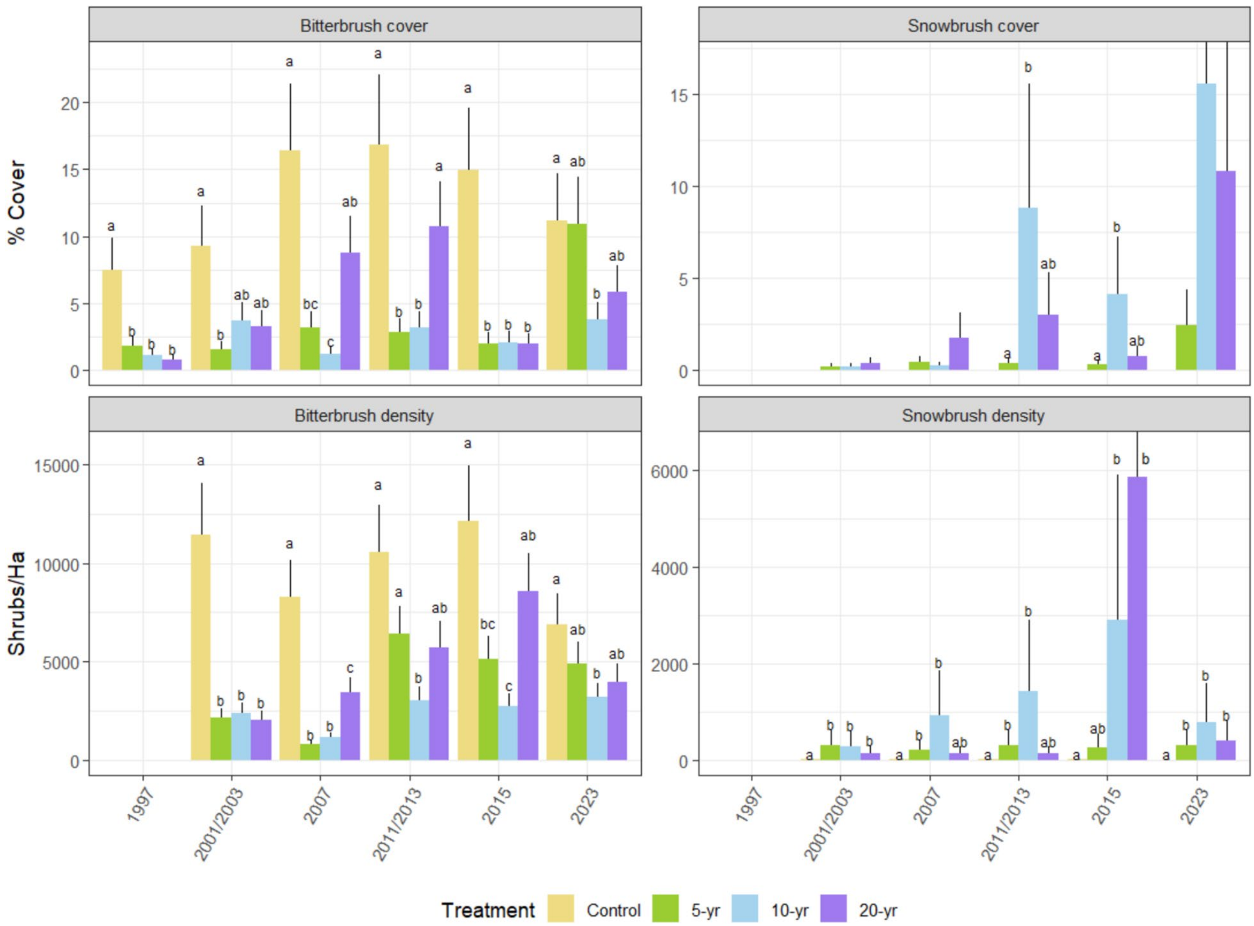

Fig. 4 Back-transformed estimated marginal means ± SE for bitterbrush and snowbrush cover and the expected number of shrubs per hectare across years and treatment. Lowercase letters denote treatment differences within year ($p \leq 0.10$). Note the control treatment for snowbrush cover and 1997 were not included. In 1997 all treatments were burned once 3–5 years prior. The second 10-year burn took place after the 2001/2003 sample. By 2015, all treatments were fully implemented: 20-year (two burns) 5-year (five burns), and 10-year (three burns). By 2023, each treatment had 9–10 years of recovery with no further burning (5-year interval skipped)

compared to the control, but the burn treatments were undifferentiated.

Rhizomatous forb/ferns were the dominant herbaceous plant group in the study area, owing largely to western brackenfern (Table 1). There was no evidence of an initial response to the burns in 1997 (Fig. 6). Burning every 5 years did not increase cover of rhizomatous forb/ferns, except for 2015 immediately after the last fires and in 2023 when one interval was missed. Ten and 20-year burning increased this plant group, especially later in the study. Non-rhizomatous forbs showed no evidence of differences between treatments throughout the course of the study (Fig. 6). Following the first burns in 1997, annual forb cover was higher for all the treatments compared to the control. However, this pattern did not endure and after 1997, cover was very low across all treatments, particularly the recovering 20-year (Fig. 6). Although treatment differences were noted, we caution interpreting such differences as meaningful. For perennial grasses, initially there was lower cover in the 20-year treatment compared to the 5-year in 1997 (5–20 $p = 0.07$), suggesting either an a priori difference or heterogeneous fire effects in response to the first burns. This trend weakened by 2007, indicating that 5-year burning eventually reduced perennial grass cover. Cover in the 20-year treatment remained low throughout the study.

Species richness and composition

Across all the years analyzed we recorded 87 understory species from herbaceous cover plots, shrub transects, and belt transects (Appendix 1 Table S1). We found no treatment effects on species richness. Results from NMDS ordinations demonstrate changes in plant community composition among treatments over the course of the study and limited within plot variability

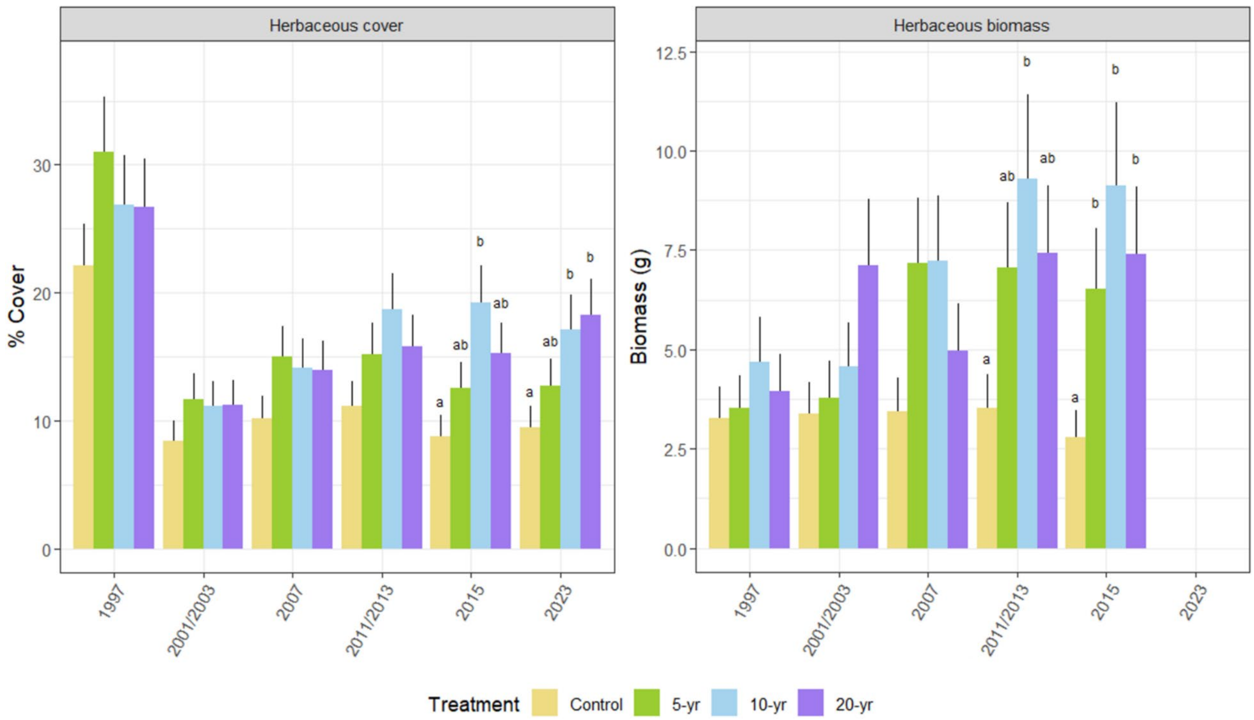

Fig. 5 Total herbaceous cover and biomass (grams/0.10 m^2) across years and treatment. Data are back-transformed estimated marginal means ± SE. Lowercase letters denote treatment differences within year ($p < 0.10$). In 1997, all treatments were burned once 3–5 years prior. The second 10-year burn took place after the 2001/2003 sample. By 2015, all treatments were fully implemented: 20-year (two burns) 5-year (five burns), and 10-year (three burns). In 2023, each treatment had 9–10 years of recovery with no further burning (5-year interval skipped; biomass not collected)

in species composition (Fig. 7). Stress was 0.18, indicating a decent representation of the data in ordination space, with some caution indicated in interpretation (McCune 1986). Initially, treatments overlapped in ordination space, but by 2007, the burn intervals were more distinct from the control, although still similar to each other, particularly for the 5- and 10-year treatments. In 2011/2013 and after four burns, the 5-year burn interval is distinct from the other two burn treatments. Treatments were less distinct in 2023 after the 5-year treatment missed one interval. Permutation tests revealed that higher litter cover was positively correlated with axis 1 and conversely, bare ground had a negative correlation to axis 1, and cover of coarse woody debris was positively correlated with axis 2.

Discussion

Many of our results were consistent with our hypotheses around burn frequency and plant responses based on plant traits. The two dominant shrub species responses differed based on burn frequency and plant traits; frequent burning favored some, but not all herbaceous plant groups, as well as resprouting or rhizomatous species in general. Frequent burning reduced both shrub species, but did not increase species richness. Our ordination results revealed that different burn frequencies created fairly distinct plant communities by the end of the study, although not maintaining the 5-year interval blurred these distinctions. However, these results were influenced by nuances around the fire frequency, recovery time and overstory conditions as detailed below.

Bitterbrush and snowbrush response differed

Bitterbrush is a key wildlife forage species of great management and restoration interest across the west (Guenther et al. 1993; Young et al. 1997; Hayden et al. 2008; Eckrich et al. 2019). Both cover and density responses to burning were often highly variable in our burn treatments, complicating broader implications around burn interval. However, some patterns were clear. Unsurprisingly, our more frequent (5- and 10-year) burn treatments suppressed bitterbrush cover but not density. Interestingly, release from 5-year burning produced a strong positive response for bitterbrush. Bitterbrush is generally considered to be highly sensitive to fire with high mortality rates; successful recovery following fire depends on its ability to resprout or to germinate from

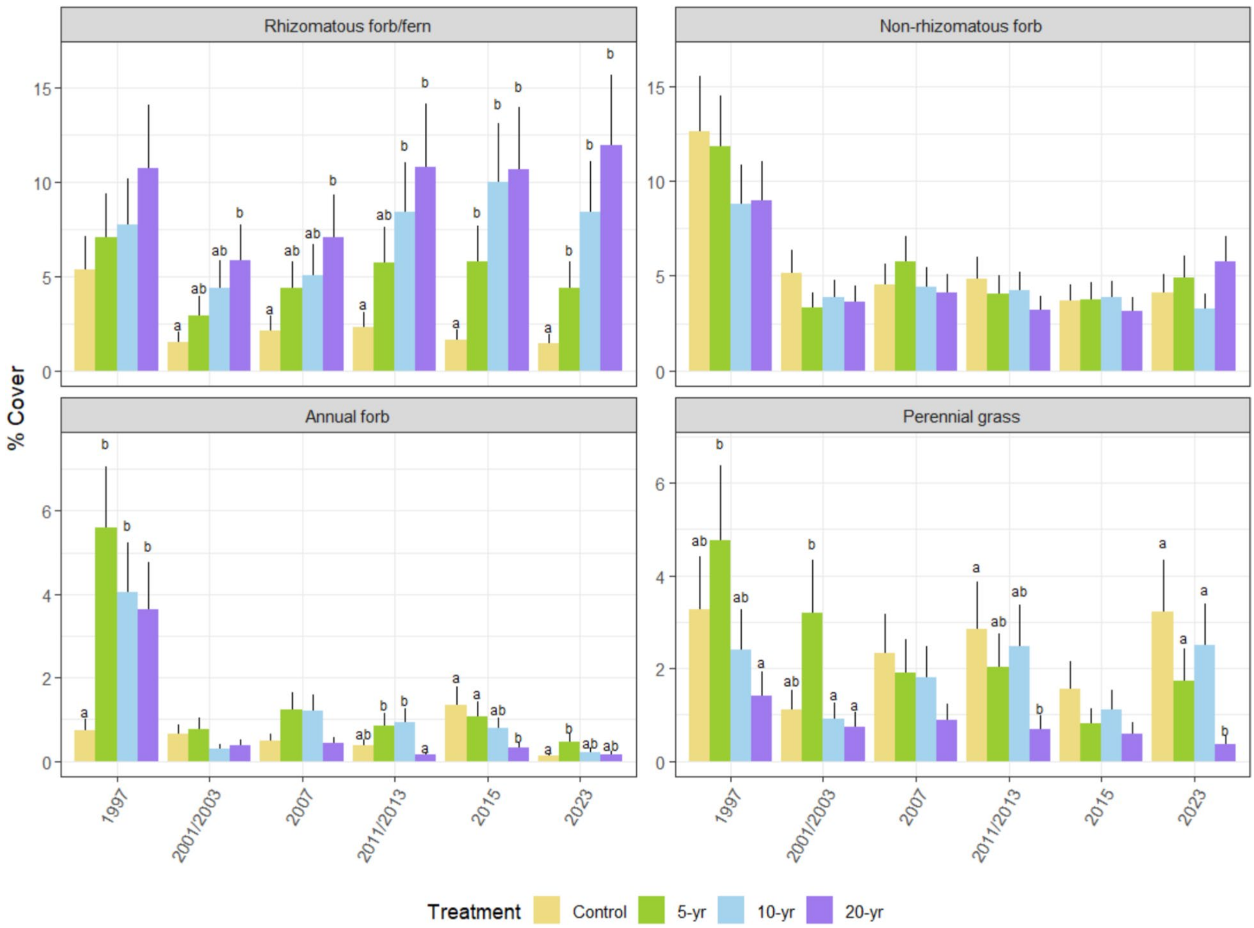

Fig. 6 Herbaceous plant group cover across years and treatment. Data are back-transformed estimated marginal means ± SE. Lowercase letters denote treatment differences within year ($p < 0.10$). In 1997, all treatments were burned once 3–5 years prior. The second 10-year burn took place after the 2001/2003 sample. By 2015, all treatments were fully implemented: 20-year (two burns) 5-year (five burns), and 10-year (three burns). In 2023, each treatment had 9–10 years of recovery with no further burning (5-year interval skipped)

rodent seed caches (Sherman and Chilcote 1972; Busse et al. 2000; Busse and Riegel 2009). Youngblood and Riegel (1999) observed that while nearly all bitterbrush was consumed in the initial spring fires in the study area, cover increased immediately as a result of rodent seed caches where litter was sparse, although seedling mortality was high after several years. Bitterbrush prefers seedbeds relatively free of surface organics for seedling establishment, and fire can stimulate copious seed germination, which likely influenced the increased density we observed post-fire (Sherman and Chilcote 1972; Edgerton 1983; Martin and Driver 1983). Resprout capability was not measured in our study but has been found to be tied to plant age and genetics and can vary substantially between populations (Sherman and Chilcote 1972; Busse and Riegel 2009).

Our data suggests that 10 years or more are needed for bitterbrush to recover after prescribed fire, consistent with other studies in the region, even if moderate post-fire resprouting is noted (Busse et al. 2000; Busse and Riegel 2009; Eckrich et al. 2019). We also found consistent patterns between higher bitterbrush cover in areas with less light; however, these are conditions more typical in unburned areas (Appendix 2 Fig. S2). The substantial increase in cover noted in 2023 in response to the release from 5-year burning (one skipped interval), more so than the patterns of a similar recovery period for 10-year, may be due to surface fuels in these areas and abundant local seed sources. Our density results demonstrated robust establishment of bitterbrush in the 5-year treatment, and less so in the 10-year until later in the study. This may also be related to the establishment of snowbrush in the 10-year treatment. Further examination of the impacts of variable prescribed fire regimes (several frequent burns followed by a longer interval) or tactics such as mosaic burn patches (Busse et al. 2000; Eckrich et al. 2019) is needed across a wider range of bitterbrush environments. Research on pyrodiversity, or the spatial

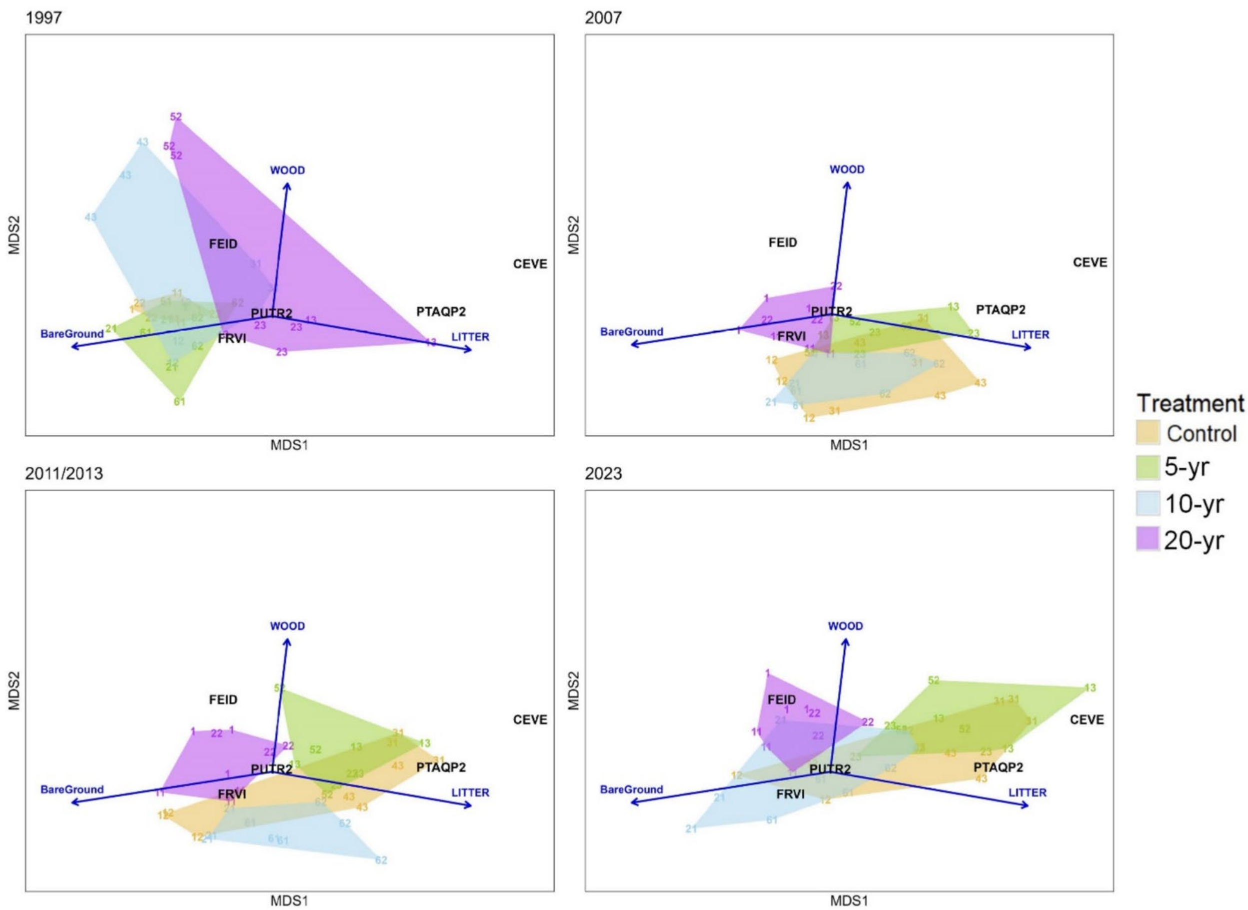

Fig. 7 Ordinations of understory cover species composition show differentiation through time owing to burn treatment (stress = 0.18). Numbers represent plots, with three transects per plot shown. Convex hulls are colored by treatment type, and the five dominant species in 2023 are shown (Table 1). In 1997, all treatments were burned once 3–5 years prior. By 2007, three 5-year and two 10-year burns were completed. In 2011/2013, four 5-year burns were complete, and 10-year reburns were continuing to recover. By 2023, burn treatments were fully implemented and treatments had 9–10 years of recovery with no further burning. Abiotic variables correlated with the ordination axes are displayed by vectors proportional to the direction and strength of the linear relationship

or temporal variability in fire effects across a landscape (Jones and Tingley 2022), is broad and/or sparse.

We found that all burn treatments increased snowbrush cover and density to some degree, although 5-year burning kept cover low. Unlike bitterbrush, snowbrush cover was absent or barely detected in the unburned control for the entire study period and density patterns confirm very few shrubs in these areas (17–39 shrubs/ha, based on raw data). Snowbrush cover and density increased slowly following the initial application of fire for the longer fire return intervals, but 10-year and 20-year reburning eventually increased snowbrush, dramatically so in some areas with substantial overstory loss. While the snowbrush response was theoretically expected based on the species resprouting traits, it was a somewhat surprising response, as the species was not recorded in any of the historical documents that exist describing the vegetation of the study area and does not typically increase in the ponderosa pine/bitterbrush plant associations that typified the area; however, a post-disturbance increase in snowbrush has been noted for the *Pinus ponderosa/Purshia tridentata-Arctostaphylos patula/Achnatherum occidentale* association (Volland 1985).

The increases we observed in snowbrush cover and density after 10- and 20-year reburning were likely due to feedbacks associated with more intense fires in areas with denser saplings and pole size trees and in areas with or near established snowbrush. While we do not have fire intensity information associated with burning in this study, more intense reburns and tree mortality were observed in plots later in the study where snowbrush had established (Fig. 3, and Gregg Riegel, personal observation). Snowbrush is considered a flammable species that can burn at high intensities when foliar moisture is low

(Cronquist and Weber 1988; Agee 1996). The species is strongly fire-adapted with long-lived soil seed banks in forests that are released through burning and vigorous basal sprouting of mature plants following fire (Bradley et al. 1992; Dietz 1980; Keeley et al. 2024). Snowbrush often dominates early recovery following fire, particularly in higher severity open areas (Conrad 1985; Geier-Hayes 1989; Jurgensen et al. 1991; Meigs et al. 2009).

Once established, snowbrush can persist on the landscape without repeated disturbance for decades or longer until overtopped by closed-canopied forests (Keeley 1991; Anderson 2004). Our data indicates that overstory canopy cover of about 25–35% may be adequate to reduce the dominance of snowbrush; however, our data are too limited to conclusively define this relationship (Appendix 2 Fig. S2). In addition, as with our bitterbrush results, we note that relative effects of fire and light are difficult to decouple in burned areas. Regardless, it is likely that further burning in snowbrush-dominated areas, additional canopy loss, and lack of forest recovery would likely maintain dominance of the species. In contrast, short fire return intervals may inhibit recovery through a combination of top killing existing plants and, in some cases, depleting seedbanks needed for reestablishment via germination by reducing the dominance of sexually mature plants (Noste 1982; Weatherspoon 1988). However, our density results did not suggest that germination in the 5-year treatment waned through time. This may be related to the longevity of snowbrush seeds in soil seed banks (Conrad 1985) or the proximity of local seed sources due to the small size of our burn units.

Herbaceous understory increased with longer fire return intervals

For the herbaceous understory, burning doubled to tripled total cover and biomass particularly for the longer fire return intervals (10- and 20-year) later in the study. Our expectation that 5-year burning would favor herbaceous species and suppress woody species was met; however, richness did not increase with 5-year burning. Herbaceous cover and biomass have been shown to respond positively to disturbances such as burning and thinning in ponderosa pine forests, although neutral or inconsistent responses are often noted and responses related to repeat burning are not common (Harris and Covington 1983; Andariese and Covington 1986; Moore et al. 2006; Abella and Springer 2015; Strahan et al. 2015; Kalies and Kent 2016; Willms et al. 2017; Kerns and Day 2018, 2024). Consistent with expectations, our results were driven by the rhizomatous forb/fern group dominated by the globally distributed species western brackenfern that responded positively to burning (particularly 10- and 20-year intervals) and likely the more open canopy conditions through time (Agee and Huff 1987; Stewart 1988; Carvalho et al. 2022). An increase in brackenfern was noted in prior work in response to the first burns (Youngblood and Riegel 1999). However, we did not find strong relationships between herbaceous cover or biomass and overstory canopy conditions. Rhizomatous species possess fire-adapted traits such as resprouting that allow rapid colonization following fire (Chapman and Crow 1981; Youngblood et al. 2006; Bowd et al. 2018; Kerns and Day 2018). Western brackenfern is a rapid resprouter following fire, and underground rhizomes can grow up to 2 m in a single season (Fletcher and Kirkwood 1979; Chapman and Crow 1981; Stickney 1986). The species can also promote fire by producing a highly flammable layer of dried fronds in the late summer and fall (Frye 1956; Agee and Huff 1987).

While there were similar results, there were deviations in patterns between total herbaceous cover and biomass. Overall, herbaceous cover was much higher in 1997 compared to the other years, which was a trend not reflected in biomass. The wet winter from 1996 to 1997 (Appendix 1 Fig. S1) may be responsible for this pattern. However, we would expect a climatically driven trend to be reflected in the biomass data, and it is not. It is most likely that the higher cover in 1997 compared to the other years is due to staff turnover, variation in species identification skills and implementation of protocols. Ocular cover estimates are particularly vulnerable to changes in personnel (Godínez-Alvarez et al. 2009). These challenges with long-term studies and data collection are mediated in part by our focus on treatment differences within years, allowing relative patterns among treatments to be more robustly compared.

We found little evidence that 5-year burn intervals increased other herbaceous plant groups, except for an initial but ephemeral flush of annual forbs. The waning effect for annual species has been observed in other repeat burn studies (Rossman et al. 2018; Kerns and Day 2018). However, annual plant species can be influenced by local weather and inter-annual differences in growing season conditions, which can overwhelm the effects of fire in some circumstances (Moore et al. 2006; Scudieri et al. 2010). It is important to note that the differences in annual forb cover between treatments after 1997 for this group were very small and may not be ecologically relevant. While we were unable to examine exotic species response to the burns due to low cover and occurrence, cheatgrass invasion has been noted in the northern portion of the study area, but has been periodically mitigated by hand pulling.

While perennial grass cover was low in the study area, we found an initial pattern of lower grass cover in 1997 for the 20-year compared to the 5-year treatment; a pattern that persisted later in the study. This may reflect a possible a priori difference for the grass understory prior to burning, potentially related to the higher tree cover found for the 20-yr treatment, or strong heterogenous fire effects from the first burns. However, we found no differences in 1997 for total herbaceous cover or biomass, and no relationship between sky visibility and herbaceous cover in 2001/2003 (Appendix 2 Fig. S2). It is unclear if this initial small difference in grass cover is meaningful. Interestingly, earlier reports suggested that the initial burns increased the perennial grass bottlebrush squirreltail, a species known to increase following fire (Youngblood and Riegel 1999; Kerns and Day 2018); we did not find evidence of this pattern, although this species was not common enough to analyze individually.

Burn frequency drove species composition divergence

Ordination results revealed differing plant communities in response to treatments with time, although we did not find any differences for species richness, suggesting differences were driven by changes in plant abundance. These results counter some prescribed fire studies that document increases in species richness after a single prescribed fire (Rossman et al. 2018; Springer et al. 2024; Webster & Halpern 2010a, b), although other studies suggest variable results and note that increases in richness are generally driven by annual forbs and invasive species (Nelson et al. 2008; Abella and Springer 2015; Strahan et al. 2015; Willms et al. 2017). However, repeat burn studies are uncommon. We did find an overall divergence in community composition between control plots and treated units in the later years of the study, largely driven by differences in snowbrush and brackenfern as noted in our univariate model results. These results are consistent with our expectation that burning would favor resprouting and rhizomatous species in general. While brackenfern is a native, early seral, shade-intolerant species common in the region, it is also known as one of the most successful global invasive species that can alter floristic composition due to aggressive colonization (Schneider 2006; Baptiste et al. 2019; Carvalho et al. 2022). As noted earlier, species in the genus *Ceanothus* can also homogenize post-disturbance environments, especially in areas with tree canopy removal (Goodwin et al. 2018; Odland et al. 2021).

Study inference and future research

While we were able to document several important patterns related to prescribed fire frequency, variability in our data was often high for the burned treatments, limiting inference from our findings. Variability is likely owing to a variety of factors, including heterogeneous fire effects, low sample size, differing post-fire recovery times from the staggered burn schedule, annual climate variability, and implementation challenges. Conducting long-term prescribed burn studies is challenging in the western US, as burning is subject to available prescription windows, adequate staffing and multiple approval processes (Quinn-Davidson and Varner 2011). While our sample size was fairly low, our study is unusual in the burn schedule only deviated slightly for one block (resulting in a 6-, 11-, and 21-year interval for the last burn period).

Like many prescribed fire and wildfire studies (Donato et al. 2009; Stevens et al. 2016; Kerns and Day 2018), we were also unable to examine the effect of pretreatment conditions, which can have a strong influence on outcomes from burning in the understory (Dodson et al. 2008). As noted above, we acknowledge some evidence for pre-treatment differences and we note that the study area had a mix of three plant associations at the study outset, reflecting localized patterns in topography and soils (Volland 1985) that we cannot account for at the plot scale. However, this variability is accounted for to some degree in our random effects model statement. Researchers looking to build upon these results or conduct similar studies could improve interpretability and statistical inference by increasing the number of replicates for each treatment, using spatial rather than temporal blocking, sampling all study plots in the same year, and collecting pre-treatment data. We acknowledge these goals can be difficult to achieve.

Management implications and conclusions

Prescribed burns are essential management tools for the restoration of many ecosystems and reduction of wildfire severity in the western US (Hessburg et al. 2015; Stephens et al. 2020; Merschel et al. 2021). As extreme weather and drought exacerbate wildfire issues in western forests, land managers are tasked with increasing the pace and scale of prescribed fire implementation (Ryan et al. 2013; Prichard et al. 2021). Ponderosa pine forests are one of the ecosystems most at risk of severe fire in the interior west due to the strong impact fire suppression has had on these historically frequent fire ecosystems, and thus these forests, along with WUI areas, are often highlighted for more proactive treatments. Examples of old-growth ponderosa pine are also vanishingly rare in many areas of the region, making them a high priority for conservation and restoration, including with controlled burning (Johnston et al. 2021). This study provides valuable information about how understory vegetation responds to reintroduction of fire and to burn frequency or maintenance burning. We caution that the smaller size of our burn treatments and close proximity of bitterbrush and snowbrush seed sources were likely important factors for our study outcomes; these results may not be representative of outcomes from larger, landscape-scale burns that are increasingly being called for and implemented (Urza et al. 2023). In addition, managers often use plant associations to generalize potential responses of vegetation to actions such as prescribed fire. Because the study area has a mix of different plant associations and localized topo-edaphic variability, we suggest that this heterogeneity be considered and our results may be less relevant for each individual plant association.

While the reintroduction of fire is critical to the restoration of dry forests, guidance for restoration of prescribed fire frequency is often lacking and is generally dependent upon site conditions and species composition. In this study, we only considered frequency which is inherently tied to fuel loads—yet, even within a fire regime, fuel loads and moisture levels can differ, leading to heterogeneous fire effects. However, we did not assess pre-fire fuel loads or connectivity. Some studies document that fire must be repeated at regular intervals for its effects on the understory to be sustained. Burning at 5-year intervals was the most effective for maintaining low levels of shrub fuels, reflecting recent findings from dry forests that experienced repeat short-interval wildfires as well as other studies that show frequent fire suppresses woody species (Grupenhoff and Safford 2024; Tortorelli et al. 2024). Such frequent burning is resource-intensive and can be difficult to implement given the resulting lack of surface fuels to carry fire. Frequent burning may also have negative impacts to winter deer habitat if bitterbrush cover is reduced. Prescribed burns following low- to moderate-severity wildfires could help achieve desired fuel reduction outcomes with less resource investment by reducing resources required for the initial entry burn (Greenler et al. 2023; Tortorelli et al. 2024). However, burning before substantial amounts of shrub fuels re-establish is a key consideration.

Wildland fire and fuel managers often face substantial tradeoffs as they plan to use prescribed fire to restore dry forests. In our study area, where wildlife habitat such as winter deer forage is prioritized, restoration projects may need to be carefully designed to maintain adequate cover of bitterbrush, which is both sensitive to fire in its mature form, yet requires bare soil for germination of seedlings (Pflug 1999; Busse and Riegel 2009). We found that burning at 5-year intervals was the most successful at reducing surface litter and flammable shrub species but came with tradeoffs for important wildlife habitat. Some patterns related to 5-year burning were still detectable even roughly a decade after the cessation of treatments, while other patterns (bitterbrush) strongly responded to the cessation of treatments. Burning at greater than 10-year intervals can sustain bitterbrush habitat for ungulates but also can constitute a ladder fuel that would be of concern in WUI settings.

To maintain bitterbrush habitat and decrease ladder fuels, landscape-scale designs that maximize variation in post-fire characteristics, a central tenant of pyrodiversity, may be more likely to succeed in a balance, as areas with mature browse plants and seed sources will be available while burned areas recover from recent treatments. For example, burn plans could include a matrix of unburned refugia and burn units with a range of fire return intervals. The benefits of this type of landscape-scale pyrodiversity for wildlife habitat are increasingly supported by the scientific literature (Roerick et al. 2019; Lewis et al. 2022). Managers engaged in this difficult balancing act may also consider multiple strategies to achieve restoration goals, such as direct seeding of native understory species following prescribed burns if soil seedbanks or propagule sources are depleted (Carr and Krueger 2012), and varying both the season and frequency of burning so that benefits are seen for a variety of species (Wayman and North 2007).

Supplementary Information

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Supplementary Material 1.

Supplementary Material 2.

Supplementary Material 3.

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Authors' contributions

BKK garnered funding for these analyses as well as data collection in 2023, guided the analytical approach, and led the writing of the manuscript. GMR co-developed the initial study design (see Acknowledgments), oversaw burning and data collection throughout the life of the study, and contributed to the analyses and writing of the manuscript. NMW and DGN assembled data and conducted QA/QC, conducted most analyses, created the figures, and contributed to the writing of the manuscript. NMW also collected data in the field. CMT and MCK contributed to the analytical approach, conducted analyses, and contributed to the writing of the manuscript. GLW and DHB collected field data, assisted with figure creation, and provided editorial comments. SP contributed to the analytical approach and the writing of the manuscript. All authors approved the final manuscript.

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Data availability
All data are archived at Open Science Framework and are available at the following URL: Frequency of prescribed fire, Metolius Research Natural Area: Understory vegetation attributes

Declarations

Ethics approval and consent to participate
Not applicable

Consent for publication
Not applicable

Competing interests
The authors declare no competing interests.

Author details
[1]USDA Forest Service, Pacific Northwest Research Station, Corvallis, OR, USA. [2]USDA Forest Service, Pacific Northwest Region, Bend, OR, USA. [3]USDA Forest Service, Pacific Northwest Research Station, and Oak Ridge Institute for Science and Education, Oak Ridge, TN, USA. [4]University of Washington, School of Environmental and Forest Sciences, Seattle, WA, USA. [5]Present Address: Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA. [6]Present Address: University of Minnesota, St. Paul, MN, USA. [7]University of Washington Tacoma, Department of Sciences and Mathematics, Tacoma, WA, USA.

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