Considering regeneration failure in the context of changing climate and disturbance regimes in western North America

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Abstract

Wildfire-mediated changes to forests have prompted numerous studies on post-fire forest recovery of coniferous forests. Given climate change, a growing body of work demonstrates that conifer regeneration in temperate and boreal forests is declining, a phenomenon often termed "regeneration failure." However, the definition and parameters are numerous and variable. Characterization of drought also varies greatly, thus hindering the ability to compare results among areas. This review discusses new perspectives on conifer regeneration failure and places these studies into the context of drought and fire activity. We focus this review on three forest types where conifer regeneration failure is well documented: western boreal forests, cold mixed-conifer forests, and dry pine forests. To place the challenges to conifer tree regeneration in the context of regional climate trends, we present a novel regional analysis that summarizes drought conditions prior, during, and following the year of a large wildfire. We demonstrate the need to assess failure in the context of specific forest dynamics and well-defined metrics. For example, tree establishment may historically occur over longer periods, and current and future climate may exacerbate this and not promote pre-fire forest structure and composition. Many forests are undergoing rapid change and the type, magnitude, and causes of changes need to be compared among areas. As such, we should be cautious of quantifying "regeneration failure" and drought without providing spatial and temporal context.

Key words: tree regeneration, drought, climate change, forest conversion, regeneration failure, wildfires

Résumé

Les modifications des forêts provoquées par les incendies de forêt ont suscité de nombreuses études sur la régénération des forêts de conifères après un incendie. Compte tenu des changements climatiques, un nombre croissant de travaux démontre que la régénération des conifères dans les forêts tempérées et boréales est en déclin, un phénomène souvent appelé « accident de régénération ». Cependant, la définition et les paramètres sont nombreux et variables. La caractérisation du phénomène de sécheresse varie également beaucoup, ce qui entrave la capacité de comparer les résultats entre les régions. Cet article présente de nouvelles perspectives sur les accidents de régénération des conifères et place ces études dans le contexte des sécheresses et des incendies. Nous nous concentrons sur trois types de forêts où les accidents de régénération des conifères sont bien documenté : les forêts boréales de l'Ouest, les forêts mixtes froides de conifères et les forêts sèches de pins. Pour placer les défis de la régénération des conifères dans le contexte des tendances climatiques régionales, nous présentons une nouvelle analyse régionale qui résume les conditions de sécheresse avant, pendant et après l'année d'un grand incendie de forêt. Nous démontrons la nécessité d'évaluer l'accident de régénération dans le contexte de dynamiques forestières spécifiques et de mesures bien définies. Par exemple, l'établissement des arbres peut historiquement se produire sur des périodes plus longues, et le climat actuel et futur peut exacerber ce phénomène et ne pas favoriser la structure et la composition de la forêt avant l'incendie. De nombreuses forêts subissent des changements rapides et le type, l'ampleur et les causes de ces changements doivent être comparés entre les différentes régions. En tant que tel, nous devrions être prudents dans la quantification des « accidents de régénération » et des sécheresses sans fournir un contexte spatial et temporel. [Traduit par la Rédaction]

Mots-clés : régénération des arbres, sécheresse, changement climatique, conversion des forêts, échec de la régénération, incendies de forêt

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Introduction

The composition, structure, and ecological function of forests, which occupy around 30% of the global landmass, are strongly patterned by landform and climate (Bond et al. 2005). Worldwide, forest cover has fluctuated substantially over time through climatic variability and resulting dynamics between vegetation, fire, and other disturbances (Calder et al. 2015). Although many forests are highly adapted to wildfire, fire may also limit the extent of tree cover. From a climatic perspective, many parts of the world that have the capacity to support closed-canopy forests are maintained as savannas, shrublands, or grasslands due to frequent fires (Bond and Keeley 2005; Krawchuk et al. 2009). For example, the role of climatic variability and fire frequency in the dynamic interface between forests and savanna ecosystems is well documented in parts of Australia, the Amazon Basin, and sub-Saharan Africa (Bradstock 2010; Pausas and Paula 2012). Expansion and retraction of tree cover have also been influenced by human-caused fires for millennia through Indigenous cultural burning practices and, more recently, through fire-management policies and land-use change (Trauernicht et al. 2015; Taylor et al. 2016).

Changes to many forest-dominated systems are mediated through large disturbances, including wildfire, and these dynamics are accelerating in many areas due to climatic changes (Krawchuk et al. 2009; Stralberg et al. 2018). In western North America, climate change has led to an increased incidence and extent of wildfires in recent decades (Jolly et al. 2015; Abatzoglou and Williams 2016; Hanes et al. 2019). Fire–vegetation dynamics are expected to markedly shift under warmer and often drier conditions (i.e., drought), with arid ecosystems becoming more fuel limited while more productive ecosystems are projected to support increased incidence of wildfires and longer fire seasons (Flannigan et al. 2009; Allen et al. 2010). The catalyzing effect of disturbances on compositional change is also evident in the paleoecology record, providing historical support for current observations and future likelihood of projected shifts in vegetation type (Higuera et al. 2009; Crausbay et al. 2017). Along with shifting fire–vegetation dynamics, droughts are expected to increase in frequency, severity, and duration throughout much of North America as the climate continues to warm (Naumann et al. 2018).

Warming and drying trends may not only alter fire regimes but also influence forest dynamics, including the mechanisms of post-fire vegetation recovery (Johnstone et al. 2010; Falk et al. 2022). Drought-induced tree mortality and post-fire regeneration failure are growing areas of study and a primary concern to many land managers tasked with implementing adaptation strategies in response to climate change (Allen et al. 2010; Falk et al. 2019; Coop et al. 2020). Wildfires, including high-severity wildfires or high-severity patches within wildfires, may create opportunities for tree establishment through reduction of competition, changes to nutrient cycling, and exposure of bare mineral soil, assuming adequate soil moisture (Kemball et al. 2006). However, increases in fire frequency and the extent of high severity burned patches

observed in recent years (Shenoy et al. 2011; Parks and Abazoglou 2020) can also trigger shifts in plant physiognomic type, including conversion of forests to grasslands or shrublands if trees are not able to regenerate following the disturbance event (Coop et al. 2016; Kolden et al. 2017; Whitman et al. 2019).

Drought and extreme events as bottlenecks to tree establishment

As the climate warms, becomes more moisture limited, and wildfire seasons grow longer and more extreme, altered frequency and severity of wildfires can set the stage for rapid changes in forest composition and successional trajectories. Dry years often drive larger areas burned (Box 1), and drought can have wide ranging ecological implications to a recovering landscape (Coop et al. 2020; Crausbay et al. 2020). Germination and juvenile survival and growth are typically the most vulnerable stages in a tree's life (Harper 1977). While mature trees may persist on a site for centuries, changing climatic conditions may reduce a species' ability to regenerate, given smaller ranges of suitable conditions at juvenile stages (Dobrowski et al. 2015). Seeds require sufficient moisture and specific temperature ranges to support germination, and favorable conditions for continued survival are critical in the first growing seasons following germination (Barton 1993; Germino et al. 2002). The seeds of many coniferous trees in temperate and boreal zones are sensitive to desiccation (Tweddle et al. 2003) and are generally viable for only a brief time (i.e., days to months) once they reach the ground (Charron and Greene 2002). Tree seedlings can quickly desiccate in dry soils due to their shallow root systems and low carbohydrate reserves (Landhausser et al. 2012). Even when establishment is successful, extreme weather events, such as pronounced drought, cold winters, or fluvial events, can kill regenerating seedlings (Petrie et al. 2016).

Given rapid global warming, arid and semiarid ecosystems will be particularly vulnerable to both regeneration failure and mature tree mortality (Kemp et al. 2019; Stevens-Rumann and Morgan 2019). Over the past several decades in North America, sparse to absent conifer tree regeneration following large wildfires has been documented across diverse biophysical settings (Brown and Johnstone 2012; Boucher et al. 2019; Davis et al. 2019), but this trend appears to be more pronounced in the moisture-limited regions of western North America. From a biogeographical standpoint, many western conifer-dominated forests occupy areas where moisture limitations can inhibit tree growth, and the climate may be more suitable to broadleaf trees or shrub dominance (Waring and Franklin 1979; Hogg 1994; Parks et al. 2018; Kemp et al. 2019). Adding to challenges of conifer regeneration, mortality of mature and old forests has been documented in many western forests and associated with prolonged drought and associated soil water deficits (Allen et al. 2010; Michaelian et al. 2011). In the state of California alone, it is estimated that more than 100 million trees died from moisture stress from a series of droughts in the 21st cen-

tury, a proportion that far exceeds the estimated mortality rates of the last two centuries (Stephens et al. 2018; Fettig et al. 2019). As such, where post-fire environments coincide with chronic water deficit, high-severity fire events may facilitate changes to non-forest more rapidly (Parks et al. 2019, Box 1).

Short fire return intervals (e.g., <20 years) are also becoming increasingly common in western landscapes under climate change. In western boreal forests, fires in rapid succession can diminish the water-retention capacity of soils by removing the soil organic matter layer and can contribute to forest type changes from conifer-dominated forests to broadleaf deciduous species (Brown and Johnstone 2012; Hansen and Turner 2019). Multiple studies in the western US have found repeated wildfires in short succession may further contribute to regeneration delays or vegetation type conversions (Harvey et al. 2016; Stevens-Rumann and Morgan 2016; Turner et al. 2019; Busby et al. 2020). More intense dry spells associated with changing climates may compound and exacerbate the effect of short-interval reburns prior to the fire by increasing tree mortality and propagule production (Mueller et al. 2005) and following the fire through increased drought conditions (Whitman et al. 2019; Hoecker and Turner 2022).

Defining regeneration failure

Because the fate of seedling survival is dependent on multiple environmental variables, seedling recruitment is often episodic and unpredictable at any given location. Thus, trajectories of tree regeneration are best assessed through regional analyses (e.g., Stevens-Rumann et al. 2018; Davis et al. 2019) or across long time periods (e.g., Johnstone et al. 2004; Moore et al. 2004). Even with the many documented field studies on post-fire tree regeneration, there is a lack of consensus on how to define regeneration "failure" (Boucher et al. 2019; Splawinski et al. 2019; Coop et al. 2020). To date, the term "regeneration failure" is often used to describe a range of post-fire tree regeneration scenarios, especially prevalent in early post-fire regeneration windows (i.e., <10–20 years) that do not meet expectations of rapid reestablishment, including a complete absence of tree seedlings or the inability to meet minimum stocking standards.

Understanding regeneration failure is dependent on the geographical context and temporal window of observation, leading to vastly different management implications. The temporal scale for regeneration failure will almost certainly vary among systems. For instance, in boreal forests where deep soil organic layers often develop, initial post-fire years are critical for tree regeneration (Johnstone et al. 2004; Dawe et al. 2022). If no regeneration occurs in that short window of time (e.g., <5 years), it is unlikely that regeneration will occur without a future disturbance to reduce the depth of the soil organic layer (Johnstone and Chapin 2006; Wirth et al. 2008). Thus, in wetter ecosystems, where surface substrates limit seedling establishment, a short time scale of observation may be valid, whereas regeneration might not be as temporally constrained in drier forests with less organic matter develop-

ment. Here, we explore various definitions of regeneration failure, which we describe as a long-term absence of tree regeneration and its variability across western North American forests.

Multiple scenarios of regeneration trajectories in North America's conifer-dominated forests have been observed and are often termed regeneration failures. In the classic model of post-fire vegetation recovery of many conifer-dominated systems, vigorous same-species recruitment occurs rapidly following the fire (Fig. 1A; Mutch 1970; Rowe and Scotter 1973). If the post-fire observation period is too short to observe regeneration establishment, *delayed and* (*or*) *prolonged regeneration* may be characterized as a failure (Fig. 1B). However, it is plausible that a vegetation shift observed in short-term (<30 years) post-fire period may eventually develop into a conifer forest (Brown and Wu 2005), although this process may be slow with gradual in-filling before becoming fully stocked. In other cases, post-fire landscapes may shift from a conifer to a broadleaf forest, indicating a *change in dominance* (Fig. 1C; Whitman et al. 2019; Baltzer et al. 2021). In this scenario, even though forest cover is maintained, major ecological and biogeochemical changes occur (Mack et al. 2021). The final case, *regeneration failure* is either categorized as a complete and enduring lack of tree regeneration (Coop et al. 2016) or enduring regeneration is occurring at a lower density than desired (e.g., below a critical stocking density threshold; Outzs et al. 2015; Chambers et al. 2016; Fig. 1D). In the three "non-classic" pathways, the resulting vegetation assemblages may provide markedly different ecosystem services than those of the pre-fire conifer-dominated forest, including fiber production, carbon stores, forest cover, and wildlife habitat (Tepley et al. 2018). Temperature and precipitation are driving factors in determining these ecosystem responses post-fire, and the climate a system experiences post-fire may not be indicative of the longer climatic trend that established the pre-fire forest structure (Figs. 1E and 1F).

Objectives

Our central goal is to review definitions of conifer regeneration failure in western North America and place this phenomenon in the context of recent patterns of drought and fire activity. Coniferous forests of western North America span a wide range of biogeoclimatic zones and support diverse species assemblages. As a basis for comparison, we consider three forest types where conifer regeneration failure is well documented: western boreal forests, cold mixed-conifer forests, and dry ponderosa pine-dominated forests. We selected three analysis areas that represent these forest types and their associated ecosystem dynamics (Fig. 2). Our specific objectives were to: (*i*) use a novel regional analysis of pre- and post-fire dry years to provide context for recent trends in post-fire forest regeneration within these forest types and conclude with proposed research topics, (*ii*) review and compare the ways in which drought may impede tree recruitment, (*iii*) compile and explain the metrics that have been used to measure regeneration failure, and (*iv*) describe patterns of regeneration failure within these three forest from a mod-

Fig. 1. Examples of post-fire conifer-dominated forest trajectories, demonstrating the importance of the post-fire observation period that may lead to an expectation of tree regeneration failure (top panel). (A) The top visual shows immediate regeneration of a forest that relatively quickly returns to a closed-canopy forest. (B) In the delayed regeneration scenario, tree establishment may be delayed long enough for short-term post-fire studies to only observe a lack of regeneration, though the long-term trajectory may ultimately result in a conifer forest. (C) In the change of dominance scenario, a shift from conifer to broadleaf forests (light green trees) may be described as a regeneration failure of conifer species. (D) Finally, the regeneration failure scenario demonstrates a long-term absence of tree establishment that regardless of the post-fire window of observation, little to no conifer trees are present and the few that do grow die indicated by the red trees. The second panel (F) shows a representation of climate for the last 2000 years, and how the climate variability in a short-term study (E) may capture conditions well outside the long-term mean conditions and may not be indicative of the long-term, 2000-year patterns observed in dendrochronology or paleo studies. Panel (G) illustrates the scientific tools used to study regional forest dynamics. Neo-ecology refers to relatively recent studies with direct observation of fire effects (including studies employing post-fire field observations and remote sensing) and offer different temporal window of observation than dendrochronology and paleoecological studies (e.g., Buma et al. 2019).
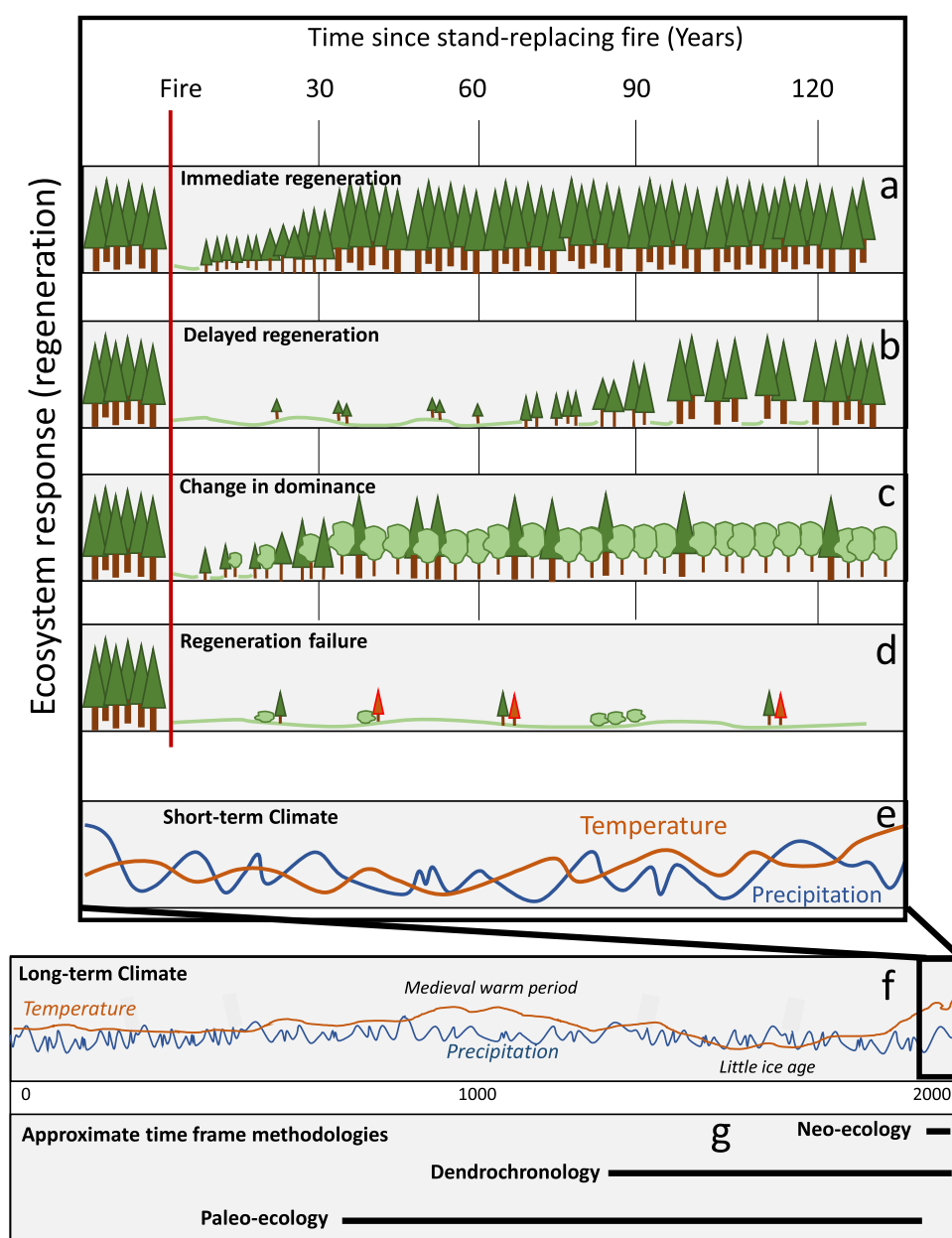
ern/contemporary and paleoecological perspective (Fig. 1G). The following sections highlight studies documenting patterns of recent post-fire tree regeneration, dendroecological reconstructions, and paleoecological research to evaluate metrics of coniferous tree regeneration. We recommend analyzing cross-regional drought and tree regeneration patterns

Fig. 2. Fire history, land cover, and climatology of forests in three analysis areas: western boreal (boreal forests comprise 100% of the forest cover), northern Rockies (cold mixed conifer comprises 28% of land cover and 77% of forest cover), and US Southwest (ponderosa pine comprises 21% of land cover, 30% of forest cover; LANDFIRE, 2016). (A) Needleleaf tree cover (CEC 2015), fire perimeters (1970–2017), and large waterbodies (CEC 2015, (B) Mean annual Climatic Moisture Index (CMI; 1981–2010; McKenney et al., 2011), and (C) Time series of annual mean CMI anomaly (blue bars = cooler and wetter than average and red = hotter and drier than average), and annual percentage area burned (black line). We report nonparametric Sen's slopes, and *P*-values from one-sided Mann-Kendall trend tests for trends in mean annual CMI anomalies (1961–1990 reference period) and annual % area burned time series (1970–2017) for each study region. Serial autocorrelation within the time series was accounted for using a variance correction to the Mann–Kendall test statistic distribution (Hamed and Rao 1998).
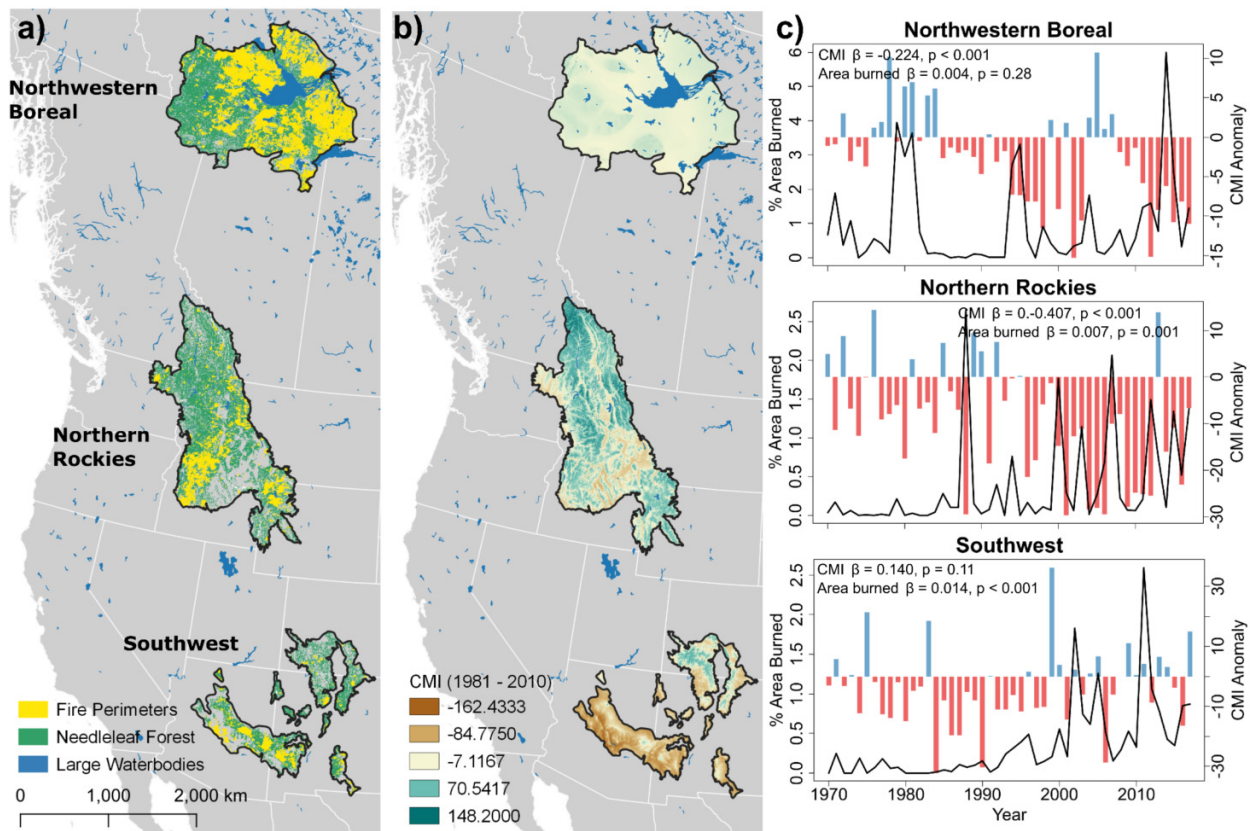
using a consistent drought metric (e.g., climatic moisture index (CMI)). Thus, we analyzed fire occurrence and drought across three regional study areas to show that dry years influence the occurrence of fire and post-fire landscapes are increasingly faced with dry years that can play an important role in the post-fire successional pathway of these forests. We illustrate a way in which drought can be incorporated in a standardized manner into post-fire regeneration studies (Box 1).

Synthesis by forest type

Western boreal forests

Large, stand-replacing wildfires are characteristic of western North American boreal forests (Burton et al. 2009; Kelly et al. 2013). This forest type and analysis area (Fig. 2) spans a broad terrain interspersed with some rolling hills and high plateaus. As in most parts of the boreal biome, the region is predominantly forested but is also composed of abundant wetland complexes and large waterbodies. Climate is

cold and continental with short growing seasons and precipitation mostly falling during the summer months. Upland forests of this region consist of a mix of northern conifers (black spruce (*Picea mariana*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*)), and broadleaf trees including quaking aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Dominant boreal tree species are adapted to high-severity fires; some species such as quaking aspen vegetatively regenerate while other species, such as jack pine and black spruce, maintain aerial seed banks that can produce a vigorous seed rain, even after an intense crown fire (Rowe and Scotter 1973). There have been reports, however, where particularly intense wildfires have depleted the aerial seedbank, thereby limiting post-fire regeneration potential (Arseneault 2001).

Provided there are sufficient propagules, post-fire forest recruitment in the western boreal typically occurs shortly after fire (<5 years), with forest patterns and composition established in these early years tending to persist until a subsequent fire (Johnstone et al. 2004; Lavoie and Sirois 1998). In these forests, the presence of a thick soil organic layer of-

Box 1. A probabilistic look at drought, wildfires, and post-fire recovery

While drought is often considered a major constraint to post-fire recruitment of conifers, how this phenomenon is characterized varies tremendously in the literature. Using a well-known drought metric, the climate moisture index (CMI; Hogg 1994), we evaluated an approach in which we compute dry year for different observation windows that are relevant to post-fire regeneration failures and delays. Specifically, we analyzed the likelihood of a dry year in three areas of analysis (Figs. 2B and 2C) the year of, prior to, and following (up to 3 years) years that have experienced many large wildfires (hereafter "large fire years") from 1970 to 2017. See Appendix A for detailed methods.

The effect of dry years after fire is increasingly well documented: associated water deficits can prevent germination or kill seedlings (Davis et al. 2019; Stevens-Rumann and Morgan 2019; Hansen et al. 2021). However, dry years can also indirectly affect tree recruitment through their effect on wildfire recurrence and behavior, which is mainly a function of climate during the year of the wildfire (i.e., insofar as it is representative of weather at the time of burning) (Littell et al. 2016). Least well documented — yet undoubtedly important in many situations — is how effects of dry years and longer-term drought and site water deficits trends on forest health prior to a fire could affect post-fire regeneration by causing parent-tree mortality, loss of vigour, and reduced (or increased, i.e., masting) fecundity.

Unsurprisingly, dry years are highly correlated with years of widespread fire in the three areas of analysis (Box Fig. 1, lag 0). There is also a significant priming effect of drier-than-average conditions in the year before a large fire year in the NW Boreal and the Southwest, but not in the N Rockies. Pronounced dry years in the years following regional fire years are common; in the N Rockies and the NW Boreal at least one dry year was observed in the first 0–3 years after fire ($P = 1$, where P is the probability). Multiple dry years are also frequent in that period, having occurred after more than half of large fire years in both the NW Boreal and the Southwest (Box Fig. 1, lag 0–3). The probability of wet years following large fire years (1–3 years) varied among areas. A wet year following a large fire year was consistently likely in the NW Boreal ($P = 0.64$), occurred at least once in 3 years ($P = 0.33$) in the N Rockies, and was never observed in the Southwest ($P = 0$).

Box Fig. 1 Superposed epoch analysis (SEA) of the relationship between departures in the median annual CMI and large fire years (LFY; 75th percentile area burned) for three analysis areas. Bars that reach the dashed and solid line are significant at $\alpha = 0.05$ and $\alpha = 0.01$, respectively. Colored bars under the plot represent the bootstrapped probability of dry years (25th percentile annual climatic moisture index (CMI)) and wet years (75th percentile annual CMI) in the years prior to and after a large fire year (75th percentile annual area burned) in the western boreal, the northern Rockies, and the Southwest US.
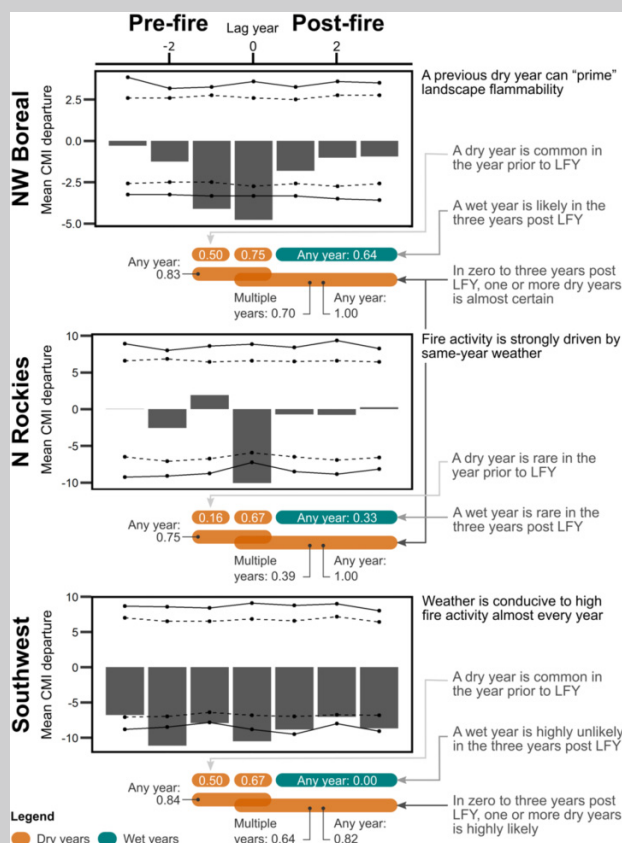
ten inhibits continued establishment (Johnstone and Chapin 2006), thus those first few post-fire years are particularly critical for conifer establishment. This contrasts with the other two forest types considered here, where episodic and long-duration establishment events may be expected. Post-fire drought in boreal forests can delay or reduce seedling establishment, with recruitment limited by the availability of seedbeds that retain soil moisture, leading to lasting effects on stand structure (Kemball and Wang 2005; Whitman et al. 2019). Delayed regeneration is possible for trees that require live seed sources, such as white spruce. In some northern forests, white spruce has regenerated slowly in uneven-aged cohorts over many years; for example, Hogg and Wein (2005) reported conifer recruitment continuing up to 24 years post-fire. Despite these observations of slow spruce establishment, initial patterns of regeneration have proven to be important to post-fire vegetation succession trajectories, as the slow-growing spruce persists in the understory for decades before occupying much of the forest canopy (Peters et al. 2005, 2006).

Although boreal tree species display extensive and diverse adaptations to disturbance that allow forests to persist, regeneration failures and rapid changes in vegetation cover have been recently observed in these forests (Boucher et al. 2019). There are well-documented cases of recent regeneration failures following wildfires in the western boreal (Brown and Johnstone 2012; Hayes and Buma 2021). Extensive fire years in recent decades have caused a biome-wide decline in spruce trees to the enhancement of other tree genera (e.g., *Pinus*, *Populus*) and non-arboreal vegetation types (Baltzer et al. 2021). Present day, post-fire regeneration failures are similar to those events that led to the establishment of the forest-tundra landscape in northern Québec (Sirois and Payette 1991). Multiple lines of paleoecological evidence suggest that the landscape was predominantly forested for about 1000 years, from 4000 to 3000 B.P., after which increased fire activity and associated climate led to a gradual opening of the forest cover, a process that was accelerated over the last 1000 years (Gajewski et al. 1993). These fires, coupled with a changing climate, led to deforestation in places where post-fire climates were not conducive to tree establishment or seed banking, relative to pre-fire conditions (Payette and Gagnon 1985; Asselin and Payette 2005).

Given a high incidence of fire in the western boreal forest, interacting or repeated disturbances have also caused regeneration failures, leading to long-term conversion to non-forest vegetation and canopy opening. At the northern tree line successive "short-interval" wildfires (<15 years) in the northern Yukon territory led to recruitment failures due to a lack of post-fire seed source (Brown and Johnstone 2012). The initial wildfires killed most overstory trees and produced a typical abundant post-fire seed rain from aerial seedbanks of semi-serotinous black spruce. Subsequent fires occurred in short succession before seedling trees reached maturity and produced viable seeds. The failure to reach sexual maturity (Johnstone et al. 2010; Viglas et al. 2013) reduces the availability of viable seeds from aerial seedbanks and creates altered successional pathways. Similar but less extreme examples exist farther from the tree line, with examples of repeated wildfires creating extensive understocked or low-seedling density

areas (Pinno et al. 2013; Hart et al. 2019; Whitman et al. 2019). While short-interval reburns have always occurred, reports of their increased prevalence signal more rapid post-fire vegetation change (Buma et al. 2022; Whitman et al. 2022).

In western boreal systems change in the dominance of tree species following fire is more common than conversion to non-forest vegetation. Specifically, pre-fire coniferous stands can be replaced, partly or in their entirety by broadleaf species when few living propagules and post-fire drought limit conifer recruitment (Johnstone and Chapin 2006; Terrier et al. 2013; Baltzer et al. 2021). Short-interval reburning and fire-free intervals had no effect on post-fire stem density of broadleaf tree species in these forests (Johnstone and Chapin 2006; Whitman et al. 2019). In contrast, conifer recruitment may be severely impeded or entirely absent following wildfires burning in close succession (Splawinski et al. 2019), often resulting in long-lasting shifts in forest structure (Johnstone et al. 2004). This phenomenon may also instigate a change in species composition (shifts from conifer to broadleaf dominance or from *Picea* to *Pinus*) (Lavoie and Sirois 1998; Baltzer et al. 2021; Dawe et al. 2022). That vigorous post-fire recruitment of trees — coniferous or broadleaf — is still observed following wildfires across the boreal biome is indicative of sufficient moisture. Moisture deficits are becoming more common (Girardin et al. 2016), and this trend will invariably lead to the inability of trees to persist in many landscapes (Stralberg et al. 2018). Other factors beyond moisture may influence tree recruitment, such as seed source availability, soil microbial processes, soil substrate, nutrient availability, and herbivory (Johnstone et al. 2004, 2010; Johnstone and Chapin 2006; Hansen et al. 2021), though these exert a control over smaller areas, rather than biome-wide conversions.

Paleoecological studies in boreal forests provide important context for recently observed patterns of rapid post-fire conifer establishment or long-term, persistent conversion. Because broadleaf species are less flammable than conifers, shifts in tree cover can create feedbacks with respect to flammability (Barrett et al. 2013) and modify fire behavior, with the potential of transforming fire regimes even in a warmer and drier climate (Rogers et al. 2015). For example, over the late Quaternary period in Alaska, flammable coniferous trees including black and white spruce dominated landscapes during cool periods were associated with increased fire activity over time; this trend was reversed when less flammable vegetation including aspen and birch became dominant and were associated with reduced fire frequencies (Hu et al. 2006; Higuera et al. 2009). In spite of highly variable fire activity and species shifts throughout the Holocene, some studies contend the biome is highly resilient to climatic changes, notably in central Canada (Carcaillet et al. 2010; Waito et al. 2018). In contrast, in the western part of the biome, even with the negative feedbacks caused by a change in vegetation dominance toward broadleaf species, recent fire activity in some western boreal forests has exceeded the levels historically observed, indicating that climate warming may have overwhelmed this historic vegetation control on fire frequency (Kelly et al. 2013). While the sensitivity of tree establishment is evidenced in paleorecords, these also show

how rapid and nonlinear change may lead to uncertain outcomes in the boreal forest (Soja et al. 2007; Young et al. 2017).

Cold mixed-conifer forests

In the montane and subalpine forests of the northern Rockies and Pacific Northwest, dominant species include ponderosa pine (*Pinus ponderosa*), Engelmann spruce (*Picea engelmannii*), western larch (*Larix occidentalis*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta* var. *latifolia*), various fir species (*Abies* spp.), and quaking aspen. Within the southwestern US, subalpine forests are mixed assemblages of Engelmann spruce, southwestern white pine (*Pinus strobiformis*), white fir (*Abies concolor*), and a broad mix of conifers in the Sierra Nevada mountain range. Across the geographic range of cold mixed conifer forests, management history is highly variable, but there has been less direct human impact in the more remote locations of these high-elevation landscapes. Fire exclusion may have influenced the transition zones of this forest type and of alpine meadows, but long fire-return intervals (50–200 years) are common within these forest types (Agee 1993). Indigenous burning of high elevation meadows and forests has been recorded in many cold mixed-conifer forests and contributed to mosaics of forested and meadow environments (Turner et al. 2011; Long et al. 2021). These complex forest structures, topography, and local site climate and moisture create mosaics of regeneration niches following wildfire.

In many ways, subalpine forests at the upper tree line experience similar limitations to tree establishment and growth as harsh lower tree line because of climate tolerances (Davis et al. 2019). For example, even with an adequate seed source, dry sites located on south- and west-facing slopes and (or) excessively drained soils in subalpine sites may offer few opportunities for tree regeneration and can become persistent meadows for decades to centuries (Appendix Table B1; Agee and Smith 1984; Coop and Givnish 2008). Conversely, high-elevation sites that have late-season snowpack and associated short growing seasons may have reduced opportunities for tree establishment and survival. Fires in these environments, especially given the lack of fire-resistant traits of many of these species, may create persistent, subalpine meadows or long delays in regeneration establishment with snowpack limiting conifer establishment and survival (Woodward et al. 1995; Cansler et al. 2018).

As managers and scientists grapple with uncharacteristic regeneration failure in some forests, these cold forests demonstrate several alternate pathways and perspectives to regeneration failure. With pronounced warming and widespread reduction in snowpack, subalpine meadows and alpine tundra are now often leading-edge environments for tree establishment and many sites with adequate moisture are being invaded by tree seedlings of nearby forests (Parks et al. 2019). Decades of fire exclusion and loss of Indigenous burning have also promoted the advancement of closed-canopy cold mixed-conifer forests at high elevations (Hessburg et al. 2015). However, increasing incidence of summer wildfires in these environments and post-fire tree regeneration failure may in some cases maintain meadows and

restore historical open-forest structure in montane and subalpine ecosystems (Cansler et al. 2018). For example, in a study of recent fires in high-elevation sites, Cansler et al. (2018) reported that fires restored heterogeneity of patch sizes and vegetation types within subalpine forests and meadows, which were often maintained by Indigenous communities across the northwestern US (Lake and Christianson 2019).

Conversely, where forests are regenerating after wildfires, transitions in species dominance to more lodgepole pine and quaking aspen have been observed after recent fires, heralded by drier post-fire conditions (Harvey et al. 2016; Schapira et al. 2021). However, lodgepole pine also has a climatic threshold that may be limiting in some areas into the future (Hansen and Turner 2019). Further, both repeated fires and interacting disturbances such as tree-killing bark beetles (*Dendroctonus* spp.) and fire have resulted in different tree regeneration patterns, often diminishing abundance of lodgepole pine (Harvey et al. 2014; Larson et al. 2013; Turner et al. 2019; Hoecker et al. 2020), which is typically a dominant early post-fire species.

Lake sediment records of charcoal and vegetation (i.e., pollen and macrofossils) demonstrate how fire frequency and vegetation assemblages have shifted during the Holocene. Studies across the western US have shown the persistence of mature cold mixed-conifer forests and that it is specific high-severity fires combined with periods of rapid climatic change that prompts forest conversion (Gavin et al. 2007; Calder et al. 2015). Multiple studies demonstrate how cold mixed-conifer forests with fire-intolerant species expanded during times of low fire frequency and shifted to more fire-tolerant assemblages such as ponderosa pine and Douglas-fir or even lodgepole pine during periods of warmer climate and higher fire frequency (Gavin et al. 2007; Whitlock et al. 2008; Chileen et al. 2020). In a related paleoecological study, Crausbay et al. (2017) documented that high-severity fire combined with changing climate often precipitated rapid vegetation change in cold mixed-conifer forests of western Washington. In each case, having broader spatial and temporal context can put short-term patterns and evidence in better perspective, especially as interacting disturbances such as repeated fires may impact tree recruitment to maturity (Littlefield 2019).

Dry pine forests

The dry pine forests described here are those of the intermountain west, dominated by ponderosa pine with associated quaking aspen, Gambel oak (*Quercus gambelli*) and juniper species (*Juniperus* spp.) in the southwestern US (e.g., Arizona, New Mexico, Colorado, and Wyoming) and can be codominant with Douglas-fir, and multiple true fir species in areas of the northern US and southern Canada (e.g., Montana, Idaho, Wyoming, Oregon, Washington, British Columbia). Ponderosa pine, a common and widespread species across the western US, is often viewed as a model of fire resistance (Falk et al. 2022). With thick bark, discontinuous crowns, and a tendency to shed lower branches after being scorched by surface fires, mature individuals can survive light to even moderate fire intensities at frequent fire intervals. Fire scar

records and tree ring studies of forest development suggest that frequent (5–25 years), low-severity fire was common in low-elevation mixed-conifer forests and favored fire-tolerant ponderosa pine and Douglas-fir (Falk et al. 2011; Veblen et al. 2000). Some ponderosa pine-dominated areas historically burned in more mixed-severity fires, with longer, or more variable fire frequencies (Brown et al. 1999). A common finding in dendroecological studies is that warm, dry conifer forests developed in uneven-aged pulses of regeneration and mortality and often not as a single-aged cohort, both tracking favorable climatic periods and slightly longer fire free intervals (Hagmann et al. 2021). These uneven-aged distributions in tree ages have been documented in dry, mixed-conifer and ponderosa pine forests throughout the intermountain west (Mast and Veblen 1999; Fulé et al. 2002; Boyden et al. 2005; Brown and Wu 2005).

Mature ponderosa pine trees are drought tolerant and can withstand periodic drought cycles. However, ponderosa pine seedlings are highly dependent on favorable moisture and temperature regeneration windows. Recent studies have reported a lack of resilience as measured by little to no regeneration following wildfires (see Korb et al. 2019 and Stevens-Rumann and Morgan 2019 for reviews). Many assessments of post-fire tree regeneration in warm, dry mixed-conifer forests document low seedling densities and reduced opportunities for regeneration associated with increasing water deficit, particularly during summer at lower elevations (Appendix Table B2; Kemp et al. 2016; Singleton et al. 2021). Davis et al. (2019) demonstrated that this phenomenon was widespread across the intermountain west where tree regeneration was highly limited by moisture and climatic stress.

Studies using post-fire field surveys identify a persistent shift in vegetation from a conifer forest to non-forested or broadleaf deciduous assemblages that have developed over several decades after high-severity fires (e.g., Roccaforte et al. 2012; Coop et al. 2016; Haffey et al. 2018; Walker et al. 2018). Across these longer-term studies, conversion to non-conifer forest was observed at some but not all locations. For example, in a study of conifer regeneration 5–25 years post-fire in the southwestern US, Haffey et al. (2018) documented regeneration on only 25% plots, while in the northern US Rockies, Kemp et al. (2016) found that only 32% of sites had ponderosa pine regeneration and only 74% had conifer regeneration of any species 5–13 years post-fire. Similarly, others have found regeneration on only 17%–43% of sites (Roccaforte et al. 2012; Stevens-Rumann et al. 2012) and this is consistent across much of the post-fire regeneration literature in this forest type (Appendix Table B3; Korb et al. 2019). While these studies did not identify a forest transition to deciduous forests, Singleton et al. (2021) found that competition with Gambel oak was a major limitation in conifer regeneration. Ponderosa pine tree establishment also is highly episodic in historical records across the range of the species. Thus, while the majority of sites in these studies lack ponderosa pine regeneration, regeneration following wildfires is highly variable, and some locations within each studied wildfire had tree regeneration in both low and high abundances.

Numerous dendrochronology studies across Arizona, New Mexico, and Colorado have demonstrated establishment pe-

riods of trees that reach maturity to be highly variable and often associated with favorable climatic windows (Brown and Wu 2005; Littlefield et al. 2020), especially within fire-free periods (Meunier et al. 2014). This is seen both in long records, such as in Brown and Wu (2005), where tree establishment pulses were associated with large fire periods that corresponded to cooler post-fire periods. In this case, 20–40 years post-fire had the largest pulses of regeneration, with minor infilling at other periods dating back to the 1550s (Brown and Wu 2005). Similarly, based on a 500-year reconstruction of compiled tree establishment dates, Everett et al. (2008) documented continuous recruitment and mortality of uneven-aged moist to dry mixed conifer sites including Douglas-fir, ponderosa pine, and western larch. Given the diversity of sites and ecosystems, it is not surprising that recent records of post-fire regeneration dynamics in montane and subalpine mixed-conifer forests report variable findings. Meanwhile, multiple other studies have identified large peaks of tree establishment since European settlement and fire suppression resulting in long fire-free periods (Fulé et al. 2002; Mast and Wolf 2004; Meunier et al. 2014). For example, Mast and Wolf (2004) reported a large establishment of trees between 1900 and 1950 that corresponded to favorable climate, livestock grazing, and active fire suppression, but prior to this period large pulses of establishment were missing from the record as far back as the 1720s.

Regional trends of increasingly severe wildfires, multi-year drought, and associated tree regeneration delays present a major concern for the future of dry pine forests. However, short-term studies of recent patterns in tree regeneration may not be able to detect tree regeneration failure or type conversions as seen in longer paleoecological records due to episodic and infrequent tree establishment (Napier and Chipman 2021). Trends of low recruitment associated with water deficit, seed source availability, and competition with broadleaf deciduous species and grasses all suggest the potential for reduction of ponderosa pine forests under future climate change and wildfires. Given the importance of fire refugia in ponderosa pine regeneration (Coop et al. 2019; Singleton et al. 2021) and evidence of highly episodic recruitment in dendroecological records, some post-fire ponderosa pine forests may be slow to recover or may convert to savannas under a warmer, often drier climate. Forest thinning and fuel reduction treatments to mitigate future fire severity and increase the probability of mature pines surviving future fires represent science-based strategies to resist forest type conversions in dry pine forests (Kalies and Yocom Kent 2016; Stephens et al. 2020; Prichard et al. 2021).

Definitions and metrics of regeneration failures

Increasing drought and the shrinking climatic windows of opportunity for tree recovery in the years following fires may herald an increasing prevalence of low tree regeneration rates or tree regeneration failure in many parts of western North America. Our analysis of drought within these study areas shows that large wildfire years are linked to drought

(Box 1), and the fate of conifers establishing afterward may be strongly influenced by the likelihood of post-fire drought, as others have found (Rother and Veblen 2016; Davis et al. 2019), exacerbating the uncertainty of post-fire recovery. As the occurrence of large and severe fires continue to increase (Parks and Abazoglou 2020) and considering that droughts influence both wildfires and post-fire vegetation recovery, having a thorough understanding of tree regeneration limitations is critical. To this effect, comparative analyses are useful for understanding the nuances of the response to drought and climate warming across the three different areas of regional analysis. There is a need to clearly identify (*i*) the metrics of failure and their criteria for identification and (*ii*) the appropriate spatial-temporal windows of observation are critical for understanding the ecological consequences and consideration of management actions.

The metrics of post-fire regeneration failure are numerous: an absence of seedlings, a comparison to standard stocking thresholds, or a quantification of low regeneration of target species (i.e., which can exclude non-target species) (Appendix Tables B1–B3). Understanding the goal for regeneration — from an ecological or management standpoint — will determine regeneration failure identification. For example, if timber resources are a priority, a regeneration metric based on stem density may be the most appropriate (Pinno et al. 2013; Rother and Veblen 2016). If vegetation-type transition is the focus of study, the metric could shift to whether there are low densities, or no (zero) tree regeneration (Kemp et al. 2016; Andrus et al. 2018; Baltzer et al. 2021). Alternatively, if one species or functional group is targeted, perhaps because of previous dominance, explicit focus on individual species dynamics and limitations is needed (Littlefield 2019). Revising stocking standards in the context of dendrochronological records of historic tree establishment and climate projections will provide better insight into reasonable expectations for a given ecosystem. Additionally, quantifying geographic areas of concern for recovery and being "climate smart" in terms of tree-planting guidelines will lead to more successful reforestation (North et al. 2019).

Further, we emphasize the importance of matching the temporal window of observations or assessment of failure to the potential longevity of the post-fire recovery period in a given ecosystem. Evidence of delays in conifer tree regeneration 0–10 years post-fire has been reported in all major biomes of western North America, thus rapid recruitment post-fire may not always be the norm (Agee and Smith 1984; Mast and Veblen 1999; Tepley et al. 2014). Longer temporal records, such as dendrochronology, also provide the necessary perspective to understand if, and under what ecological circumstances, past regeneration was generally even-aged or uneven-aged and how long of a recruitment period should be expected for specific conifer forests (Brown and Wu 2005; Napier and Chipman 2021). For example, ponderosa pine has been historically episodic in its regeneration establishment, demonstrating opportunistic regeneration during favorable climatic or forest conditions (Meunier et al. 2014; Littlefield et al. 2020). Using a timber management metric based on forest stocking, most post-fire sites in the SW did not achieve high-enough densities to be considered fully stocked and

could be defined as regeneration failure even 20 years post-fire (Chambers et al. 2016; Rother and Veblen 2016; Singleton et al. 2021). Stocking thresholds in Outzs et al. (2015) were set at a lower density based on historic range of variability targets and thus more sites (4 out of the 8 studied) were considered fully stocked. Further, growth and yield models often do not incorporate regeneration delays or low levels of stocking and will need to be adjusted according to climate change uncertainties (Crookston et al. 2010; Medlyn et al. 2011).

In western boreal forests, by contrast, studies of post-fire regeneration often cover a relatively short time period following a fire (<20 years). Post-fire recruitment of serotinous conifers, namely black spruce, jack pine, and lodgepole pile, is rapid in this harsh biome and the vegetation trajectory is often "set" within a few years (Greene and Johnson 1999). For instance, 70%–90% of all post-fire regeneration may occur in the first 10 years and long-term studies confirm that such patterns are persistent in black spruce-dominated forests (Johnstone et al. 2004; Johnstone et al. 2020). Post-fire regeneration potential in black spruce forests deteriorates over time due to declining seedbed quality, soil organic material development, and competition from understory vegetation and non-vascular plant species (Johnstone et al. 2004; Brown and Johnstone 2012; Splawinski et al. 2019). Delayed recruitment is still possible in the western boreal forest, either through the contribution from obligate-seeder species (e.g., white spruce), the eventual opening of serotinous cones (i.e., black spruce is semi-serotinous), or during long fire-free interval through the asexual reproduction (i.e., layering) of some conifers (Légère and Payette 1981).

The spatial extent and configuration of regeneration delays are critical in dictating the rate of ecosystem change (whether transient or long term) and whether they should truly be termed a "regeneration failure." For example, as more fires occur in dry ponderosa pine forests, conversion to non-forest vegetation may restore mosaics that resemble those prior to European settlement and promote feedback to future fire and vegetation patterns (Prichard et al. 2017). In both ponderosa pine and cold mixed-conifer forests, patchworks of grasslands can carry low-intensity surface fires to forests that create more resilient stand and landscape patterns of forests (Hessburg et al. 2019). In addition, increasing aridity in some forested sites will also continue to cause mature tree die-back, lower forest cover, and reduced fine-fuel accumulations (van Mantgem et al. 2009; Michaelian et al. 2011). Increasing aridity may create a negative feedback to fire through a reduction in vegetation and fine-fuel accumulations that support fire spread, especially at ecotone boundaries (Krawchuck et al. 2009). Although fine-scale measurements of tree recruitment are essential for investigating potential regeneration success (or failure), many sites must be considered to allow any generalization on regeneration "success" for a given geographic area.

Evaluating the long-term evidence collected at broad spatial scales (e.g., >1 Mha) demonstrates that some forests have historically been one component of a shifting mosaic of disturbance-maintained forest and non-forest vegetation (Schwarz and Wein 1997; Whitlock et al. 2008; Hessburg et al. 2019). In some parts of western North America, many

meadows and grasslands are undergoing shrub and tree invasion over the last century due to land-use change and effective fire suppression, including the suppression in Indigenous cultural burning (Stockdale et al. 2019; Lake and Christianson 2019). Some of the local regeneration "failures" may represent a partial restoration of the shifting mosaic of forest and non-forest vegetation that existed under historical fire regimes and will be essential to create more fire-resilient landscapes under a warmer, often drier future in these forests (White and Long 2018; Hessburg et al. 2019). Conversely, large-scale studies that demonstrate consistent and widespread regeneration failure (Stevens-Rumann et al. 2018; Davis et al. 2019; Baltzer et al., 2021) highlight landscapes experiencing unprecedented change that will likely continue with a continued warming and drying climate (Coop et al. 2020).

Future research needs

Although we do not advocate a single metric describing "regeneration failure" across western North America, we encourage more uniformity in the nature of the measurements and spatiotemporal frame of observation. In particular, we urge caution when extrapolating short-term (e.g., approximately 1- to 25-year post-fire regeneration) studies to make statements about forest regeneration failure where delayed regeneration is possible (i.e., forests dominated by non-serotinous species). Regeneration patterns are species- and forest-type specific; for example, the same inferences that may be made in much of the western boreal biome may not be adequate in describing long-term regeneration potential in dry conifer forests of the southwestern US. Furthermore, we focus here on early post-fire regeneration windows, but even when post-fire climatic conditions are conducive to tree reestablishment, pronounced drought at seedling and sapling stages can substantially alter forest successional trajectories (e.g., Johnstone et al. 2010; Kemball et al. 2006).

Forest dynamics are expressed across a range of time scales; thus research is needed that combines multi-scale, multi-proxy records to more fully understand past regeneration dynamics and likely trajectories of post-fire vegetation (Falk et al. 2011; Napier and Chipman 2021). For example, in two studies of post-fire recovery in a subalpine ecosystem of the Rocky Mountains, Harvey et al. (2016) and Schapira et al. (2021) documented low recruitment densities of two shade-tolerant, mesic species (subalpine fir (*Abies lasiocarpa*) and Engelmann spruce), however given their shade tolerance this may be due to longer regeneration windows than these post-fire observation windows of up to 20 years post-fire. A network of lake sediment records in the same location provides a longer-term and broader-scale perspective on post-fire tree regeneration in subalpine forests. These records demonstrate that large, severe wildfires have occurred in the past and, combined with sudden warming, resulted in mosaics of non-forest (meadows) to develop with measurable reductions in moist-site species such as Engelmann spruce (Calder et al. 2019). This longer-term perspective lends support for shorter-term evidence that rapid warming and drought could

strongly influence tree establishment patterns and forest resilience to wildfire in these subalpine forests.

Second, there is a need for long-term post-fire forest regeneration studies to increase the understanding of the mechanisms and drivers of whether forest regeneration is accelerated, delayed, or in line with historical rates. Short term studies are valuable but may not always show the long-term trajectory of an area. The design of longer-term studies can include: (*i*) field observations of forest regeneration across fires that occurred up to 100 years ago, (*ii*) design of space-for-time sampling strategies (Pickett et al. 1989; Bond-Lamberty et al. 2014) in combination with remote sensing techniques (i.e., lidar) to assess regeneration across different site-level factors, and (or) (*iii*) combine neo-ecological research queries with paleo or dendrochronological research ones (Buma et al. 2019) to extend recent observational fire impact datasets with longer-term pollen and tree-ring studies. Alternatively, where these types of data are unavailable, spatial models based on solid field-based observations and well-understood forest dynamics may provide important insights on vegetation change and resilience (cf. Hart et al. 2019; Falk et al. 2019).

Third, we recommend the development of species- or trait-specific ecophysiological drought indices (Kattge et al. 2020; Stevens et al. 2020). Efforts in that direction have been initiated (e.g., O'Brien et al. 2017), but have yet to incorporate future potential conditions and the potential stressors added in post-fire environments. To understand the specific impacts of drought on tree regeneration, we need a better understanding of how individual trees and cohorts respond to dry and hot conditions at different locations within a species and within fine-scale variation in the landscape (Harvey et al. 2016; Hill and Ex 2020). Additional research is needed on the limitations at different stages of tree growth (e.g., germination, seedling, sapling stages), and on quantification of where and when drought-mediated plant die-off events occur. Furthermore, many of the species highlighted here have large geographic ranges and the phenotypic variation across the range may make some locations more prone to climate-induced tree-regeneration failures (Isaac-Renton et al. 2018; Leal-Saenz et al. 2020). It will be important to identify whether the climate envelope is suitable for such tree species, as some previously forested landscapes may no longer support species that were historically present or dominant (Parks et al. 2019; Davis et al. 2020). Paleoecological studies are particularly important to assess how individual species have responded to past changes in climate and how species assemblages have shifted over time (e.g., Gavin et al. 2007; Higuera et al. 2009). Under rapid climate change, even if species can migrate to more suitable climates (e.g., higher altitudes or latitudes), there is no guarantee that they can survive under novel drought cycles and disturbance regimes.

Fourth, interactions between fire, drought stress, other disturbances (e.g., tree disease, insect outbreaks, windthrow, and permafrost thaw) are another critical aspect of understanding the direction of future (mid to long term) forest dynamics in the three forest types of this study, and globally (Kautz et al. 2017). Existing literature on insect–fire interactions is mixed, with some studies demonstrating a reduction in tree regeneration after interacting biotic and abiotic dis-

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turbances (Harvey et al. 2013) and some not (Stevens-Rumann et al. 2015; Schapira et al. 2021). Similar to insect outbreaks, large wind disturbances can affect the structure of forests and influence both propagule availability and subsequent fire behavior in reburn events (Grandpré et al. 2018). In northern latitudes, the combined effect of wildfire and permafrost thaw is not well understood but has the potential to cause profound and long-lasting impact on vegetation communities (Holloway et al. 2020). This paper has focused on post-fire landscapes; however, the increasing fire footprints combined to other disturbances (i.e., insect outbreaks and drought) that may also become more widespread and severe — in addition to the possibility of novel climates — may lead to unanticipated consequences with respect to conifer regeneration and subsequent vegetation trajectories (Johnstone et al. 2016).

Finally, as western forests experience ongoing climate changes, *in situ* experiments within burned areas to understand where and why tree regeneration fails are needed. There are numerous avenues to pursue climate adaptation research, and incorporation of researchers and managers in silviculture and restoration will be critical to drive the state of knowledge forward. For example, the US Forest Service plants thousands to millions of trees in burned National Forest land across the western US, yet little data exist on the success of these plantations. Similarly, in Canada the government has created the 2 Billion Trees Commitment to encourage reforestation over the next decade (https://www.canada.ca/en/campaign/2-billion-trees.html; last accessed 21 February 2022). Numerous silvicultural experiments are currently underway to understand ecosystems' ability to adapt to climate change (e.g., Nagel et al. 2017), and this work should continue in burned areas, especially in climate-vulnerable parts of the continent.

Conclusions

Conifer tree regeneration is extremely variable, with a growing consensus across these three forest types that climate and drought play a large role in driving regeneration success or failure. It is important for managers and scientists to quantify spatial and temporal scale when discussing "regeneration failure." In some cases, a failure to regenerate to a forested landscape may in fact be the re-establishment of meadows or alternate species compositions historically found across these landscapes. The expectation that tree regeneration meets a minimum threshold of establishment may warrant careful consideration, especially in the face of both prolonged tree establishment periods for some species and ecosystems, and climate change, where similar pre-fire forest structure may not be desired or resilient in a novel climate. Further, we should enhance our comparisons of regeneration failure across forest types and examine the drivers of these patterns, especially where drought and climate change may herald changes from historical establishment patterns. There is no doubt that the forests of western North America are shifting, and post-wildfire environments often provide an early indicator of these changing forests, but we should be cautious of quantifying "regeneration failure" without providing spatial and temporal context.

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Data generated or analyzed during this study are available in the OSF repository and can be found at https://osf.io/ufw7y/?view_only=f598f0a834284399ad962509d558690f

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Author contributions

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Appendix A. Drought and fire activity analysis methods

We defined three analysis areas within North America: the western boreal forest, the northern Rockies, and the Southwest (Fig. 1). In these three areas, we used fire perimeter atlases to map the area burned over time. Study area boundaries were adapted from the Commission for Environmental Cooperation (CEC) North American terrestrial ecoregions (CEC 2015). In the western boreal forest, we used the Canadian National Fire Database (CNFDB; Natural resources Canada 2019) to identify all fires that burned between 1970 and 2017. In the Northern Rockies analysis area, we combined the CNFDB, in the north, with perimeters provided by the Monitoring Trends in Burn Severity (MTBS) program (1984–2017). We represented earlier (1970–1983) wildfires in the US portion of this study area with data from a fire history atlas covering much of Idaho and Montana (Morgan et al. 2008). We used MTBS fire perimeters (1984–2017) for the southwestern analysis area as well and supplemented the earlier period with two additional historical fire atlases for the Santa Fe and Gila National Forests (1970–1983; Snyderman and Allen 1997). All fire data for the two study areas that were partially or entirely in the United States was limited to a minimum fire size of $\geq$404.7 ha, for consistency with the minimum fire size mapped by MTBS. For all analyses, annual area burned was normalized as a percentage of the analysis area for which fire maps were available, due to the smaller fire atlas extent in the US portions of analysis areas during early periods (1970–1983 fire atlas recording areas; 1984–2017 full analysis areas). We represented historical climate moisture using the raster grids of the annual climate moisture index (CMI; McKenney et al. 2011). We conducted a time series anal-

ysis of mean CMI anomalies (reference period 1961–1990), and % annual area burned. We calculated Theil–Sen nonparametric slopes and Mann–Kendall trend tests for significance of the trend in mean CMI anomalies and % area burned (1970–2017). The time series of mean CMI anomalies was derived from the full extent of the analysis areas, and not a smaller atlas proportion. All analyses were conducted in R (R Core Team 2021).

To examine the likelihood and role of dry years in fire occurrence, as well as in post-fire periods, we examined the probabilities and coincidence of "large fire years," "dry years," and "wet years." The CMI data for this analysis were limited to the extent of the recording area for which fire data were available in earlier atlas periods (1970–1983), allowing the climate and analysis areas to match one another in spatial extent and through time. We defined a large fire year in each of the three analysis areas as a year with 75th percentile area burned. Similarly, we defined a dry year as one with 25th percentile median annual CMI (negative values indicate dry years). We defined a wet year as a year with 75th percentile CMI. We then used superposed epoch analysis in the burnr package (Malevich et al. 2018; v 0.3.1) to examine the significance of departures from mean CMI prior to, during the year of, and following large fire years (year 0 = large fire year). For each study area, we also calculated the bootstrapped mean probability of drought in years −1, 0; any drought in years −1 or 0; any drought in years 0, 1, 2, and 3; and multiple droughts in years 0, 1, 2, and 3. We also calculated the bootstrapped mean probability of experiencing any wet year in years 0, 1, 2, and 3.

Appendix B

Table B1. Evidence of conifer tree regeneration delays or failure in western boreal forest. Study findings were categorized into absence of seedlings, low density/stocking or delayed regeneration or having identified a shift in conifer species if the majority of sites (>50%) was identified as such. Most studies in this forest type identified sites rather than number of wildfires seen in Appendix Tables B2 and B3.

Metric	Time since fire (years)	Spatial context	Drivers/Causes	Literature
Total regeneration failure (postfire density of the prefire dominant is zero)	2–13	1538 sites across the North American boreal biome	Drought stress, lack of propagules due to short-interval reburns, non-tree competition; study focused specifically on black spruce (*Picea mariana*); species failed to regenerate in 18% of sites.	Baltzer et al. 2021
	≤50	150 sites, Saskatchewan Boreal Shield	Site moisture limitation leading to post-fire recruitment failures on well-drained sites, and when the interval between fires was <50 years.	Hart et al. 2019
Change in dominance (simple majority, number of stems)	5–19	34 sites, interior Alaska and central Yukon Territory	Short-interval reburns (<25 years) exhibited reduced recruitment of black spruce, but no reduction in quaking aspen (*Populus tremuloides*); broadleafs persist under a range of fire intervals due to low availability of conifer seeds, and fast-growing aspen suckers.	Johnstone and Chapin 2006
	2–4	90 sites, interior Alaska	Short interval reburns support conversion to broadleaf forests; recruitment of black spruce strongly linked to environmental conditions; self-replacement of black spruce mostly at moist sites with low fire severity; widespread replacement by quaking aspen.	Johnstone et al. 2010
	4–17	50 sites, northwestern boreal region	Lack of propagules due to short-interval reburns, exacerbated by drought stress; 72% of short-interval sites had <50% conifer stems than corresponding long-interval sites (>30 years).	Whitman et al. 2019
	13	89 sites, interior Alaska	Broadleaf seedling establishment strongly controlled by fire effects (combustion and residual organic layer depth), whereas black spruce seedling density was insensitive to fire effects and instead driven by environment.	Johnstone et al. 2020
	13	75 sites, Alaska	Soil organic matter loss, plant-soil-microbial feedbacks, differential growth rates/competition.	Mack et al. 2021
	2–13	1538 sites across the North American boreal biome	Black spruce lost dominance after fire in 38% of sites.	Baltzer et al. 2021
	12–16	50 sites, interior Alaska	Repeated short-interval fires caused a sharp decline in black spruce; Alaska birch (*Betula noalaskana)* and other broadleaf became increasingly dominant with each additional fire; spruce persisted in wetter lowland sites with greater organic matter; after three burns, conifers were virtually eliminated from all sites.	Hayes and Buma 2021
Stocking/seedling density	5–28	24 sites, northern Yukon	Low recruitment due to short-interval fires; black spruce recruitment limited by seed availability after short-interval fires; seed limitation does not take advantage of post-fire recovery on seedbeds.	Brown and Johnstone 2012
	1	56 sites, northeastern Alberta	Young stand (<30 years) have much lower stocking than older (>60 years) stands; greatest regeneration in moderate-severity burns; 1164 stems/ha considered understocked (potentially 130 500 of a 658 000 ha wildfire).	Pinno et al. 2013

Table B1. Continued

Metric	Time since fire (years)	Spatial context	Drivers/Causes	Literature
Regeneration delay	59	20 sites, east-central Alberta	Study focused on white spruce (*Picea glauca*) in boreal mixedwood; regeneration dominated by initial (<20 years; 7 stands), delayed (≥20 years; 6 stands), or both types (7 stands); delayed regeneration peaked 38–44 years post-fire; ageing of *P. glauca* is problematic and requires dendrological analysis.	Peters et al. 2006
	43–44	12 sites, southern Yukon Territory	Study focuses on quaking aspen and white spruce; area is in one of the driest parts of the North American boreal forest; reduced growth and regeneration due to episodic droughts; both species exhibited episodic regeneration.	Hogg and Wein 2005
Forest productivity (annual growth increment)	~170–185	4 sites, northern Manitoba	Multiple pulses in recruitment due to high mortality episodes; high temperature and low precipitation caused significant mortality and delayed tree recruitment; effects are persistent many decades following mortality events.	Bond-Lamberty et al. 2014
	34–340	75 site, Alberta and west-central Saskatchewan	Climate drying the major cause of growth decline and subsequent mortality; 57 of 75 stands exhibited significant decline; no difference in decline as a function of stand age.	Hogg et al. 2017

Table B2. Evidence of conifer tree regeneration delays or failure of cold mixed conifer forests across the intermountain regions of the Rockies and Pacific Northwest. Study findings were categorized into absence of seedlings, low density/stocking or delayed regeneration or having identified a shift in conifer species if the majority of sites (>50%) was identified as such.

Metric	Time since fire (years)	Location	Drivers/Causes	Literature
Delayed regeneration (distance to seed source)	11	1 wildfire east Cascades, Washington	High lodgepole pine (*Pinus contorta*) regeneration but significantly lower with distance to seed source for Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasicarpa*).	Littlefield et al. 2019
	18	6 wildfires, Idaho	Subalpine mixed conifer forests generally had high seedling recruitment but significantly lower with distance to seed source. Dense invasion of montane sites previously dominated by Douglas-fir (*Psuedotsuga menziesii)* and ponderosa pine (*Pinus ponderosa)* with lodgepole pine.	Stevens-Rumann and Morgan 2016
Delayed regeneration/low density at high elevation mixed conifer sites is common	200	2 wildfires Olympic Mtns, Washington.	Long periods of seedling recruitment into meadows, limited by moisture on dry sites and snow on moist sites.	Agee and Smith 1984
	300	Subalpine meadow study central Cascades, Oregon	Conifer recruitment is episodic and facilitated by early invaders into subalpine meadows.	Halpern et al. 2010
	30	2 wildfires central Cascades, Washington	Sparse regeneration in first 3 decades following fire. Conifer tree establishment associated with warm, dry spring and low snowpack.	Little et al. 1994
	60	Subalpine meadow study central Cascades, Washington	Continuous recruitment of conifers in subalpine meadows for >60 years. Snowpack limits tree regeneration. Heather–shrub assemblages facilitate conifer regeneration.	Rochefort and Peterson 1996
	>300	Subalpine meadow study Olympics Mtn, Washington	Snow historically limited tree regeneration in the western Olympics, whereas drought limited post-fire tree regeneration in the eastern Olympics.	Woodward et al. 1995
Delayed or absent regeneration with shrinking climatic windows	40	Regional study in high elevation forests of the southern Rockies	Recruitment of Engelmann spruce and subalpine fir are limited by moisture availability and will be impacted by warmer, drier summers.	Andrus et al. 2018
	20	10 wildfires, northern Rockies	Abundant lodgepole pine regeneration but recruitment of other subalpine conifers limited by post-fire drought.	Harvey et al. 2016
	4–30	52 wildfires, Rockies	Compared regeneration trends between 1985–1999 vs 2000–2015. Significant reductions in regeneration in latter period including high elevation forests.	Stevens-Rumann et al. 2018
Conifer vegetation type change	20	10 wildfires, northern Rockies	Recent lodgepole pine has been favored over Engelmann spruce due to lack of moisture and seedling density declined with severity.	Harvey et al. 2016
	8	1 wildfire, northern Rockies, Montana	Lodgepole pine densely invades first-entry fire areas, but rapid succession reburns can favor ponderosa pine.	Larson et al. 2013
	7–18	6 wildfires, northern Rockies, Idaho	Repeat wildfires reduce regeneration – 31% lower mixed conifer seedling densities in reburn areas.	Stevens-Rumann and Morgan 2016
Fire-maintained subalpine meadows	10–100	Subalpine meadow study. High elevation north Cascades and northern Rockies	Fire restores subalpine forest/meadow mosaic and maintains heterogeneity in alpine environments.	Cansler et al. 2018
	60	Treeline study, New Mexico	Invasion of subalpine grasslands by conifers mediated by fire. Conifers are expanding with higher minimum temperatures.	Coop and Givnish 2007, 2008

Table B3. Evidence of conifer tree regeneration delays or failure in dry ponderosa pine (*Pinus ponderosa*) and dry mixed conifer forests of western North America. Study findings were categorized into absence of seedlings, low density/stocking or delayed regeneration or having identified a shift in conifer species if the majority of sites (>50%) was identified as such. HRV = historical range of variability.

Metric	Time since fire (years)	Location	Drivers/Causes	Literature
Delayed or absent regeneration across regions	11–18	5 wildfires, Colorado	High severity fire patches 70% of area and seedling density <49 trees/ha over 50 m away from remnant forests.	Chambers et al. 2016
(Limited climatic window)	0–30	33 wildfires across w US 1988–2015	Regional study of post-fire regeneration of dry mixed conifer forests. Demonstrated that since 1995, climatic windows have significantly declined for post-fire ponderosa pine regeneration.	Davis et al. 2019
	5–13	21 fires, central Idaho and w Idaho	Regional study of post-fire regeneration in low elevation dry mixed conifer forests. Evaluated same dataset as Kemp et al. (2016) and found strong correlation between maximum summer temperatures and tree regeneration with evidence for regeneration failure on the warmest sites.	Kemp et al. 2019
(Limited seed source)	7-17	8 fires, Arizona, New Mexico	No regeneration observed >225m from seed source. Only 43 of 175 plots had ponderosa pine regeneration.	Haffey et al. 2018
	28–45	2 wildfires, Arizona, New Mexico	Seedling densities significantly declined >150 to 200 m from mature conifers. Long-term regeneration failure in high severity patches was observed in almost all long-distance plots.	Haire and McGarigal 2010
	5–13	21 fires, central Idaho and w Idaho	Regional study of post-fire regeneration in low elevation dry mixed conifer forests. Across all fires, 75% of the area burned was high severity and associated with seed source limitations.	Kemp et al. 2016
	8–15	6 fires, Colorado	Distance to seed source and xeric settings (south aspects) were associated with limited tree regeneration in low elevation burned sites following high severity fire in the Colorado Front Range.	Rother and Veblen 2016
Recruitment does not meet minimum stocking standards and/or historical range	11–18	5 fires, Colorado	Stocking min standard = 370 trees/acre for ponderosa pine. Measured 211 stems/ha near forests but a mean of 10 stems/acre >200m from surviving forest.	Chambers et al. 2016
	10	8 fires, Arizona, New Mexico	Four out of eight sites did not reach target density based on HRV of 56–138 stems/acre.	Outzs et al. 2015
	9–21	10 fires, Arizona, New Mexico	Seven out of 10 fires had median conifer densities that do not meet min 125 stems/ha of HRV and restoration targets.	Singleton et al. 2021
	5	1 fire, New Mexico	Sites that had prior wildfire or prescribed fire had lower burn severity than previously unburned sites and highest probability of conversion of forest to nonforest within the 5-year monitoring period.	Walker et al. 2018
Conifer recruitment limited due to competing vegetation	1–18	11 fires, Arizona	Conifer regeneration lacking in 50% –57% of sites. Competing shrublands and grasslands are barrier to long-term post-fire establishment.	Roccaforte et al. 2012
	9–21	10 fires, Arizona, New Mexico	Even within high severity patches, there were small refugia that provided a seed source. Regeneration most influenced by veg competition with Gambel oak cover but not by conifer cover.	Singleton et al. 2021