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Anticipating fire-mediated impacts of climate change using a demographic framework

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Abstract

1. Climate change indirectly affects forest ecosystems through changes in the frequency, size, and/or severity of wildfires. In addition to its direct effects prior to fire, climate also influences immediate postfire recruitment, with consequences for future vegetation structure and fire activity. A major uncertainty, therefore, is if, when and where vegetation shifts will occur.

2. With an emphasis on species traits, we use a demographic framework to examine how the interaction of changing climate and fire will affect postfire woody vegetation recruitment and the likelihood of vegetation shifts. Each demographic stage – adult mortality, propagule availability, seed germination, seedling establishment, and seedling survival – serves as a filter through which a species must pass for establishment and recovery to occur.

3. We apply this framework to case studies in western North American forests, including boreal and southwestern U.S. *Pinus ponderosa* forests, to help understand the mechanisms behind recent postfire vegetation changes. The case studies highlight how changes in climate and fire properties will make it increasingly difficult for some species to pass through each demographic filter in the future.

4. As climate warming continues, we expect increased dominance of species that resprout following fire, maintain canopy or soil seed banks, have long distance seed dispersal, produce drought-tolerant seedlings, and/or reach reproductive maturity quickly. The persistence of postfire vegetation shifts will depend the on ratio of recovery time to disturbance interval(s).

5. An advantage of the demographic-filter framework is that it places emphasis on mechanisms, thus improving our ability to anticipate future vegetation shifts. As such, it highlights the clear need for more mechanistic studies of postfire recruitment to disentangle the relative effects of multiple drivers in postfire environments.

KEYWORDS
alternative stable state, climate change, conifer forest, fire, fire effects, postfire regeneration, vegetation shift, western North America

1 | INTRODUCTION

Climate change will affect forest ecosystems directly through warming and drought (Allen et al., 2010; Jiang et al., 2013) and indirectly through increases in forest disturbances, including insects and pathogens (Anderegg et al., 2015; Weed, Ayres, & Hicke, 2013), and wildfires (Flannigan, Logan, Amiro, Skinner, & Stocks, 2005; Westerling, Hidalgo, Cayan, & Swetnam, 2006). Potential changes in vegetation composition and structure in turn have important consequences for carbon and water cycles, and subsequent climate feedbacks (Bonan, 2008). The sensitivity of fire activity to climate change, and the dominant role of fire and climate in shaping postfire vegetation dynamics, make understanding climate/fire-mediated changes in forests a major challenge for anticipating the impacts of global environmental change. Here, we examine the potential for these changes to occur by taking a demographic approach to postfire woody vegetation recruitment with an emphasis on western North American coniferous forests.

Climate warming over the past several decades has led to an increase in the duration and magnitude of fire-conducive weather conditions across much of the globe (Jolly et al., 2015). This pattern is particularly pronounced and directly linked to increased fire activity in forest ecosystems of western North America, where average annual area burned in many regions has increased by over 1,000% in the 21st century (e.g., 2003–2012 vs. 1973–1982, Westerling, 2016). Large wildfires are facilitated by seasonal climate conditions that lead to low fuel moisture (i.e., drought; Littell, Peterson, Riley, Liu, & Luce, 2016), conditions that have become increasingly common over the past several decades due to earlier springs, warmer summers and/or decreased summer precipitation. Combined, these trends have resulted in an increase in the duration of the fire season, by as much as 3 months, and increased annual area burned (Jolly et al., 2015; Littell, McKenzie, Peterson, & Westerling, 2009; Westerling, 2016). With warming climate, increased frequency of fire-conducive conditions is expected in the future (Jolly et al., 2015; Moritz et al., 2012; Young, Higuera, Duffy, & Hu, 2017). Area burned across forests in western North America is projected to increase in proportions similar to or greater than those observed over the past several decades (e.g., >1,000%; Balshi et al., 2009; Littell et al., 2010; Westerling, Turner, Smithwick, Romme, & Ryan, 2011; Young et al., 2017).

Anticipating future fire activity, however, inherently depends on postfire vegetation change, which may lead to positive or negative fire vegetation feedbacks, depending on whether postfire vegetation is more or less flammable than prefire vegetation. For instance, while statistical models suggest dramatic increases in area burned, fuel-limitations will likely moderate climate-driven increases in fire activity and limit the amount of burning that can be sustained (Parks, Holsinger, Miller, & Nelson, 2015; Westerling et al., 2011). Thus, anticipating future fire activity inherently depends upon vegetation response to the combined impacts of climate change and increased burning. It is important that, the same climate conditions

that facilitate burning—that is increased moisture deficits—directly influence the postfire environment and vegetation response. A key question, therefore, is if, when and where postfire vegetation shifts will occur in the future.

Fire has been shown to be a catalyst for vegetation shifts (Crausbay, Higuera, Sprugel, & Brubaker, 2017; Donato, Harvey, & Turner, 2016; Gavin, Brubaker, & Greenwald, 2013; Stralberg et al., 2018), accelerating climate-driven changes that would otherwise take decades or centuries to unfold. Vegetation shifts can be caused by a single large fire event (Crausbay et al., 2017; Donato et al., 2016) or by a series of fires over a time period shorter than the dominant species require for maturation (Buma, Brown, Donato, Fontaine, & Johnstone, 2013). These dynamics ultimately reflect how changes in climate (i.e., temperature, precipitation and associated variability) and fire (i.e., frequency, intensity or size) interact with vegetation to determine postfire vegetation recruitment. Because postfire recruitment, particularly in the first few years immediately following fire, strongly determines long-term vegetation composition (Johnstone, Hollingsworth, Chapin, & Mack, 2010; Turner, Whitby, Tinker, & Romme, 2016), vegetation that recruits immediately following fire can be the fuel for the subsequent fire. These dynamics can set up a feedback loop involving vegetation, fire behaviour, fire effects and postfire recruitment (Figure 1).

To help anticipate when, where and why postfire changes in vegetation will occur, we propose to use a demographic framework focused on the mechanisms driving fire-mediated vegetation changes, through the lens of plant functional attributes and demographic filters (Figure 2). This framework is based on the simple rationale that plant community persistence requires that rates of recruitment and survival to maturity roughly match adult mortality rates (Lloret, Escudero, Iriondo, Martinez-Vilalta, & Valladares, 2012). After mortality events, such as wildfires, compensation through higher recruitment of prefire vegetation can prevent vegetation shifts (Lloret et al., 2012); however, climate limitations or changes in fire effects may prevent this compensation from occurring after one or multiple fires (Enright, Fontaine, Bowman, Bradstock, & Williams, 2015). It follows that a mechanistic understanding of how changes in climate and fire will affect important demographic stages will allow us to identify the processes that may contribute to vegetation shifts in different forest ecosystems.

The importance of demographic processes influencing the dynamics of plant populations and the mechanisms driving long-term successional dynamics have long been acknowledged (Connell & Slatyer, 1977; Harper, 1967). Focus has also been given to the distinct physiology of early and later successional species (Bazzaz, 1979; Finegan, 1984) as well as to plant traits associated with distinct life-history strategies (Wright et al., 2004) relevant during succession (Grime, 1977). Surprisingly, however, the majority of studies on postfire regeneration rely on correlative evidence to make inferences on how factors such as fire characteristics, climate and microsite conditions influence
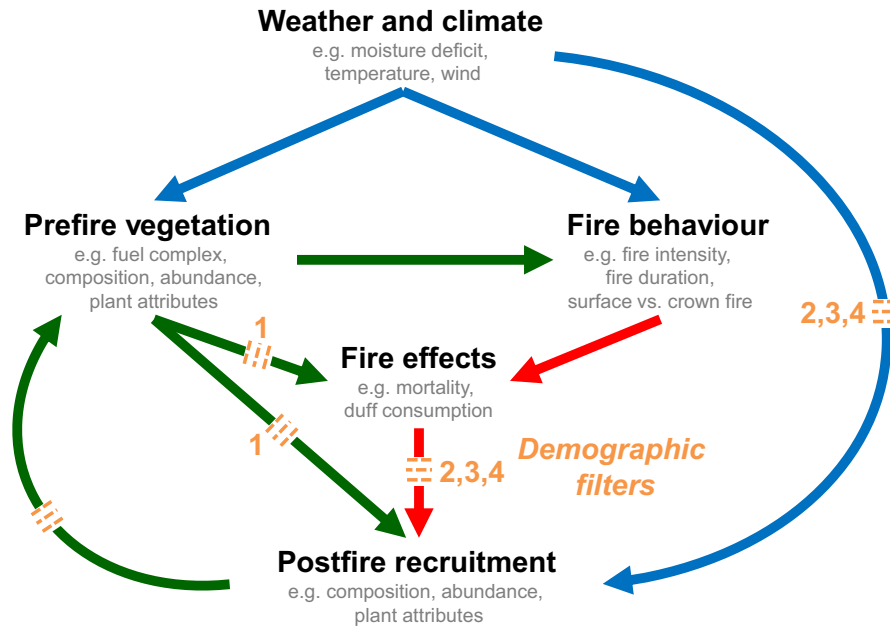
FIGURE 1 Fundamental linkages among weather and climate, fire activity (i.e., behaviour and effects), and vegetation (i.e., pre- and postfire), which ultimately determine how an individual fire interacts with prefire vegetation to dictate postfire recruitment. Arrows reflect the influence of weather and climate (blue), vegetation (green) and fire (red). Arrows linking vegetation, fire and recruitment (green and red) highlight pathways that can lead to fire-vegetation feedbacks, whereby the postfire vegetation sets up key attributes of the fuel complex (e.g., fuel loading, bulk density, canopy base height) for the next fire. Numbers designate the specific demographic filters passed through at each point along the path to postfire recruitment, and they correspond to the numbered filters in Figure 2. Demographic filters will also operate from postfire recruitment to prefire vegetation in the longer term, though they are not our focus (and hence not numbered)
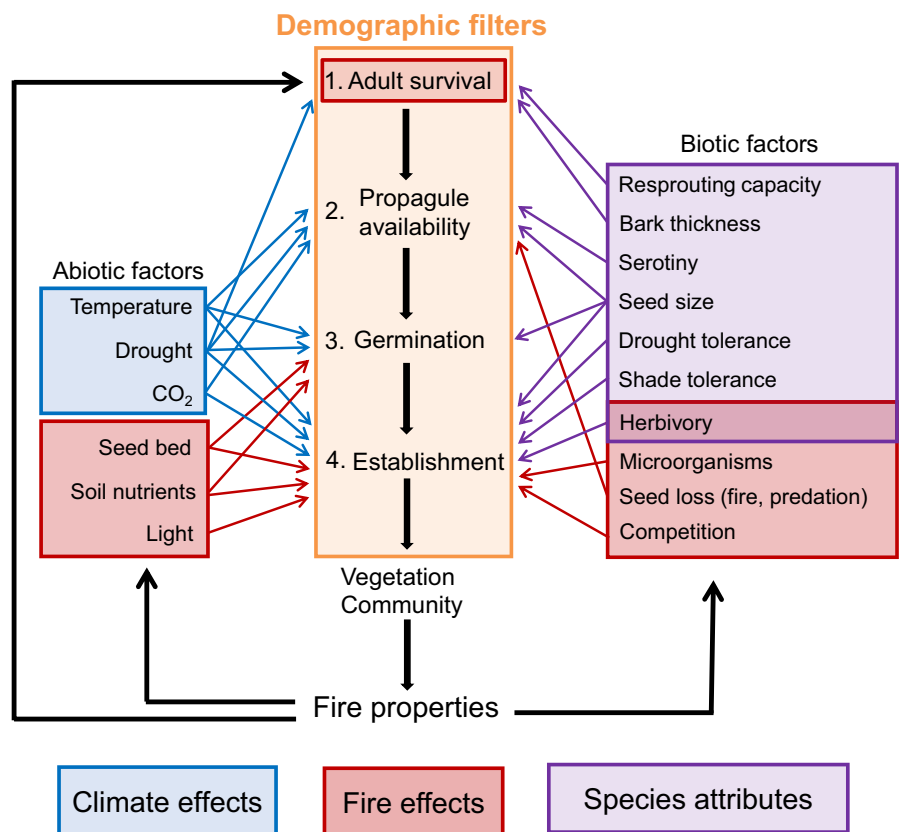
FIGURE 2 Simplified conceptual model highlighting factors that affect a species' ability to pass through the four demographic filters following fire: adult survival, propagule availability, germination and establishment. Box and arrow colours correspond with the type of factor: climate effect, fire effect, or species attribute

postfire recruitment. To date, a demographic framework for understanding postfire vegetation development is lacking, but it is critical for empirical, theoretical and modelling efforts aimed at

understanding global change. Further, a key assumption in existing models of succession is that the climate that led to the prefire vegetation is similar to that during postfire recruitment, which is

no longer true. Here, we build upon the existing body of work to develop a framework that identifies which species will dominate landscapes immediately following fire and explicitly incorporate the effects of changing abiotic conditions following the initial disturbance, including changing fire regimes and climate conditions. The framework draws on the idea from species coexistence theory that large-scale processes, such as dispersal, determine which species are available to colonize postdisturbance landscapes, and small-scale environmental filtering determines which species ultimately establish (Zobel, 1997). We then use case studies in different forest ecosystems to illustrate the generality of the framework, and end by exploring expectations and uncertainties in fire-vegetation feedbacks.

2 | DEMOGRAPHIC FILTERS DETERMINE POSTFIRE VEGETATION COMMUNITIES

The demographic filter framework is based on the premise that dominant prefire species must pass through successive demographic stages to transition from fire-caused mortality to reproductive maturity, including propagule dispersal, seedling germination, establishment and survival. Each demographic stage serves as a filter through which a species must pass for vegetation recovery to occur. The ability to pass through a given filter depends on the combination of prefire vegetation, species attributes, fire properties and properties of the abiotic environment, including weather and climate. In many fire-prone ecosystems, these properties are not independent, with species traits often tightly associated with the historic fire regimes (Keeley, Pausas, Rundel, Bond, & Bradstock, 2011). Postfire shifts in vegetation, relative to prefire vegetation, are thus most prominent when there is a misalignment among fire properties, species attributes and postfire abiotic conditions (Johnstone et al., 2016). Below we examine how changes in fire behaviour (individual or collectively in a fire regime) and climate interact with species attributes to determine the likelihood of a species passing through each demographic filter, and ultimately the likelihood of postfire shifts in vegetation communities. We focus on woody plants, although the same framework could be applied to herbaceous species as well.

2.1 | Adult mortality

The immediate impacts of a fire on vegetation—first-order fire effects—determine the potential for postfire vegetation change: community dynamics after fire depend, in part, on what survives the fire. First-order effects are a function of key fire behaviour metrics and plant species traits or attributes (Figures 1 and 2). The latter can be considered an "information legacy," a type of biological legacy that exists in fire-prone ecosystems (Johnstone et al., 2016). Fire intensity, a physical measure of the rate of energy release per unit distance of fire line (kW/m), dictates the temperature that plants are exposed to, and fire rate of spread (m/s) dictates the duration of this exposure. For a given heat exposure, plant traits that insulate

living cells (e.g., cambium or buds) facilitate survival. For instance, in conifers of western North America, bark thickness largely determines the degree to which cambium is insulated from lethal temperatures and is thus a good predictor of postfire mortality (Hood, McHugh, Ryan, Reinhardt, & Smith, 2007). Thick-barked species like ponderosa pine *Pinus ponderosa*, Douglas-fir *Pseudotsuga menziesii* and western larch *Larix occidentalis* are considered "fire resistant," based on of their ability to survive low- to moderate-intensity surface fires, while thin-barked species like lodgepole pine *Pinus contorta* and spruce *Picea* are considered "fire sensitive" (Baker, 2009). In broad-leaf deciduous trees and shrubs (e.g., *Alnus*, *Betula*), survival of below-ground tissues facilitates resprouting, despite mortality of above-ground biomass. Likewise, graminoids with bunch grass lifeforms (e.g., *Festuca* spp.) and rhizomes (e.g., *Carex* spp., *Calamagrostis* spp.) can also regenerate new shoots after fire (Baker, 2009).

Because the direct impacts of fire on plants vary with fire behaviour, altered fire behaviour is a key mechanism through which fire mediates the impacts of global change. For example, under conditions with greater fuel availability—due to seasonal drought or increased fuel accumulation—fire intensity in any single fire will likely increase. This not only exposes plants to greater rates of energy release, but it also facilitates the transition of surface fire into crown fire, which can significantly increase tree mortality—or fire severity—through crown scorch or consumption. We use the term "fire severity" here to refer to the ecological impacts of a fire, focusing primarily on the impacts of fire on plant survival (Keeley, 2009). Increased crown fire activity, particularly in ecosystems historically characterized by surface fire, is a major mechanism catalyzing postfire vegetation shifts (Johnstone et al., 2016; Savage & Mast, 2005).

Climate change also interacts with plant physiology to alter fire-caused tree mortality, independent of the physical attributes of a fire. Across the western United States, evidence suggests that increased drought stress prior to a fire lowers the likelihood of survival in coniferous trees, independent of fire intensity (van Mantgem et al., 2013). That is, when exposed to a similar intensity and duration of heat from prescribed fires, drought-stressed, thick-barked conifer species (e.g., *Pin. ponderosa*, *Ps. menziesii*, *L. occidentalis*) have lower survival rates than nondrought-stressed trees of the same species, presumably due to reduced xylem conductivity prior to the fire (van Mantgem et al., 2013).

2.2 | Propagule availability

After a fire, population persistence for species killed (above and below-ground) by fire depends on propagule availability. In Western conifers, seed banks that are not consumed during a fire are limited by a loss of viability over time, in addition to seed predation (Farmer, 1996; Johnson & Fryer, 1996), although many common shrub species do have persistent soil seed banks. Therefore, two important mechanisms that determine propagule availability for many conifer species of western North America are seed dispersal by wind and animals, and seed release from aerial seed banks from serotinous cones or canopy seed banks (Larson & Franklin, 2005). For species

with wind-dispersed seeds (i.e., nonserotinous conifer species), the distance to live seed sources is one of the most important factors determining the rate and pattern of conifer regeneration in burned areas. Regeneration generally decreases sharply when live seed sources are greater than 100–400 m from a site (Johnstone, McIntire, Pedersen, King, & Pisaric, 2010; Stevens-Rumann et al., 2018; Tepley, Thompson, Epstein, & Anderson-Teixeira, 2017; Welch, Safford, & Young, 2016). When dispersal distances exceed these distances, typically within large high-severity patches, postfire vegetation is dominated by species with a persistent soil or canopy seed bank (e.g., *Ceanothus* spp., *Arctostaphylos patula*, *Pin. contorta*), effective long-distance dispersal (e.g., *Populus tremuloides*), or resprouting capabilities (e.g., *Quercus* spp., *Ceanothus* spp., *A. patula*) (Barton, 2002; Collins & Roller, 2013; Coop, Parks, McClernan, & Holsinger, 2016; Johnstone, Hollingsworth, et al., 2010; Savage & Mast, 2005; Welch et al., 2016). Animals can also be critical for seed dispersal; for example, Clark's nutcracker facilitates regeneration of whitebark pine *Pinus albicaulis* into large high-severity patches in subalpine forests (Tomback, 1982). Likewise, rodent dispersal promotes *A. patula* persistence despite recurrent fires that may be lethal to seed banks (Moore & Vander Wall, 2015). However, animals can also determine postfire seed availability by preferentially predating seeds in burned relative to unburned areas (Zwolak, Pearson, Ortega, & Crone, 2010).

In western North American conifers, aerial seed banks from serotinous cones are a dominant strategy facilitating postfire recovery, particularly in high-elevation and high-latitude forests (e.g., *Pin. contorta*, *Pinus banksiana*, *Picea mariana*). However, if fire return intervals become shorter than the time to reproductive maturity, even species with serotinous cones may have reduced postfire regeneration (Brown & Johnstone, 2012; Buma et al., 2013). This highlights the important role that age at reproductive maturity, in combination with fire frequency, can play in determining propagule availability.

Propagule dispersal is also influenced by climate variability, through two main mechanisms. First, seed production is linked to interannual climate variation, and second, changes in wind conditions affect dispersal distances for wind-dispersed seeds. Seed production in the dominant conifer species in western North America varies temporally (Buechling, Martin, Canham, Shepperd, & Battaglia, 2016; Greene & Johnson, 2004; Mooney, Linhart, & Snyder, 2011; Sala, Hopping, McIntire, Delzon, & Crone, 2012), with populations experiencing large seed production every 2–15 years (i.e., masting). The timing of mast years relative to fire occurrence is important in determining postfire regeneration density (Larson & Franklin, 2005; Peters, MacDonald, & Dale, 2005). Seed production and masting have been linked to climate signals for many tree species and often depend on the occurrence of specific seasonal conditions (Buechling et al., 2016; Mooney et al., 2011; Moreira, Abdala-Roberts, Linhart, & Mooney, 2015; Roland, Schmidt, & Johnstone, 2014). Current warming trends have been linked to both increased (Buechling et al., 2016) and decreased (Redmond, Forcella, & Barger, 2012) seed production, making it difficult to generalize climate-change impacts. Furthermore, it is unclear if seed production is a bottleneck to

seedling establishment. In contrast, there is an increasing consensus that surface wind speeds are declining in North America (Pryor et al., 2009) and globally (McVicar et al., 2012), which has significant implications for wind-dispersed seeds (Thompson & Katul, 2013). As fire size increases, reduced winds are expected to favour small- relative to large-seeded species as well as species with seed banks or that resprout after fire.

2.3 | Seed germination, seedling establishment, and seedling survival

Once the demographic filter of seed availability is passed, postfire recruitment depends on the remaining filters of seed germination, establishment and survival. We define tree recruitment as the combined results of seed germination, seedling establishment and seedling survival to reproductive age. Recruitment is thus the outcome of multiple interacting factors (Figure 2), the strength of which is context-specific and varies spatially and temporally. Although long-term demographic data spanning all processes are lacking for tree species (but see Conlisk, Castanha, Germino, Veblen, Smith, & Kueppers, 2017), the consensus in the literature is that first year seedling survival is the most important demographic bottleneck for conifer regeneration (Johnson, McCulloh, & Reinhardt, 2011).

Aside from climate effects on seed dormancy break and germination (see below), direct fire effects on germination may be caused by smoke cues or heat shock (Keeley et al., 2011) and by temporary pulses of nutrients after fire (Certini, 2005; Dzwonko, Loster, & Gawronski, 2015; Perkins, 2015b). While certain shrub species in western North American are known to have heat and/or smoke-stimulated germination (Keeley, McGinnis, & Bollens, 2005), conifers in this region are not known to respond to smoke cues. However, lodgepole pine seed germination was enhanced by simulated fire-heating of serotinous cones (Despain, Clark, & Reardon, 1996). Once seeds germinate, one of the most important fire effects on initial seedling establishment is alteration of seedbed quality and the amount of the organic soil layer consumed. To prevent rapid desiccation and death, germinants must send radicles to stable moisture sources to secure water. Relative to porous organic layers, mineral soil is generally more buffered from fluctuations in moisture and temperature (Helgerson, 1990; Johnstone & Chapin, 2006), thus serving as a more reliable water source. In a consistent manner, seed proximity to the mineral soil via reductions of the organic layer enhances establishment across a variety of species and forest types (Gaertner, Lieffers, & Macdonald, 2011; Hesketh, Greene, & Pounden, 2009; Johnstone & Chapin, 2006; Keyes, Maguire, & Tappeiner, 2009). Such an effect, however, may disappear under very dry conditions when a thin organic layer may slow down soil surface evaporation or become irrelevant under very moist conditions that render the organic layer a stable moisture source (Johnstone & Chapin, 2006). Thus, moisture availability and rates of radicle elongation are important in predicting postfire seedling establishment. These rates are species-specific and depend in part on seed size: smaller seeds generally require closer proximity to the mineral soil (Hesketh et al.,

2009) due to lower seed reserves to support initial root development (Lazarus, Castanha, Germino, Kueppers, & Moyes, 2017). Therefore, where organic layer consumption is incomplete, larger-seeded conifers generally exhibit higher postfire recruitment than smaller-seeded broadleaved species (Brown, Liu, Yan, & Johnstone, 2015; Johnstone & Chapin, 2006; Johnstone & Kasischke, 2005). Among conifers, black spruce *Pic. mariana* develops shorter radicles than Engelmann *Picea engelmannii* and white spruce *Picea glauca*, while pine species tend to have slightly longer radicles (Hesketh et al., 2009). In boreal conifers, longer radicles in jack pine *Pin. banksiana* relative to black spruce (Thomas & Wein, 1985) may help to explain the unexpected pattern of prolific jack pine recruitment after low-severity fires (with only partial consumption of the organic layer) in black spruce-dominated stands (Boiffin & Munson, 2013). Other fire-induced changes to the soil that can affect early establishment include potential toxic effects of ash leachates in severely burned soils (Herr & Duchesne, 1995; Thomas & Wein, 1990, 1994) and hydrophobicity of ash layers at the soil surface (Certini, 2005; Huffman, MacDonald, & Stednick, 2001).

Alteration of nutrient availability and below-ground interactions as a result of fire may also influence seedling establishment. For instance, pulses of nutrients shortly after low-severity fire are common (Certini, 2005) and have been correlated with abundant postfire recruitment (Dzwonko et al., 2015). Similar to that, higher whitebark pine germination and growth in prescribed burned relative to unburned plots has been attributed to improved phosphorous availability (Perkins, 2015b). In other cases, however, nutrient availability had minor (Lilles, Purdy, Macdonald, & Chang, 2012) or no effect (Romme, Tinker, Stakes, & Turner, 2009) on seedling establishment and/or growth. Postfire effects on below-ground processes could also be mediated via positive effects of charcoal on microbial activity (DeLuca, MacKenzie, Gundale, & Holben, 2006). In contrast to conifers, it appears that soil chemistry has greater effects on the establishment and growth of deciduous species (Calder, Horn, & St Clair, 2011). Such an effect could have important consequences if climate–fire–vegetation interactions alter soil chemistry.

The rapid development of postfire vegetation due to resprouting can also influence conifer seedling growth and survival. Effects of light availability on young (1–3 years old) seedling establishment are mixed and may not necessarily relate to shade tolerance of adults. On the one hand, low light can limit carbon assimilation and growth (Weber, Gilbert, Kimmins, & Prescott, 2003; York, Battles, Eschtruth, & Schurr, 2011), but excessive light can damage the photosynthetic apparatus and increase mortality (Johnson et al., 2011). In a consistent manner, studies have shown positive effects of artificial shade or neighbouring vegetation on early conifer seedling survival (Baumeister & Callaway, 2006; Haugo, Bakker, & Halpern, 2013; Keyes et al., 2009; Perkins, 2015a), although dense shrubs after high-severity fire can be associated with reduced conifer regeneration or growth (Crotteau, Varner, & Ritchie, 2013; Tepley et al., 2017). Grass and herb cover, however, more consistently decrease conifer seedling survival (Harmon & Franklin, 1989; Perkins, 2015a; Redmond, Cobb, Clifford, & Barger, 2015), likely due to the combination of reduced light and more efficient competition for below-ground resources by the fibrous roots of grasses in surface layers. Similar to nutrients, faster-growing deciduous species tend to respond more positively to light availability than conifers (Calder et al., 2011). Through the above mechanisms, changes in fire frequency or intensity will alter postfire site conditions, with cascading impacts on establishment success and species composition (Crawford, Wahren, Kyle, & Moir, 2001; Crotteau et al., 2013).

In addition to competition, biotic interactions involving mutualisms or herbivory can alter postfire recruitment. Early seedling establishment is facilitated by mycorrhizae (Baar, Horton, Kretzer, & Bruns, 1999; Horton, Bruns, & Parker, 1999; Nuñez, Horton, & Simberloff, 2009). Fire alters the species composition of ectomycorrhizae, although how fire affects mycorrhizal species richness and diversity, and the resultant impacts on recruitment remain unclear (Taudière, Richard, & Carcaillet, 2017). Herbivory following fire can be high enough to limit regeneration (Bartos, Brown, & Booth, 1994) and has the potential to alter postfire vegetation trajectories (Mills, 1983). In some cases, herbivory rates can vary with fire intensity (Moreno & Oechel, 1991), however, this has not been universally found.

By altering local weather conditions, climate change could affect all stages in initial seedling establishment, given high sensitivity to temperature and, particularly, moisture. Dormancy break, a physiological process independent of germination, is triggered by a number of genetically determined environmental cues and depends on temperature regimes (Walck, Hidayati, Dixon, Thompson, & Poschlod, 2011). While warming generally enhances germination in alpine plants (see Hoyle et al., 2013), high maximum temperatures can reduce germination in some conifer species (Kaufmann & Eckard, 1977; Petrie, Wildeman, Bradford, Hubbard, & Lauenroth, 2016). Importantly, whether and how climate warming may modify the timing of germination relative to the timing of environmental factors conducive to seedling emergence and establishment is unknown.

Temperature can also limit recruitment after successful germination. Young seedlings are susceptible to stress or death from excessive soil surface temperatures via girdling and vascular impairment (Helgerson, 1990; Kolb & Robberecht, 1996), an effect that varies by species (Daubenmire, 1943; Petrie et al., 2016). In addition, experiments in subalpine (Conlisk, Castanha, Germino, Veblen, Smith, Moyes, et al., 2017; Kueppers et al., 2017) and montane forests (Rother, Veblen, & Furman, 2015) have shown negative effects of warming on seedling survival and growth, even with supplemental moisture.

There is consensus that drought is one of the most limiting factors for conifer recruitment after fire (Barton, 1993; Savage, Brown, & Feddema, 1996; Shinneman & Baker, 2009; Stevens-Rumann et al., 2018; Tepley et al., 2017). Drought can also limit postfire recruitment of shrubs establishing from seed, such as *Artemisia tridentata* (Nelson, Weisberg, & Kitchen, 2014). It is likely that the strongest bottleneck occurs during the very early stages of germination, in the first few weeks after emergence, when securing a reliable water source is critical (Moser, Walthert, Metslaid, Wasem, & Wohlgemuth,

2017). Despite the importance of the delivery of water from roots to above-ground tissues, we know very little about hydraulic traits or drought tolerance strategies of young seedlings, and how these vary by species (Johnson et al., 2011). Seedlings <10 weeks old maximize water supply to growing tissues (consistent with the critical role of moisture for establishment), but at the cost of greater risk of hydraulic failure at the onset of drought (Miller & Johnson, 2017). Therefore, seedlings with greater access to moisture tend to have higher survival rates (Balducci et al., 2015; Rother et al., 2015). As climate change reduces moisture availability, seedlings that rely on newly established root systems may be at a disadvantage following fire compared to species that resprout and can take advantage of existing root systems. However, even resprouting shrubs can experience high mortality if intense drought occurs in the year following fire (Pratt et al., 2014).

3 | DEMOGRAPHIC FILTERS EXPLAIN RECENT CHANGES AND HIGHLIGHT FEEDBACK MECHANISMS

We use two case studies to explore in detail how fire, climate and fire vegetation feedbacks affect the ability of the dominant prefire conifer species to pass through key demographic filters (Figure 2): high-latitude boreal forests of western North America, and ponderosa pine forests in the south-western United States. These systems have contrasting fire regimes and land-use and management histories, but are both subject to climate-induced changes in fire activity and vulnerable to fire-catalyzed vegetation shifts. Our framework, however, can be applied to other case studies to understand fire-mediated vegetation changes across forest ecosystems (Table 1).

3.1 | Increased fire frequency and severity in boreal forests

In the boreal forests of western North America, recent observations suggest key mechanisms that may explain postfire vegetation shifts from white or black spruce to aspen (*Po. tremuloides*) and other deciduous species (Johnstone, Hollingsworth, et al., 2010; Johnstone, McIntire, et al., 2010). Boreal fire regimes in western North America are characterized by infrequent crown fires (i.e., return intervals >80 years) that lead to widespread above-ground mortality of the dominant, thin-barked tree species (*Pic. mariana*, *Pic. glauca*, *Po. tremuloides*, *Betula* spp.). What varies most among and within fires is the amount of surface organic matter consumed, rather than the amount of tree mortality; thus, unlike temperate coniferous forests, "fire severity" in these systems is defined mainly by organic matter consumption (Dyrness & Norum, 1983; Miyanishi & Johnson, 2002).

The dominant species in these systems differ in key species attributes such as seed size, serotiny, seedling climatic tolerances and resprouting ability, which affect their likelihood of passing through each demographic filter. Different species attributes allow spruce

and aspen to persist on the landscape via different mechanisms. While both species of spruce tend to experience high adult mortality from fire, aspen and other deciduous species can resprout from top-killed stems, allowing them to successfully pass through the adult mortality filter. Despite high adult mortality in black spruce, this species' semi-serotinous cones are an effective postfire dispersal mechanism (Viereck, 1983) that allow it to pass through the propagule availability filter and persist in fire-prone landscapes. Aspen propagules also tend to be available postfire because aspen's small seed size and seed appendages make it particularly effective at long-distance dispersal (Perala, 1990). White spruce does not have serotinous cones or the ability to resprout, and thus it depends mostly on dispersal from living trees for postfire recruitment, making it less effective at colonizing the interior of large burned areas (but see Michaletz, Johnson, Mell, & Greene, 2013).

Given sufficient propagule availability for both spruce and deciduous species, demographic filters affecting seed germination and seedling establishment become critical in determining the postfire dominance of spruce vs. deciduous species. Seedbed quality in boreal forests is directly related to the depth of the soil organic layer. Spruce and aspen both have higher germination rates in areas with less organic matter (Charron & Greene, 2002; Zasada, Norum, Vanveldhuizen, & Teutsch, 1983). However, sites with lower consumption of the organic layer by fire (i.e., lower fire severity) favour spruce over aspen; this pattern likely arises because the larger seeds of spruce provide energy reserves to support larger germinants and longer radicles that are more likely to access moisture in mineral soil beneath the organic layer (Greene et al., 2007; Johnstone & Chapin, 2006; Johnstone & Kasischke, 2005). Furthermore, black spruce recruitment on sites with high organic matter consumption (i.e., high fire severity) is negatively correlated with aspen recruitment, suggesting that aspen out-competes spruce seedlings or that aspen litter creates an unsuitable seedbed for black spruce (Johnstone & Kasischke, 2005). Therefore, after fires that burn with a high enough intensity or duration to reduce or remove the deep soil organic layer, stands are expected to be dominated by aspen, while those that leave a deeper soil organic layer are expected to be dominated by black or white spruce (Johnstone, Chapin, et al., 2010; Johnstone, Hollingsworth, et al., 2010), assuming the propagule availability filter is met.

Differences in the climatic tolerance of seedlings from different species further determine their ability to pass through the recruitment filter. For example, spruce seedlings are sensitive to moisture stress, especially in combination with warmer temperatures (Balducci et al., 2015; Hogg & Schwarz, 1997), whereas aspen seedlings are sensitive to low soil temperatures (Landhausser & Lieffers, 1998). Therefore, postfire recruitment of black and white spruce tends to be higher on moister sites, while aspen dominates on warmer sites (Johnstone, Hollingsworth, et al., 2010; Johnstone, McIntire, et al., 2010). Where aspen dominates, plant traits conducive to greater photosynthetic rates such as higher leaf specific area (Wright et al., 2004) may further enhance competitive ability. After recent fires, warmer sites that were dominated by white spruce prior to fire were colonized more strongly by aspen than white spruce, potentially due

TABLE 1 Additional case studies highlighting outcomes of individual or multiple fire events, and potential feedbacks between postfire vegetation change and the likelihood or behaviour of future fires

Ecosystem	Fire properties	Demographic filters	Outcome	Feedbacks	Refs.
California mixed conifer	Increased size and extent of high-severity patches after periods of fire suppression	*Adult mortality*: more shade-tolerant species on landscape due to fire suppression; thick-barked species killed in crown fires; resprouting shrubs top-killed but survived *Propagule availability*: conifers limited to dispersal from live trees; some shrubs have soil seed banks *Recruitment*: high-severity patches dominated by shade-tolerant seedlings at edges, and shrubs	Increased shrub dominance in large high-severity patches; increased dominance of shade-tolerant species	High-severity patches more likely to burn at high severity in next fire	1, 2, 4, 6, 9
Montana mixed conifer	Two short-interval fires after long fire-free period	*Adult mortality*: thin-barked PICO killed; largest thick-barked PIPO survived both fires *Propagule availability*: serotiny allows PICO to dominate after first fire, but juveniles killed by second fire before reproductive maturity *Recruitment*: PICO juveniles from first postfire pulse did not survive second fire	More open forest with large remnant PIPO and reduced PICO in understory	Future fires likely to burn at lower severity due to altered stand structure	3
Greater Yellowstone Ecosystem montane Douglas-fir	Large area burned with moderate and high severity	*Adult mortality*: despite thick bark, PSME died in areas with high-intensity fire *Propagule availability*: PSME depends on dispersal from live trees, higher seedling density near seed source *Recruitment*: in dry sites more seed required to get established seedlings; in moist sites seedlings established even at long distances from a seed source; suggests dry conditions limited recruitment	Regenerating PSME forest in moist sites, conversion to grass/sage steppe in dry sites	Future fire severity may be reduced for up to 20 years; if burned again before PSME matures, may see different postfire outcomes	5, 7, 8

Notes. Refs., references; PICO, *Pinus contorta*; PIPO, *Pinus ponderosa*; PSME, *Pseudotsuga menziesii*.
1. Miller, Safford, Crimmins, and Thode (2009); 2. Collins and Roller (2013); 3. Larson et al. (2013); 4. Dolanc, Safford, Dobrowski, and Thorne (2014); 5. Parks et al. (2014); 6. Coppoletta, Merriam, and Collins (2016); 7. Donato et al. (2016); 8. Stevens-Rumann and Morgan (2016); 9. Welch et al. (2016).

to increasing drought stress with warming temperatures (Johnstone, McIntire, et al., 2010).

Ongoing warming and increased fire frequency across North American boreal forests are expected for the remainder of the 21st century (Kasischke & Turetsky, 2006). Predicted climate warming will increase the climate suitability for fire (Balshi et al., 2009; Stralberg et al., 2018; Young et al., 2017), likely leading to more frequent fire, with higher burn severity. Both trends would favour deciduous aspen over coniferous spruce after fire, mainly through demographic filters that depend on reproductive traits. Shorter fire return intervals would limit the ability of black spruce to reach reproductive maturity and develop seed banks, resulting in reduced black spruce regeneration (Brown & Johnstone, 2012), and thinner organic layers from higher fire severity would favour aspen regeneration from seed. While this may result in stand-level shifts from conifer to deciduous dominance, increased dominance of deciduous species at landscape scales could reduce overall landscape flammability and create a stabilizing feedback (Higuera, Brubaker, Anderson, Hu, & Brown, 2009; Johnstone, Chapin, et al., 2010; Kelly

et al., 2013; Stralberg et al., 2018). Palaeoecological records suggest that such negative feedbacks between fire and postfire vegetation change may have operated during the Medieval Climate Anomaly (*c.* 950–1450 CE), when warming temperatures (relative to prior) led to increased fire severity and increased deciduous dominance, but fire frequencies remained relatively stable (Kelly et al., 2013). Past and ongoing changes in the boreal forest thus highlight how fire properties (e.g., size, intensity, duration) interact with species traits (e.g., bark thickness, resprouting capacity, seed size, temperature and drought tolerances) to set up feedbacks between fire activity and postfire vegetation change.

3.2 | Climate and land-use change in *Pinus ponderosa* forests of the south-western United States

Low-elevation ponderosa pine forests in the south-western United States highlight the combined impacts of climate change and altered vegetation due to land use and land management, as well as the potential for fire to catalyze state changes from forest to
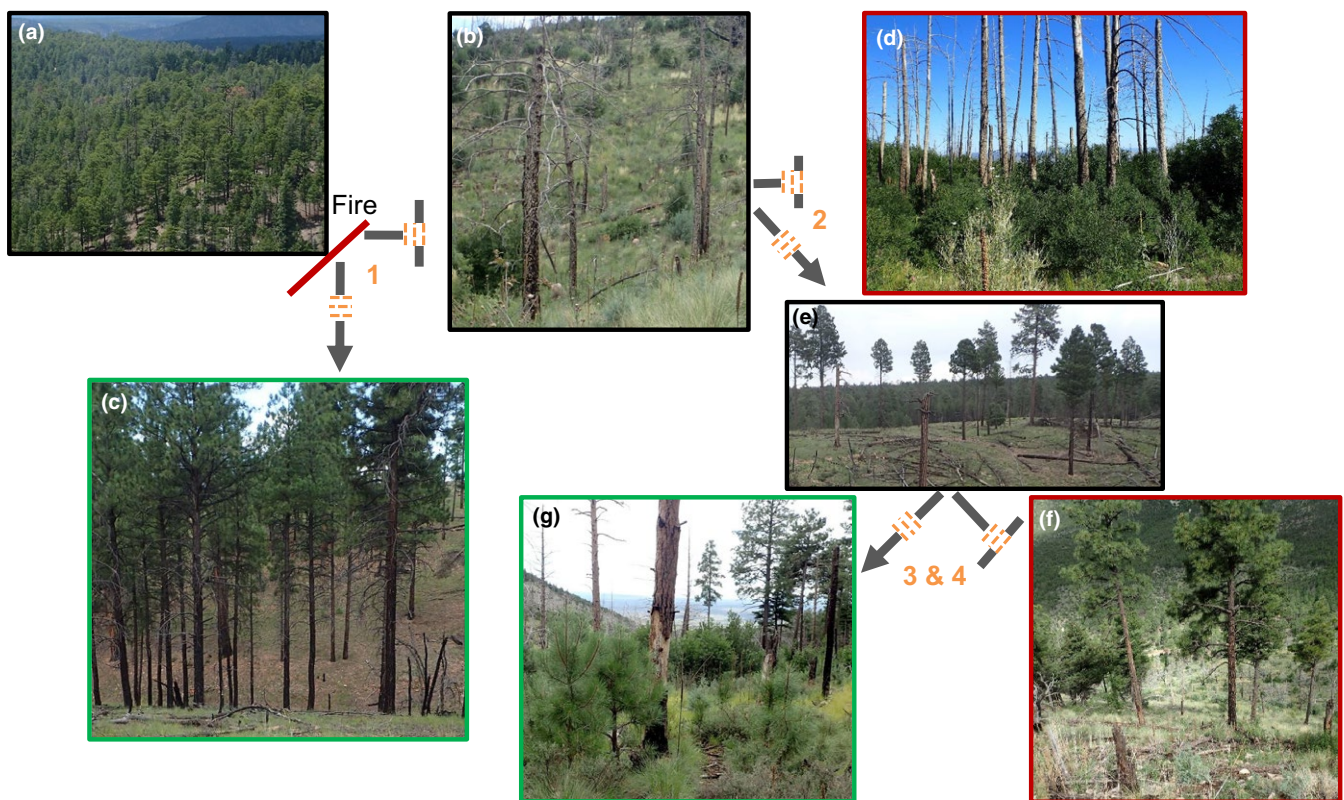
FIGURE 3 Diagram of potential outcomes following fire in south-western U.S. *Pinus ponderosa* (ponderosa pine) forests. At each stage, ponderosa pine either passes through (arrows) the demographic filter (dashed orange lines) or does not pass through (perpendicular lines) the demographic filter, resulting in different trajectories. Numbers correspond to the numbered filters in Figure 2. Photographs of outcomes are outlined in green if a vegetation shift is unlikely (c, g) and red if a shift from forest to nonforest is likely (d, f). Stages shown include a mature ponderosa pine forest (a); a ponderosa pine stand that did not pass through the adult mortality filter (high-severity fire; b); and a ponderosa pine stand that did pass through the adult mortality filter (low-severity fire; c). After failing to pass through the adult mortality filter, ponderosa pine stands can also fail to pass through the propagule availability filter resulting in resprouter dominance (d), or they can pass through the propagule availability filter (e). At last, stands with available propagules can either fail to pass through the seedling establishment filter due to climate or other factors (f), or they can pass through the seedling establishment filter and have some level of pine recruitment (g) Photographs: K. Davis

nonforested ecosystems (Figure 3; Coop et al., 2016; Roccaforte, Fulé, Chancellor, & Laughlin, 2012; Savage & Mast, 2005; Walker, Coop, Parks, & Trader, 2018). Prior to European settlement, south-western ponderosa pine forests experienced low-severity fires with average return intervals *c.* 5–40 years (Allen et al., 2002; Fulé, Covington, & Moore, 1997). Due to land use (e.g., grazing) and fire suppression since the early 20th century, fuel loading and fire hazard across many low-elevation forests have increased. As a result of changes in fuels, in combination with climate warming, recent fires have more easily transitioned from surface to crown fires, with important consequences for postfire vegetation trajectories (Allen et al., 2002; Holden, Morgan, Crimmins, Steinhorst, & Smith, 2007). The demographic filter framework highlights the likelihood of shifts from forest to nonforest states and elucidates the mechanisms responsible for postfire vegetation changes in this system.

Key species traits that determine which species pass through each demographic filter in these forests include bark thickness, regeneration strategies such as seed banks, resprouting and off-site seed dispersal, and drought tolerance. Adult tree mortality depends on the intensity of surface fires, and/or if surface fires transition to crown fires. Ponderosa pine has thick bark that allows mature individuals to survive low-intensity surface fires, but mortality is high following crown fires (Figure 3b; Baker, 2009). Other dominant tree and shrub species in this system, such as *Quercus* spp., *Juniperus deppeana* and *Robinia neomexicana*, may experience mortality of above-ground biomass in high-intensity fires, but below-ground organs survive and permit resprouting (Foxx, Hansen, Oertel, Haffey, & Beeley, 2013; Johnson, Mukhtar, Mapston, & Humphrey, 1962), even after repeated burns (Coop et al., 2016).

The likelihood of passing through the propagule availability filter is also affected by species traits. For example, some shrub species (e.g., *Ceanothus* spp.) have seeds that remain in the soil seed bank and whose germination is stimulated by fire (Foxx et al., 2013), whereas ponderosa pine is entirely dependent on seed dispersal from remnant trees (Baker, 2009). Ponderosa pine seed availability may be further limited temporally to masting years (Mooney et al., 2011) or reduced by high rodent seed predation in burned areas (Zwolak et al., 2010). Thus, many shrub species have traits, such as the ability to resprout or soil seed banks, that allow them to easily pass through the adult mortality and/or propagule availability filters, while crown fires and propagule limitation may restrict ponderosa pine's ability to pass through these same filters. Therefore, we would expect to find abundant pine regeneration only near the edges of high-severity patches, whereas shrubs should be abundant within high-severity patches (Figure 3d), a pattern which has been observed after crown fires across the south-west (Coop et al., 2016; Crawford et al., 2001; Haire & McGarigal, 2008; Roccaforte et al., 2012; Shive, Sieg, & Fulé, 2013).

The demographic filter of seedling survival may further favour resprouting species over conifers (Figure 3f), because the developed root systems of resprouting species allow better access to soil nutrients and water, relative to the shorter roots of conifer seedlings. Ponderosa pine seedling growth and survival are limited by competition with grass (Larson & Schubert, 1969) which can exacerbate moisture stress (Pinto, Marshall, Dumroese, Davis, & Cobos, 2012). Ponderosa pine seedling emergence and survival also decline with increasing temperatures (Petrie et al., 2016; Rother et al., 2015), and dendrochronological studies show that recruitment occurs primarily during years with above-average precipitation (League & Veblen, 2006; Savage et al., 1996). Given this combination of species traits, resprouting plants recover more rapidly following high-severity fire than ponderosa pine. Some species such as *Quercus gambelii* and *R. neomexicana* can resprout within days of the fire (Foxx et al., 2013) and reach prefire levels of cover within 2–3 years (Coop et al., 2016). In contrast, 16 years after the La Mesa Fire in New Mexico, cover of naturally regenerating ponderosa pine in plots adjacent to a live seed source was less than one per cent (Foxx et al., 2013). Even where ponderosa pine seedlings were planted postfire, the average seedling survival 5–8 years after planting was only 25% (Ouzts, Kolb, Huffman, & Meador, 2015), highlighting the potential climate limitations to ponderosa pine recruitment. Thus, fire-mediated impacts of climate warming in the south-west United States highlight the interaction between altered fire behaviour (e.g., crown fires) and an increased frequency of postfire drought that leads to shifts from forest to shrub- or grass-dominated systems (Feddema et al., 2013; Seager & Vecchi, 2010).

As in the boreal forest case study, postfire vegetation change impacts the likelihood and behaviour of future fires, but these dynamics in south-western ponderosa pine forests create positive feedbacks with increased fire activity. Specifically, areas that burn at high severity are more likely to burn at high severity in subsequent fires, due to high fuel loadings from crown scorch and tree mortality in the initial fire or conversion to shrub-dominated systems (Holden, Morgan, & Hudak, 2010; Parks, Miller, Nelson, & Holden, 2014). Thus, given trends of increasing fire activity (Westerling, 2016; Westerling et al., 2006), many areas will likely experience multiple high-severity fires in the upcoming decades, which may reinforce vegetation shifts away from forests (Coop et al., 2016). In contrast, in areas that remain unburned for extended periods, it is possible that tree recruitment will eventually expand towards the centre of high-severity patches from their edges (Haire & McGarigal, 2008). However, this process can be slow and depend on local factors such as topography. For example, after a crown fire in 1867 in montane forests of southern Arizona, ponderosa pine stands on southerly aspects converted to oak-shrub fields that still persist today, while northerly aspects regenerated with pine (Iniguez, Swetnam, & Baisan, 2009). Areas that previously burned at lower severities will likely be more resistant to future burns due to reduced fuel loads (Parks et al., 2015; Walker et al., 2018) and may have higher ponderosa pine survival and recruitment postfire due to the presence of seed sources (Foxx et al., 2013; Shive et al., 2013). However, successful recruitment will still depend on climate conditions favourable for tree growth and survival.

4 | FIRE VEGETATION FEEDBACKS, FUTURE EXPECTATIONS AND KEY UNKNOWNS

Given expected climate warming and subsequent increases in area burned, and potentially more high-severity fires, the demographic framework suggests key "winners" and "losers" under future conditions. We expect that species with the ability to resprout, maintain soil or canopy seed banks, or small-seeded species with highly effective long-distance dispersal mechanisms will increase in relative abundance in areas with large, high-severity burned patches. The boreal forest and the south-west ponderosa pine forest case studies suggest that plants with these traits are more abundant following recent large, high-severity fires. Similar patterns have been found in mixed-conifer forests throughout western North America (Cocking, Varner, & Knapp, 2014; Collins & Roller, 2013; Kemp, Higuera, & Morgan, 2016; Welch et al., 2016).

With expected increased fire frequency (Littell et al., 2010; Parks, Holsinger, Miller, & Parisien, 2017; Westerling et al., 2006; Young et al., 2017), we also expect changes in vegetation composition away from species that have long life cycles towards species that are able to reproduce at young ages (e.g., *Pinus attenuata*) or withstand more frequent fires (e.g., grasses, resprouting shrubs and oaks), particularly in areas that experience repeated high-severity fire over decades ("repeat burns"). Recent studies of repeat burns support this expectation, from Canada to New Mexico (Brown & Johnstone, 2012; Coop et al., 2016; Prichard, Stevens-Rumann, & Hessburg, 2017). The severity of the fires in repeat burns can greatly influence postfire vegetation trajectories, with two high-severity fires in close succession resulting in limited conifer regeneration (Stevens-Rumann & Morgan, 2016). In contrast, in dry mixed-conifer forests with high tree densities, repeat low-intensity fires may result in lower tree densities and species composition dominated by more fire-resistant conifers (Larson, Belote, Cansler, Parks, & Dietz, 2013; Stevens-Rumann & Morgan, 2016). The key mechanism leading to these alternative outcomes is the rate and intensity of burning, relative to the time it takes a species to reach reproductive maturity; this ratio between fire return intervals and regeneration time is thus a critical determinant of future vegetation trajectories (Enright et al., 2015).

Changes in climate will also influence future postfire vegetation dynamics. We expect resprouting species that have access to deeper soil water or tree species with drought-tolerant seedlings to increase in relative abundance following future fires. Fires can catalyze climatically driven shifts in vegetation by killing adult trees that generally have broader climatic tolerances than juveniles of the same species (Dobrowski et al., 2015). Thus, although climatic conditions on a site may have supported a given species composition prior to a fire, the higher climatic sensitivity of seedlings can lead to a shift in species composition following fire (Crausbay et al., 2017; Johnstone, McIntire, et al., 2010). Although our knowledge of species-specific seedling drought tolerance is limited, particularly in young seedlings, our case studies highlight that inter-species differences in the climatic tolerance of seedlings can determine which species pass through the seedling establishment filter, thus determining future vegetation trajectories. As conditions become warmer and drier, the relative importance of this filter in determining postfire outcomes will likely increase.

Despite these predictions, there are a number of important uncertainties in how climate change will directly and indirectly impact postfire regeneration. For example, while an abundance of current studies has examined postfire regeneration in the years to decades following recent fires (Roccaforte et al., 2012; Stevens-Rumann et al., 2018; Welch et al., 2016), the persistence of these postfire vegetation patterns over multiple decades is yet to be determined (Gill, Jarvis, Veblen, Pickett, & Kulakowski, 2017). Recent observations are consistent with at least two long-term outcomes, each with different implications. We may be witnessing changes in the rates of postfire vegetation change, due in part to changing fire regimes and climate. Provided prefire species are not locally extirpated, recent observations are consistent with prolonged early successional states that may eventually return to similar forest composition, provided a sufficient fire-free period. Alternatively, if lower postfire recruitment persists, then we may truly be witnessing the start of vegetation state changes (Stevens-Rumann et al., 2018). These new vegetation states dominated by resprouting species like oaks, shrubs and grasses may actually be more resilient to the predicted heightened fire activity (Coop et al., 2016) and warmer temperatures (McIntyre et al., 2015). The ratio of fire return intervals to recovery time will strongly determine whether the observed vegetation changes will be transient or persist. For example, some systems experience prolonged postfire establishment (Tepley, Swanson, & Spies, 2014), while in others, most establishment occurs within 3–15 years of the fire (Donato et al., 2016; Turner, Romme, Gardner, & Hargrove, 1997). Systems with prolonged establishment periods have more opportunities for years with favourable climate conditions to facilitate establishment. However, in species that generally establish immediately following fire (e.g., *Pin. contorta*), the increasing temperatures and the increasing rarity of wet years will increase the likelihood of postfire regeneration failures (Conlisk, Castanha, Germino, Veblen, Smith, Moyes, et al., 2017). Changes in disturbance interval will affect the persistence of vegetation shifts because increased fire frequency may result in repeated fires before establishing trees have reached reproductive maturity or a size large enough to survive the next fire (Buma et al., 2013; Larson et al., 2013; Odion, Moritz, & DellaSala, 2010).

Important uncertainties also remain regarding how climate and fire affect key demographic stages in different species. There is a large body of literature describing patterns of postfire regeneration, and many highlight the environmental conditions that correlate with recruitment. Several studies have also undertaken experimental seed planting after fires, tracking survival with environmental conditions. However, studies that attempt to elucidate the specific mechanisms at different demographic stages that underlie patterns of recruitment, the relative strength of these mechanisms, and their combined effects are surprisingly

rare for western North America (for similar work in Australia see: Nield, Enright, & Ladd, 2016; Nield, Monaco, Birnbaum, & Enright, 2015). It is unfortunate that, of the mechanistic studies that do exist, many are decoupled from the context-specific environments that occur after fire. We suggest that a more mechanistic understanding of the factors that allow species to pass through each demographic filter will provide insight into potential responses to fire and global change, including warming and changes in precipitation regimes. To address this gap, future studies could monitor individual plants over time to identify the timing and causes of mortality (Harper, 1967) or take a more experimental approach to disentangle the relative effects of dispersal limitation, seed predation, seedling predation and microclimate on postfire vegetation trajectories (Brown et al., 2015). More information is also needed on how changes in climate and CO_2 may alter plant reproduction, seed size and seed quality, which could have implications for postfire regeneration. Likewise, fire- and climate-driven changes in vegetation will most likely influence higher trophic levels, with impacts on herbivory, seed predation and dispersal, all of which can feedback on vegetation responses (Belsky & Blumenthal, 1997).

At last, mechanisms acting on plants at different demographic stages and temporal and spatial scales may interact in complex and nonintuitive ways (Ettinger & HilleRisLambers, 2013). More experimental, observational and modelling work that integrates multiple plant stressors at each demographic stage is necessary to better understand these interactions and the potential implications. In addition, although a demographic framework addresses potential local-scale changes in vegetation, feedbacks at larger spatial or temporal scales may result in the inability to scale predictions up to landscape and regional spatial scales, and decadal or centennial temporal scales. Therefore, it is important that the role of feedbacks and scale be considered when predicting future vegetation changes.

Despite these uncertainties, we provide examples of how the postfire demographic framework explains postfire vegetation development using two distinctly different case studies; the outcome in either case study would have been difficult to predict without consideration of demographic filters. Such predictive ability highlights the value of this framework as a unifying tool. Focusing on the mechanisms operating at different demographic stages that lead to fire-mediated vegetation shifts (e.g., dispersal limitation, failure to meet germination requirements, drought-induced seedling mortality) increases our ability to anticipate and model climate- and fire-driven shifts across distinct ecosystems. This approach is an improvement over a posteriori interpretations of fire-related vegetation shifts based on correlative analyses. It also highlights important knowledge gaps, such as the paucity of mechanistic studies, which are critical for predicting into the future. Applying the demographic framework to anticipate the future of conifer forests in western North America, we expect the combination of increased fire frequency and/or severity with increasing moisture stress to lead to shifts from long-lived conifers

to species that resprout, maintain canopy or soil seed banks, are capable of long-distance seed dispersal, and/or reach reproductive maturity at a young age.

AUTHORS' CONTRIBUTIONS

All authors contributed equally to the development of the framework and researching and writing the manuscript.

DATA ACCESSIBILITY

This article does not contain data.

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