Wildfire-Driven Forest Conversion in Western North American Landscapes

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Changing disturbance regimes and climate can overcome forest ecosystem resilience. Following high-severity fire, forest recovery may be compromised by lack of tree seed sources, warmer and drier postfire climate, or short-interval reburning. A potential outcome of the loss of resilience is the conversion of the prefire forest to a different forest type or nonforest vegetation. Conversion implies major, extensive, and enduring changes in dominant species, life forms, or functions, with impacts on ecosystem services. In the present article, we synthesize a growing body of evidence of fire-driven conversion and our understanding of its causes across western North America. We assess our capacity to predict conversion and highlight important uncertainties. Increasing forest vulnerability to changing fire activity and climate compels shifts in management approaches, and we propose key themes for applied research coproduced by scientists and managers to support decision-making in an era when the prefire forest may not return.

Keywords: climate change, ecological transformation, high-severity fire, tree regeneration, tree seedlings, stand-replacing fire, wildfire, vegetation type conversion.

When a forest burns in a wildfire, should we expect it to return as it was before? If the fire burns at low severity—such as a surface fire that does little damage to large, thick-barked trees—the forest character may remain essentially unchanged. However, following a high-severity fire that kills most trees, the near-term postfire environment may include some combination of dead snags, nonforest vegetation (e.g., grasses, resprouting shrubs) or tree seedlings. Given similar climate and disturbance regimes, well-understood successional processes are expected to lead, over time, to the recovery of prefire forest composition and structure. But under changing disturbance regimes and climate, can we still count on the return of the forest as it was before fire?

Across western North America—as in many other locations—the last several decades have been marked by increasing forest fire activity (figure 1; Westerling 2016, Hanes et al. 2018). These changes are coupled with the direct effects of rising temperature and evaporative demand (figure 1) on postfire vegetation dynamics. Western North American forests have long been shaped by wildfire (box 1), and most tree species exhibit fire-adaptive traits (Rowe and Scotter 1973, Baker 2009, Pausas and Keeley 2014). These include survival mechanisms that confer individual-level resistance to fire-caused mortality, and population-level mechanisms that promote postfire regeneration; collectively, these processes confer ecological *resilience*—the capacity to absorb disturbance and recover toward prior composition, structure, and function (Gunderson 2000, Reyer et al. 2015, Ghazoul et al. 2015, Falk et al. 2019). However, specific traits are adaptive only within particular fire regimes, and altered fire regimes can render formerly well-adapted species vulnerable (Keeley et al. 1999, Brown and Johnstone 2012). Fire size, frequency, or intensity outside the ranges to which dominant species are adapted can overcome both resistance and recovery mechanisms of forest ecosystems (Johnstone et al. 2016). Climate warming is also creating local postfire environmental conditions outside of the regeneration niche of dominant tree species (Stevens-Rumann et al. 2018, Davis et al. 2019a). As such, heightened vulnerability

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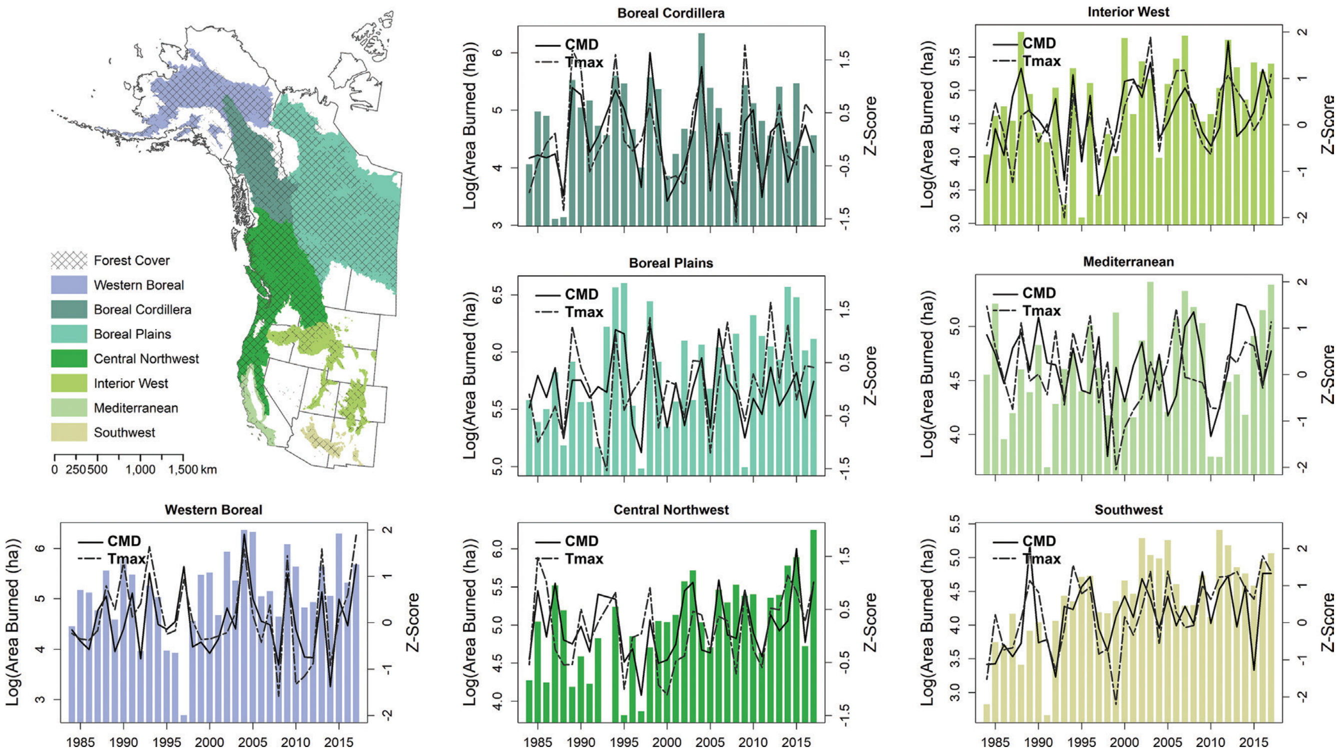

Figure 1. Trends in annual log-scale area burned and mean annual Z-scores of climatic moisture deficit (CMD), and mean July temperature (Tmax) in forested western North America (1984–2017). Z-scores are based on a 1981–2010 reference period. The annual area burned and the number of fires have significantly increased in all regions except the Mediterranean and Western Boreal. The burn area data are from the Monitoring Trends in Burn Severity for American fires and Canadian National Fire Database for Canadian fires (with a threshold at the same minimum fire size of at least 400 hectares), the forested area is derived from 2001 and 2018 MODIS Land Cover product, the climate data are from TerraClimate, and the ecoregions are adapted from the Commission for Environmental Cooperation North American Terrestrial Ecoregions.

to the combined impacts of changing fire regimes and climate raises concerns that, for some forest types, resilience to fire may be increasingly compromised (for a review, see Johnstone et al. 2016, Davis et al. 2018, Falk et al. 2019, Hessburg et al. 2019).

A direct outcome of declining forest resilience to fire is an increase in the proportion of a burned landscape with postfire vegetation that diverges considerably from its prefire state. Where altered postfire vegetation is spatially extensive and temporally enduring (i.e., longer than the known historical postfire recovery time), such changes may be referred to as *conversion*. This terminology (e.g., forest conversion, site conversion, and type conversion), although lacking a formal definition, is increasingly used by natural resource managers and researchers alike. Conversion implies major, extensive, and enduring changes in dominant species, life forms, or functions (e.g., shifts from one forest type to another, or from a forest to nonforest vegetation). Conversion may be considered inclusive of a suite of other terms used to portray major and abrupt changes to ecological systems, including reorganization (Falk 2017), regime shift (Anderson et al. 2009), state shift (Barnosky et al. 2012), state transition (Stringham et al. 2003), critical transition (Scheffer et al. 2009), and transformation (Folke et al. 2010).

In the present article, our focus is *fire-driven forest conversion*, which can be viewed as a two-step process. First, major vegetation shifts are initiated by high-severity fire that removes large areas of mature forest from the landscape. Second, recovery mechanisms are inhibited by the absence of seed sources, short-interval reburning, or postfire climate and other environmental conditions unfavorable to seedling recruitment. Return of the prefire forest is protracted or prevented, and fire-initiated changes persist, although subject to the influences of subsequent fire–vegetation feedbacks. The direction of conversion is dependent on the specific factors that lead to loss of system resilience. In some cases, for example, fire may catalyze vegetation change expected under future climate (e.g., conversion to grassland at trailing edge lower forest ecotones; Donato et al. 2016); in other cases, change may be linked to shifts in subsequent fire regime (e.g., conversion to highly flammable chaparral; Tepley et al. 2017).

Box 1. Forests and fire regimes in western North America.

Temperate and boreal forests in western North America are dominated mostly by conifer species (including fir, *Abies*; juniper, *Juniperus;* spruce, *Picea;* pine, *Pinus;* Douglas fir, *Pseudotsuga;* and hemlock, *Tsuga* spp.), but with some important components of broadleaf species including trembling aspen (*Populus tremuloides*), birch (*Betula* spp.), maple (*Acer* spp.), and oak (*Quercus* spp.). Forest types vary predictably along moisture and temperature gradients, which interact with vegetation to shape fire regimes—the characteristic frequency and severity of wildfire over decades to centuries—via differing constraints on fire activity (Schoennagel et al. 2004, Baker 2009, Littell et al. 2018). Generally, forests in warm and dry settings (e.g., ponderosa pine (*Pinus ponderosa*) and dry mixed-conifer forests) experience climatic conditions suitable for burning on subdecadal to decadal frequencies. Productivity in these systems is moderate to low, and historically, fuel quantity and continuity were reduced by frequent, low-intensity fires. Historical fire regimes in these systems are considered to be more fuel limited than climate limited. Consequently, although fire may have been frequent, severity was typically low to moderate. Systems characterized by such a regime may be termed *frequent-fire* forest types. Conversely, in cooler and wetter settings (e.g., boreal, subalpine, and mesic Pacific Northwest forests), fire activity is considered climate limited: Biomass is usually sufficient to support high-intensity fire, but conditions required to dry out fuels occur less often. Conditions suitable for burning occur on multidecadal or multicentury frequencies. However, under warm, dry, and windy conditions, these forests can support crown fires, resulting in large patches of tree mortality (e.g., Turner and Romme 1994). Such systems may be termed *infrequent-fire* forest types. Frequent- and infrequent-fire forests represent the extremes of a continuum, between which many forests share some characteristics of both.

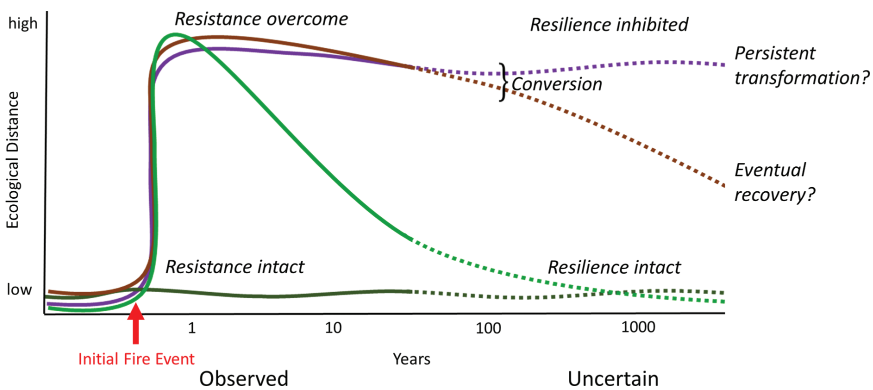

Figure 2. Hypothetical ecological outcomes of fire. The **x*-axis represents time since the initial fire; the*** **y*-axis represents ecological (e.g., compositional) dissimilarity relative to the prefire state. A low value indicates little change, and a high value indicates substantial change, such as a shift from dominance by one species or functional group to another. A forest stand with high resistance may be essentially unchanged following a fire—for example, when a surface fire burns through a ponderosa pine (*****Pinus ponderosa*****) forest. When resistance is overcome, a resilient system may change substantially, but still return toward its predisturbance state over time—for example, tree regeneration from seed following high-severity fire in a high-elevation lodgepole pine (*****Pinus contorta*****) forest. When resilience processes are overwhelmed, recovery toward a predisturbance state may be severely protracted or entirely precluded. Conversion refers to this condition. However, studies of recent postfire dynamics are limited to only a few decades postfire, represented by the solid lines; the time scales of these processes are highly uncertain. The dashed lines represent possible but uncertain future trajectories that cannot be known because of changes in climate, fire regimes, and society.***

Fire-driven conversion represents one potential outcome on a continuum of postfire vegetation dynamics (figure 2). Climate variability and disturbance have interacted over millennia to drive ecosystem change (Nolan et al. 2018). In fact, some contemporary vegetation patterns still bear the imprint of long-past conversion events, where succession toward the prefire state has been prevented (e.g., meadows generated by ancient fire and climate change; Lynch 1998) or drawn out over centuries (e.g., protracted aspen to conifer succession following high-severity fire; Margolis et al. 2007). Given the relatively short periods (years to decades) of recent postfire observations, the ultimate duration of contemporary changes cannot be known—a fundamental uncertainty in our understanding. However, accumulating evidence suggests that long-term conversions are increasingly taking place across a range of western North American forest types, and that we are likely to face substantially altered ecosystems on timescales exceeding management planning horizons and human lifespans.

A growing body of observations, empirical work, and understanding of causal processes calls for a synthesis of fire-driven forest conversion. In the present article, we begin by cataloguing the mechanisms that can generate and maintain conversions of forested landscapes across western North America. In compiling these mechanisms within the framework of conversion, we build on earlier reviews exploring and emphasizing key components of forest resilience and vulnerability (Johnstone et al. 2016, Davis et al. 2018, Falk et al. 2019, Hessburg et al. 2019, Stevens-Rumann and Morgan 2019), illustrating recent observations of their operation, considering interactions

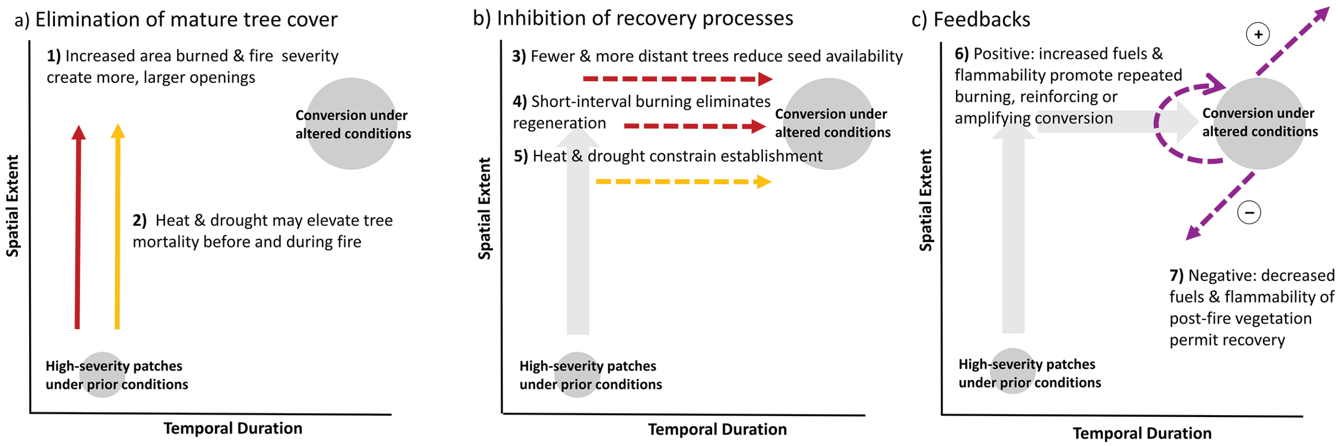

Figure 3. Processes that may give rise to fire-driven forest conversion. (a) Conversion is initiated by processes that result in extensive areas of adult tree mortality (the solid arrows; red represents fire, and yellow represents climate). (b) Conversion is maintained by processes that impede regeneration of prefire tree species (dashed red and yellow arrows) and protract vegetation change temporally. (c) The duration of forest conversion may be further influenced by positive and negative fire–vegetation feedbacks (dashed purple arrows), which respectively promote or inhibit additional burning.

and feedback processes, and highlighting their consequences and implications on the ground. Next, we draw from this mechanistic understanding to assess our capacity to predict future fire-driven forest conversions. Throughout, we identify key uncertainties. Finally, we outline a management framework for navigating conversion, in which we propose four themes for applied and coproduced research to better inform decision-making in a time of certain change, but of uncertain rate, magnitude, and extent.

Mechanisms of forest conversion

Fire-driven conversion results when forest resilience is overcome, inhibited, or otherwise absent. In what follows, we consider how increasing fire activity and warming and drought can break down resistance and recovery processes through increased tree mortality (prior to and as a result of fire; figure 3a) and reduced postfire tree regeneration (figure 3b). Subsequently, the duration and extent of conversion may be modulated by fire–vegetation feedbacks (figure 3c).

Changing fire regimes. Fire that kills most or all trees is a requisite first step toward fire-driven conversion (figure 3a). Fire regimes across western North America have undergone profound changes in the modern era. In most of this region, recent trends of increasing annual area burned, the number of fires, and the average fire size have been observed (figure 1; Dennison et al. 2014, Westerling 2016, Hanes et al. 2018). In addition, the proportion of area burned at high-severity has also increased in some ecoregions (Miller et al. 2009, Harvey et al. 2016b, Singleton et al. 2019). These increases are driven wholly or in part by anthropogenic climate change (Abatzoglou and Williams 2016), increasing human ignitions (Balch et al. 2017), and in formerly frequent-fire forest types, fuel accumulation due to fire exclusion (Steel et al. 2015).

Expanding annual area burned at high severity increases the landscape fraction of early seral postfire vegetation, but long-term conversion is contingent on impeded forest recovery processes, which may also be imparted by increasing fire activity. In some cases a single large and severe fire can effectively lead to conversion through the elimination of biological legacies vital to recovery (Turner et al. 1998, Johnstone et al. 2016). Where forests are composed of obligate seeding, nonserotinous tree species (e.g., ponderosa pine), large high-severity patches can limit postfire establishment because distances to live tree seed sources exceed characteristic seed dispersal distances (figures 3b and 4). These constraints may be further enhanced by the loss of climate buffering by the forest canopy (Davis et al. 2019b) and the development of competing vegetation (Stevens-Rumann et al. 2018). Where high-severity patches are exceptionally large, recovery may require multiple generations of tree colonization, maturation, and dispersal (Haire and McGarigal 2010, Chambers et al. 2016, Harvey et al. 2016c). Although the prefire forest type might eventually return within large patches created by high-severity fire, delays increase the likelihood of persistent change as seedling establishment becomes increasingly untenable under a warming climate (Liang et al. 2017).

As annual area burned increases, so too does the probability that a fire burns over a recently burned area (i.e., short-interval fires or early seral reburning; Prichard et al. 2017). Where frequent-fire forests have departed from historic fire regimes, intense fires occurring in short succession may surmount fire resistance and postfire recovery. The first fire shifts vegetation from obligate-seeding conifers to resprouting species while also producing abundant dead and down woody debris; this fuels the second fire, which eliminates conifer seedlings and any remaining seed sources, and further expands resilient resprouting

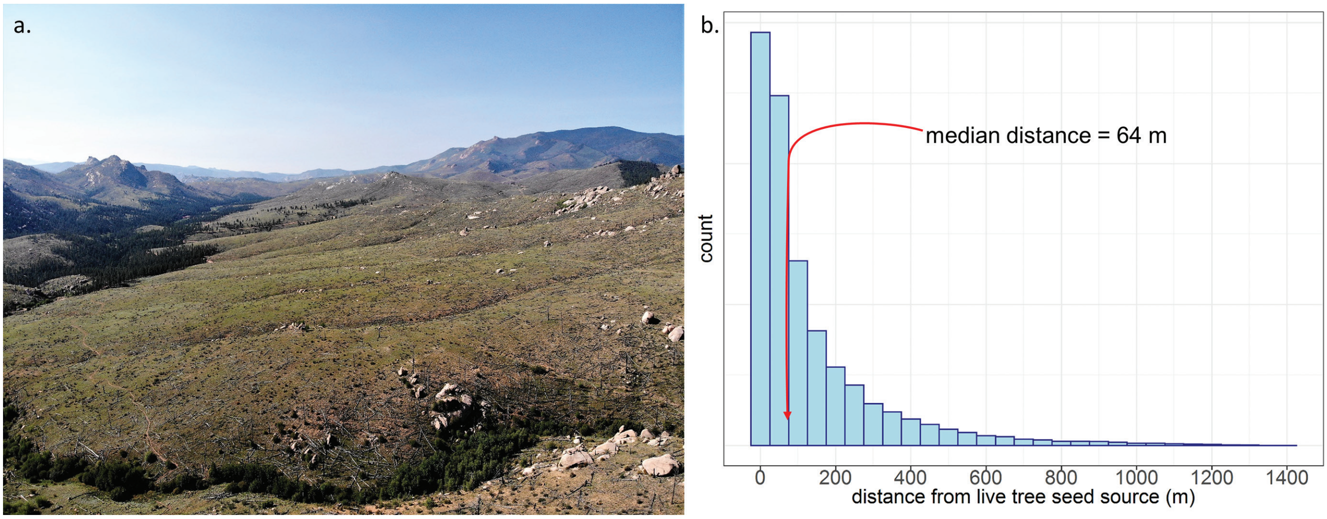

Figure 4. Exceptionally large high-severity patches in a frequent-fire forest type. (a) The postfire landscape of the Hayman fire in Colorado; (b) distribution of distances from high-severity patches to surviving tree seed sources within the burn perimeter. Fifteen years after a fire, Chambers and colleagues (2016) found that sites less than 50 meters from tree seed sources were not recovering toward prefire forest densities, and most of this landscape is now dominated by shrubs and herbs. Photograph: O. Rhoades. The data are from Jonathan D. Coop.

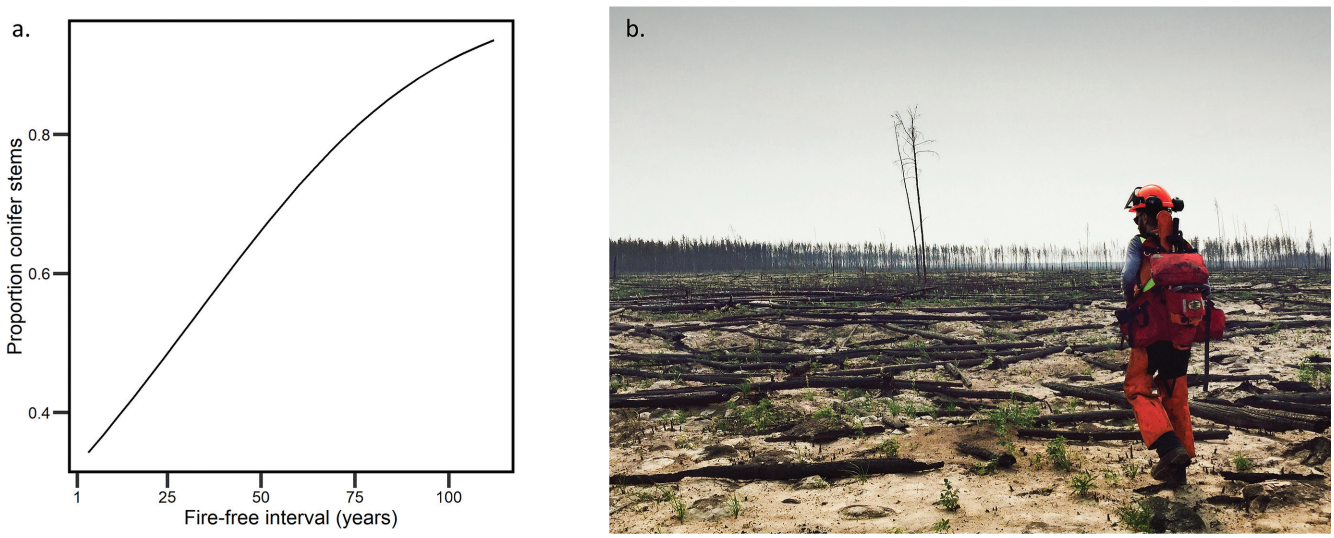

Figure 5. Shortening fire-free intervals lead to a shift from conifer to broadleaf boreal forests. These fire regime changes also lower the stem densities of stands, creating a more open forest type, and, in extreme cases, result in regeneration failure. (a) The relationship between the fire-free interval and the proportion of conifer seedlings (versus broadleaf tree regeneration) in the postfire cohort from burns in the Northwest Territories, Canada. (b) A short-interval reburn (10 years between severe fires) in Wood Buffalo National Park, Canada, showing exposed mineral soil and charred logs. There are no residual in situ seed or sucker sources for either conifers or broadleaves at the center of the reburn. Photograph: Ellen Whitman. The data are from Whitman and colleagues (2019).

species (figure 3b; Coop et al. 2016, Coppoletta et al. 2016). Short-interval fires can also undermine mechanisms conferring resilience to high-severity fire (figures 3a and 5). Serotinous or semiserotinous cones allow species such as lodgepole pine (*Pinus contorta*) and black spruce (*Picea mariana*) to maintain canopy seedbanks and disperse seeds locally following intense fire. With an adequate fire-free interval, forest composition and structure recover (Buma et al. 2013). However, when reburning occurs before tree maturation, postfire seed sources are absent (Keeley et al. 1999, Brown and Johnstone 2012, Turner et al. 2019). In these cases, infrequent-fire forest types are vulnerable to

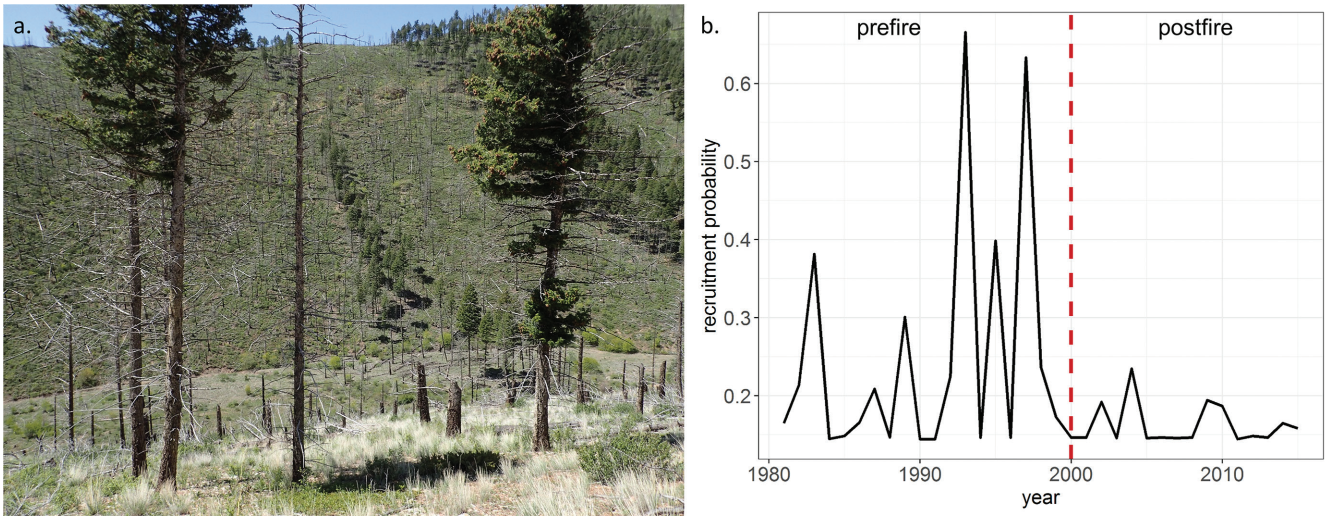

Figure 6. Shrinking windows of climatic opportunity for postfire regeneration. After 2000, conditions conducive for postfire regeneration in ponderosa pine and Douglas fir (Pseudotsuga menziesii) forests became less prevalent (Davis et al. 2019a). (a) Photo of Canyon Ferry burn in Montana, 17 years postfire, where postfire surveys suggest that there has been little to no recruitment at lower elevations. (b) Modeled probability of recruitment (above the 25th percentile of the annual rate) at this site (Davis et al. 2019a). Photograph: Kimberly T. Davis.

transitions from one forest type to another (e.g., from pine to aspen; Hart et al. 2019, Whitman et al. 2019), or to conversion from forest to grassland or shrubland (Brown and Johnstone 2012).

Direct effects of a changing climate. In addition to shaping fire regimes, climate change also contributes directly to forest conversion through effects on pre- and postfire tree population dynamics. Warmer and drier conditions can stress trees and cause mortality in the absence of fire, or predispose trees to fire-induced mortality (figure 3a; van Mantgem et al. 2013, 2018). Severe drought associated with climate change has triggered major tree die-offs via hydraulic failure or carbon starvation, or mediated through insects and pathogens (Anderegg et al. 2015). Such die-offs may hasten conversion by removing potential seed sources and increasing dead fuels.

Where prefire tree species cannot regenerate under contemporary climate, conversion is maintained (figure 3b). Even where sufficient seed sources are available, warmer and drier postfire conditions can lead to tree recruitment failures (Stevens-Rumann et al. 2018, Hansen and Turner 2019), upholding shifts to nonforest vegetation or tree species with different physiological tolerances or regeneration strategies (Hansen et al. 2016). Postfire tree regeneration is highly sensitive to climate, and directional change, as well as intra- and interannual fluctuations, shape the likelihood of regeneration success (Davis et al. 2018). Postfire recruitment pulses in dry forest types are most common in wet years that are more favorable for seedling establishment (Brown and Wu 2005, O'Connor et al. 2017) but are projected to become less frequent (figure 6; Davis et al. 2019a).

Postfire tree regeneration failures are most likely to occur, and conversion most likely to endure, at the lower elevation treeline or trailing edge ecotone (Rother et al. 2015, Donato et al. 2016, Parks et al. 2019). Low-elevation sites with high incoming solar radiation, minimal upslope water subsidies, and low moisture availability experience the greatest stress and the highest tree seedling mortality rates (Simeone et al. 2019). In such settings, high-severity fire is expected to catalyze conversions from forest to nonforest that would be anticipated to occur eventually, but more slowly, under directional climate change.

Though recent studies have documented postfire declines in regeneration when fires are followed by warm and dry conditions, the ultimate duration of these changes cannot be known. Constraints on postfire regeneration associated with warmth and drought are documented across elevations (Harvey et al. 2016c, Stevens-Rumann et al. 2018, Whitman et al. 2019) and in some locations there has been a lack of postfire regeneration many decades postfire (Savage and Mast 2005, Donato et al. 2016, Stevens-Rumann et al. 2018). However, although much attention is paid to evidence of recent tree regeneration failure, less is known about episodic postfire recruitment during periods of high moisture availability (but see Brown and Wu 2005), challenging our ability to confidently predict that the prefire tree assemblages will not return.

Fire–vegetation feedbacks. The potential for changing fire regimes and climate to sustain forest conversion is modulated by feedbacks between fire and vegetation (McKenzie and Littell 2017). Patterns of fire-induced tree mortality and postfire vegetation development influence the probability of

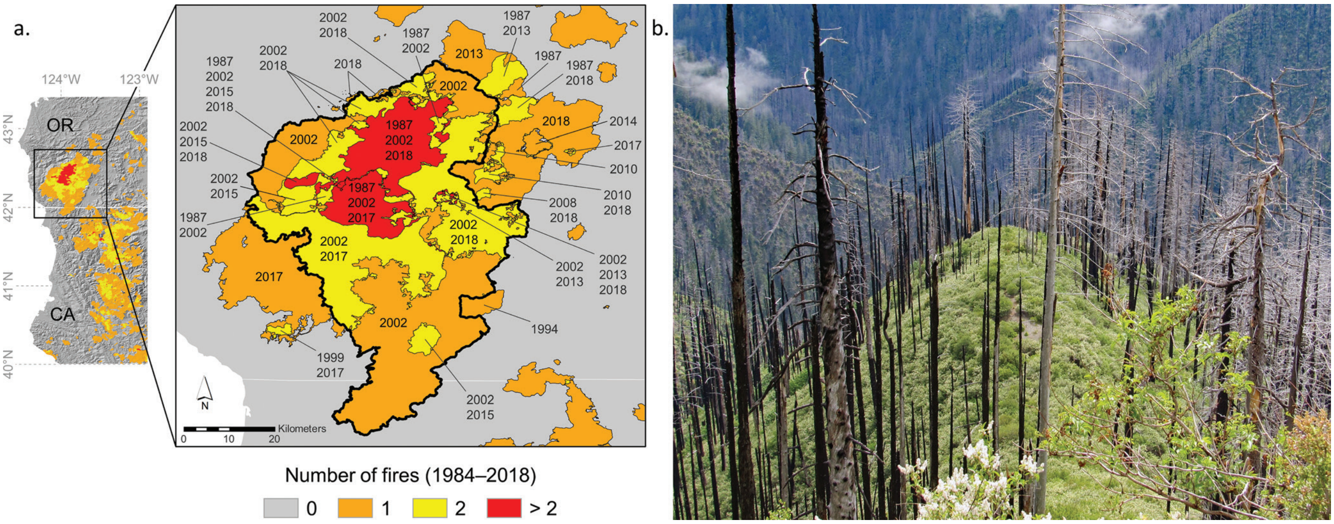

Figure 7. High-severity reburns perpetuate and expand flammable shrub cover at the expense of forest. (a) Recent fire history in the Klamath Mountains, with the inset showing reburns (1984–2018) within and adjacent to the 2002 Biscuit Fire (200,000 hectares; the thick outline). The Biscuit Fire completely reburned a 1987 fire, and much of the Biscuit Fire was burned again by smaller fires in 2013 and 2015, and large fires in 2017 and 2018. (b) The photo depicts an area that burned in 1994 and 2008. The 1994 fire burned at high severity on the left side of the photo, killing nearly all trees and initiating shrub-dominated vegetation. The 2008 fire burned both sides of the photo at high severity, perpetuating the shrub cover on the left, and expanding it farther into the forest on the right (note the difference between the blackened snags with few branches on the left, which were dead before the 2008 fire, compared to the gray snags with intact fine branches on the right, which survived the 1994 fire and were killed in 2008). Photograph: Alan Tepley.

tree regeneration, growth, and survival (Davis et al. 2018). These changes in turn influence future fire probability and effects (Archibald et al. 2018).

A positive feedback is one in which a fire-initiated vegetation shift is reinforced or amplified through ensuing positive effects on fire activity (figure 3c). High-severity fire can produce abundant dead and down fuels and dense vegetation regrowth (Nelson et al. 2016) prone to reburning and perpetuating nonforest cover. Furthermore, high-severity fire may drive shifts from forests toward more flammable, shrub-dominated vegetation types (Tepley et al. 2018). These scenarios represent self-reinforcing feedbacks in which severe fire begets severe fire (figure 7). In low-elevation forests in California, large forested areas were converted to shrubland when they burned in high-severity fires between 2000 and 2010 (Coppoletta et al. 2016). When these patches reburned in 2012, much of the area reburned at high severity, perpetuating the shrub-dominated vegetation (Coppoletta et al. 2016). This pattern of high-severity fire begetting high-severity fire has been seen in multiple areas across the western United States (e.g., Collins et al. 2009, Harvey et al. 2016a). In some cases, the second fire may burn at even higher severity than the first (Turner et al. 2019).

A negative feedback occurs when fire creates conditions that limit future burning, which may foster the return of the prefire forest (figure 3c). Reduced burn potential may arise because of slow fuel buildup after fire (Parks et al. 2018b), or a shift from relatively flammable conifers to less flammable deciduous species (e.g., shifts from conifer forests to early seral vegetation dominated by aspen or birch in boreal landscapes; Héon et al. 2014, Whitman et al. 2019). Low burn probabilities following fire represent a dampening feedback that may permit tree seedling establishment, growth, and survival. These effects, however, are generally temporary. Furthermore, negative feedbacks may be overridden by severe fire weather (Parks et al. 2018b, Harvey et al. 2016a) and climate change-driven increases in wildfire activity (Hart et al. 2019).

Spatial and temporal variation in fire–vegetation feedbacks has important implications for understanding vulnerability to fire-catalyzed conversion as the climate warms and becomes increasingly conducive to wildfire. Where the feedbacks are positive, relatively small increases in wildfire activity could lead to abrupt and extensive shifts to persistent nonforest cover. In systems with negative feedbacks, the period of low flammability following high-severity fire provides a degree of resistance to conversion by increasing the fire-free period during which forests can recover. Feedbacks may also change over a sequence of disturbances. For example, abundant dead and down fuels produced by a high-severity fire may promote a second high-severity fire (Lydersen et al. 2019). However, the consumption of such fuels during the second fire can lead to major reductions in fuels, reducing the probability of a third high-severity fire.

What does the future hold for western North American forests?

In western North America, fire activity is expected to continue to increase in association with climate change throughout this century (Kitzberger et al. 2017, Abatzoglou et al. 2019). Furthermore, in many locations, postfire climate conditions are likely to become increasingly unfavorable to tree regeneration, even if seed sources are nearby (Kemp et al. 2019, Liang et al. 2017). Given these projected changes in fire and climate, we anticipate that many forest ecosystems will face increasing risk of fire-catalyzed change, although the nature of change will depend on forest type and fire–vegetation feedbacks.

Forecasts of forested area susceptible to fire-driven conversion project varying degrees and rates of change across forest types by mid- to late-twenty-first century. In the Sierra Nevada in California, for example, Liang and colleagues (2017) project that fire and climate change will reduce forest extent by 5.8% (averaged over GCMs and transects) by the year 2100. Within the intermountain western United States, 1.6% to 15.1% (depending on ecoregion) of forest area has been modeled to be at risk of fire-catalyzed conversion to nonforest by mid-twenty-first century (Parks et al. 2019). In the southwestern United States, where extreme fire weather was incorporated into fire severity estimates, a more substantial 30% of forested area may be vulnerable to fire-driven conversion (Parks et al. 2019). Similarly, on the Kaibab Plateau of northern Arizona, 3% to 49% of the landscape (depending on forest type and climate scenario) was predicted to be nonforest by 2090 when fire was included in simulations, compared to only 0% to 0.3% when fire was excluded (Flatley and Fulé 2016). In the Klamath region of northern California and southern Oregon, approximately one third of conifer-dominated forest could transition to shrub- or hardwood-dominated ecosystems by the late-twenty-first century (Serra-Diaz et al. 2018). In the mountains of central Idaho, climate change and increased fire activity are expected to substantially reduce the prevalence of four common conifer species (Campbell and Shinneman 2017). In Alberta, Canada, wildfire could catalyze conversion of about 50% of upland mixed-wood and conifer forests to more climatically suited mosaics of grassland, shrubland, and deciduous woodland by 2100 (Stralberg et al. 2018). As a very broad generalization across western North America, bioclimatic models suggest that forested areas will have climate and fire regimes more suited to drier forest types and nonforest vegetation (Parks et al. 2018a).

Because forest recovery—or lack thereof—following high-severity burning is predicated on regeneration, studies focusing on seedling establishment and survival under future climate also inform estimations of vegetation change. In New Mexico, for example, a substantial reduction in successful ponderosa pine regeneration is expected along the dry, lower-elevation boundary of its range (i.e., the trailing edge; Allen and Breshears 1998, Feddema et al. 2013). Decreases in postfire ponderosa pine and Douglas fir (*Pseudotsuga menziesii*) seedling densities are also predicted by mid-twenty-first century at sites in Idaho and Montana, with effects being most pronounced at lower elevations (Kemp et al. 2019). If these trailing-edge forests experience high-severity fire, conversion to nonforest is probable. Similarly, more than 50% of the area currently suitable for montane forest in the Klamath region could have minimal postfire conifer regeneration by the late-twenty-first century, even if seed sources are available (Tepley et al. 2017). Concurrence between process-based (Serra-Diaz et al. 2018) and statistical models (Tepley et al. 2017) provides more confidence in the prediction that conversions are highly likely in this system.

We cannot ignore, however, uncertainties that currently hinder our ability to predict where, when, and how widespread conversions may be in coming decades. For example, whereas there is near-universal agreement among global climate models that temperatures will continue to rise this century, projected changes in precipitation at regional to global scales are variable (Knutti and Sedláček 2013), and this may impart cascading uncertainties in predictions of future fire and regeneration. However, any potential increases in precipitation may be insufficient to offset the effect of rising temperatures on fire activity (Flannigan et al. 2016) and declines in snowpack (with implications for soil moisture; Harpold and Molotch 2015). In one field experiment, ponderosa pine and Douglas fir seedlings that received a combination of warming and supplemental watering demonstrated lower rates of survival than did untreated controls (Rother et al. 2015). Elevated water use efficiency by plants resulting from carbon fertilization may also partially buffer seedlings against warming temperatures (Keenan et al. 2013), although the net effect remains uncertain and may vary with species and age (Peñuelas et al. 2011, Anderson-Teixeira et al. 2013). Continued research (e.g., Battipaglia et al. 2013) is needed to clarify the influence of carbon fertilization on tree establishment under projected future climate.

No-analog or novel climatic conditions challenge existing models built on observed interactions and feedbacks among climate, vegetation, and fire, potentially limiting the ability of retrospective studies to accurately project future dynamics. When informed by empirical research, process-based (i.e., mechanistic) simulation models have the potential to overcome some of the limitations imposed by no-analog conditions (Gustafson 2013, Loehman et al. 2020). However, process-based models may be constrained by an incomplete understanding of underlying mechanisms such as propagule production and dispersal, inter- and intraspecific interactions within a postfire community, as well as genetic variation and phenotypic plasticity. Additional research on these topics is also needed to improve projections of future changes in western North American forests and bolster existing demographic frameworks (e.g., Enright et al. 2015, Davis et al. 2018).

Properly incorporating fire–vegetation feedbacks into predictions of future conversion is also challenging. For example,

Box 2. Fire-driven forest conversion in the paleological record.

Paleoecological records offer unique insights into past wildfire-driven vegetation conversions that ground our understanding of contemporary and future change. Numerous paleological records feature vegetation shifts associated with climate change (Nolan et al. 2018), but most paleological records that address fire highlight ecological resilience to wildfires (e.g., Minckley et al. 2012). However, during periods of rapid climate change, the paleological record illustrates how wildfire can catalyze ecological changes that either would have taken centuries to unfold or may not have occurred at all.

In a lowland forest of the Pacific Northwest, for example, high-resolution pollen and charcoal records indicate two major vegetation conversions over the Holocene (i.e., the past 11,700 years) that were catalyzed by individual high-severity wildfires at the local scale (Crausbay et al. 2017). While the regional expansion of these new vegetation types was ultimately driven by millennium-scale climate change, the timing of conversion was determined by fire. More recently during the Medieval Climate Anomaly (c. 1000 years ago), a change toward a century-long period of elevated wildfire activity caused a continuous subalpine forest landscape to shift abruptly to a ribbon forest (i.e., alternating bands of meadow and forests) that persists today (Calder et al. 2019).

Conversion in these examples occurred via the interaction of two processes: high-severity wildfire, which killed adult trees that could have otherwise persisted for decades or centuries even under a changing climate, and rapid, directional climate change, which created unsuitable conditions for regeneration of the dominant tree species. Both processes are currently interacting across western North America. The paleological record offers another line of evidence that enduring forest conversion is a potential outcome of contemporary high-severity fires under a changing climate.

the long-term impact of repeated fires on vegetation and fuels is not well understood across biophysical gradients, and will be conditional on factors such as tree mortality following the initial or second fire, exact time interval between fires, postfire climate, and dominant species (McKenzie and Littell 2017, Hurteau et al. 2019a). Fortunately, quantifying ecosystem responses to short-interval fires is an extremely active area of research that is filling knowledge gaps (Coop et al. 2016, Coppelletta et al. 2016, Harvey et al. 2016a, Tepley et al. 2017, Collins et al. 2018, Parks et al. 2018b, Lydersen et al. 2019, Turner et al. 2019, Whitman et al. 2019, Buma et al. 2020).

Human activities also complicate our ability to project forest conversion, through both direct and indirect influences on land use and land cover, fire regimes, and postfire vegetation change. Human land use practices, acting in concert with a warming climate, have led to a disequilibrium (Svenning and Sandel 2013) between the existing distribution of forests and current climatic conditions in parts of western North America, setting the stage for rapid fire-catalyzed forest conversions (Serra-Diaz et al. 2018). As one important example, ongoing fire suppression in some regions has resulted in a fire deficit, whereas in other regions, the introduction of nonnative invasive grasses and increased human ignitions have expanded the spatial and temporal fire niche and resulted in a fire surplus (Parks et al. 2015, Balch et al. 2017). Pre- and postfire management can also influence the likelihood of conversion. Large-scale fuel reduction is predicted to reduce fire-induced mortality under future climatic conditions (McCauley et al. 2019), and widespread tree planting could also forestall conversion. Consequently, future patterns in human development (e.g., the expanding wildland–urban interface) and human actions (e.g., pre- and postfire management actions, fire suppression and ignition) are additional factors that could be considered when predicting fire-catalyzed forest conversions. Though some process-based models already incorporate these dynamics at a coarse spatial scale (Lawrence et al. 2016), their influences at finer scales is an important area for future study.

Resolving these uncertainties and identifying where there is convergence across the growing body of research can improve our confidence in predictions of where and when fire is most likely to drive forest conversion. Nevertheless, with the preponderance of evidence—from the paleoecological record (box 2), present-day observations, *in situ* experiments, and future projections—we can state with confidence that fire-driven conversions will unfold across many forested landscapes as climate change proceeds. However, perhaps the most important question is the most elusive: How should society respond to these conversions?

A framework for supporting management decisions around forest conversion

Given our developing understanding of wildfire-driven forest conversion and a wide range of inherent uncertainties, how might science and policy best support management decisions? Western North American forests support a wide range of ecological and social values and services, ranging from utilitarian and economic (e.g., timber production) to aesthetic and spiritual. Many of these services will be changed by the forest losses and shifts we describe in this article (box 3). Sustaining these values and services has guided management policy in Canada and the United States for over a century. However, in a time of pervasive and intensifying change, the implicit assumption that the future will reflect the past is a questionable basis for land management (Falk 2017). Increasing forest vulnerability to changing fire regimes and climate compels revised management paradigms, strategies, and tactics, with a robust scientific foundation.

Box 3. Consequences of fire-catalyzed forest conversion.

The direct and indirect effects of fire-driven forest conversion are numerous and wide ranging, but will depend largely on the characteristics and dynamics of postconversion vegetation assemblages, an area requiring further research. In conifer-dominated systems of western North America, most recent studies have examined fire-driven conversion toward vegetation dominated by genera of resprouting broadleaf trees (in particular, aspen and birch), shrubs (such as oak and ceanothus, *Ceanothus*), and herbaceous communities (Savage and Mast 2005, Abella and Fornwalt 2015, Stevens et al. 2015, Airey Lauvaux et al. 2016, Coop et al. 2016, Guiterman et al. 2018, Barton and Poulos 2018). Given recent historic conifer increases in some systems, contemporary fire-catalyzed conversion to nonconifer dominated systems may, in some cases, represent a return to conditions similar to the early twentieth century (Hessburg et al. 2019). However, the spatial and temporal scale of patchiness of fire-catalyzed conversion may not mirror the opposing pattern of recent conifer densification or encroachment. In other cases, conversion could be viewed as an adaptive change that creates a new system better suited for warmer climate with more fire activity. Severe fire serves as a filter with warm- and fire-adapted species (e.g., resprouters, annuals, some invasives) succeeding at the expense of fire-sensitive species (Abella and Fornwalt 2015, Stevens et al. 2015). However, with implications for ecosystem function, as well as the provision of ecosystem services, particularly carbon sequestration, any shifts will necessarily have a range of local, regional, and global impacts.

Fire-driven forest conversion can lead to reduced carbon storage, altered hydrologic dynamics, plant- and animal-community turnover, and impacts on a wide range of human social and economic values. Forests are a substantial contributor to climate regulation through the uptake and storage of carbon (Pan et al. 2011), and conversions, particularly to nonforested vegetation types, are generally expected to result in reduced productivity and carbon storage. However, in temperate regions, the effect of forests on Earth's energy balance is also a function of local climatic conditions. In semiarid regions, for example, forest cover decreases albedo and low water availability limits the latent heat flux from evapotranspiration, suggesting that a wildfire-induced state change may yield a net cooling effect (Jackson et al. 2008). Widespread forest loss and the associated changes in albedo and land-surface energy balance scale up to affect the entire climate system, with global consequences. For example, models suggest that loss of forests in western North America could lead to drying and reduced net primary productivity in other parts of the world (Stark et al. 2016). Forest conversions may also affect erosion rates and water quality and quantity by decreasing transpiration and increasing overland flow (Wine et al. 2018). Forest conversion will also necessarily drive complex changes to biotic community composition and diversity. High-severity fire can generate habitat for some species dependent on postfire attributes such as snags (e.g., some woodpeckers; Hutto et al. 2015), but these may ultimately be diminished if long-term forest recovery is compromised. For example, the capacity for landscapes to harbor species that rely on shrubs or meadows may increase, but forest- or old-growth obligate species will be increasingly susceptible (e.g., lichens; Miller et al. 2018). Nonnative species may also benefit from fire-driven conversion (Abella and Fornwalt 2015, Stevens et al. 2015).

Over the past decade, consensus has built around a three-part concept of the universe of potential management responses (Aplet and Cole 2010) expressed in terms of resisting, accepting, or directing change. Resisting wildfire-driven forest conversion means attempting to sustain existing forests by supporting prefire resistance or postfire recovery. Accepting conversion concedes the replacement of extant forests by other vegetation types after fire without intervening, accommodating modified communities and altered ecosystem services. Directing conversion uses management interventions to favor particular postfire outcomes aligned with human values (e.g., Aplet and Cole 2010, McWethy et al. 2019).

Contemporary forest management policies, mandates, and science generally fall within the paradigm of resisting conversion, through on-the-ground tactics such as fuel reduction or tree planting. Given anticipated disturbance trajectories and climate change, science syntheses and critical evaluations of such resistance approaches are needed because of their increasing relevance in mitigating future wildfire severity (Stephens et al. 2013, Prichard et al. 2017) and managing for carbon storage (Hurteau et al. 2019b). Managers seeking to wisely invest resources and strategically resist change need to understand the efficacy and durability of these resistance strategies in a changing climate. Managers also require new scientific knowledge to inform alternative approaches including accepting or directing conversion, developing a portfolio of new approaches and conducting experimental adaptation, and to even allow and learn from adaptation failures.

Science to support decisions around resisting, accepting, or directing forest conversion is best formed within coproduction models between scientists and managers, where both parties meaningfully engage (e.g., Meadow et al. 2015) and target decision-making processes. Decision-making processes such as the Climate-Smart Conservation Cycle (Stein et al. 2014) provide a framework highlighting how science can support decisions to resist, accept, or direct ecological change. In the present article, we propose four central themes toward an array of coproduced science to support decisions around wildfire-driven forest conversion. These include (1) *characterizing vulnerability to fire-driven conversion*, (2) *providing plausible scenarios of post-fire ecological futures* under shifting climate and fire regimes, (3) *assessing the feasibility of directing or resisting conversion*, and (4) *understanding the social and ecological consequences* of the choice to resist, accept, or direct change.

The first theme, *characterizing vulnerability to fire-driven conversion*, offers crucial support to the initial steps in a decision-making process. There are many opportunities to further develop and synthesize knowledge about the likelihood of wildfire-driven conversion, including mapping and modeling the locations of fire refugia (Krawchuk et al. 2016), trailing-edge forests (Parks et al. 2019), climate futures for fire weather (Wang et al. 2017), and postfire recruitment (Davis et al. 2019a). As was described previously, however, there are inherent uncertainties associated with each of the mechanisms that can lead to conversion. These are compounded by interactions among processes (Temperton et al. 2004), and potentially exacerbated by expected no-analog climates of the twenty-first century and nonstationarity of ecological processes. However, uncertainty need not be a limitation for forward-looking managers to engage in proactive thinking about the general vulnerability of the forests they manage to fire-driven conversion in the near future.

The second theme, *providing plausible postfire ecological futures* under shifting climate and fire regimes, will allow managers to consider the consequences of accepting ecological reorganization. Research on interactions between disturbance and climate-driven species, habitat, and biome range shifts will provide more plausible postfire ecological scenarios under climate change. As with the first theme, there is currently high uncertainty around the characteristics of the ecological communities most likely to replace any particular forest. In addition, the field lacks a commonly accepted means of forecasting ecological scenarios. Before decisions can be made about resisting, accepting, or directing conversion, land managers will require some degree of clarity, or ability to incorporate scenarios, about the likelihood and probable character of forest conversion.

The third theme, *assessing the feasibility of resisting or directing conversion*, is a call to expand our paradigm outside the traditional narrow focus on ensuring resilience of existing forest communities (Falk et al. 2019). Currently, a large body of work supports tactics to resist conversion, although these pertain primarily to frequent-fire forest types. Well-established fuel reduction techniques emphasize the retention of larger-diameter trees with thick bark and other adaptations to fire, the removal of understory and ladder fuels that promote the transition from surface to crown fire, and maintenance burning (Stephens et al. 2013). Such interventions have been demonstrated to reduce tree mortality during subsequent wildfire (Prichard et al. 2020). Recent work also highlights support for treatments that promote landscape heterogeneity through creation of clumps and gaps (Churchill et al. 2013); stand- and landscape-level heterogeneity have also been shown to increase forest resilience to wildfire (Koontz et al. 2020) and other disturbances such as beetle outbreaks (Seidl et al. 2016). At broader spatial scales, vegetation management projects and strategic fuel breaks can be used to restore more resilient patch mosaics and limit future fire spread into communities or vulnerable late-successional habitat (Hessburg et al. 2016, 2019).

Heterogeneity may be achieved by direct management intervention (mechanical thinning and prescribed fire), but strategically allowing wildfires to burn at low-to-moderate severity under tolerable fire weather conditions also reduces fuels and creates heterogeneity. In particular, where frequent-fire ecosystems are not substantially departed from historic norms, repeated low-to-moderate-intensity burning may confer resilience to forests by maintaining a reduced fuel load and perpetuating a low-severity fire regime (Larson et al. 2013, Walker et al. 2018, Kane et al. 2019). Furthermore, fires burning under benign to moderate conditions may interact with topography to support fire refugia (Krawchuk et al. 2016) that promote forest recovery (Coop et al. 2019). Following high-severity wildfires, strategic tree planting and forest management can also generate heterogeneous forest structure and composition (North et al. 2019). A synthesis of these many existing strategies to resist conversion could provide insight into whether and how long these tactics will be viable under climate change, and also inspire the development of new approaches to mitigate conversion in infrequent-fire forest types, where fewer management interventions are in use.

Although directing forest conversion is within the spectrum of management choices, it currently lacks adequate scientific underpinnings and is therefore poised to become an increasingly important research field. For example, ecological and ethical questions associated with managed relocation or assisted migration of genotypes, species, and vegetation types cover very broad terrain. Topics for applied research include the role of dispersal limitations, habitat connectivity, multispecies interactions, native and nonnative species interactions, no-analog climates, and probability of long-term establishment (Schwartz et al. 2012). In addition, a general framework is needed for conducting experimental adaptation for directing change, testing the efficacy of various tactics, and assessing how different approaches might interact and be sustained across larger spatial scales.

The fourth theme, to better *understand the ecological and social consequences of the choice to resist, accept, or direct conversion*, is key to creating operational models for adapting to change. Ecological and social values will be strongly affected by how the postfire assemblage of species that replaces a particular forest will translate to biodiversity and habitat availability, ecosystem processes and functions (e.g., hydrology), and ecosystem services, economic health, and cultural identity. Connecting science on these ecosystem functions and services to a diverse array of plausible vegetation types for each option to resist, accept, or direct conversion will be key to supporting experimental adaptation and a portfolio of informed management approaches.

Even with strong scientific support, managers may be constrained by agency practices and public expectations. Although there are risks, ultimately managers will require broader social license and support to operate outside of traditional models. Social science is needed to inform and support decisions about forest conversion (e.g., McWethy et al. 2019), with a better understanding of how society values particular forests, and how those values, social acceptability, and agency mandates constrain a manager's decision space (Higuera et al. 2019). These topics each merit their own assessment of management-focused research needs. Furthermore, an era of profound and global ecological change may demand a strengthened ethical framework within which to consider decisions likely to have wide-reaching and lasting consequences.

Conclusions

Wildfire-driven forest conversion occurs when ecological resilience of forests to wildfire is overcome, leading to extensive and enduring areas of altered vegetation. Conversion is initiated by high-severity fire that removes areas of mature trees, and is maintained by a range of processes that impede tree regeneration, including distant tree seed sources, short-interval fires, or unfavorable postfire climate, further shaped by fire–vegetation feedbacks. An emerging body of research from across western North America highlights the strong potential for anthropogenic climate change and other human-induced changes to create conditions leading to fire-driven forest conversion. Numerous key uncertainties currently limit our capacity to project future changes, but also present research opportunities. However, the prospect of directional climate change beyond historical ranges of variability, and increased frequency and magnitude of extreme disturbance, compels us to consider the possibility of profound and persistent ecological change across forested ecosystems. As such, management and conservation efforts should align with expectations of increasing forest vulnerability to conversion. In an era of change, the forest that was there before the fire may not return.

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