




REVIEW

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# Tree regeneration following wildfires in the western US: a review



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## Abstract

**Background:** Wildfires, like many disturbances, can be catalysts for ecosystem change. Given projected climate change, tree regeneration declines and ecosystem shifts following severe wildfires are predicted. We reviewed scientific literature on post-fire tree regeneration to understand where and why no or few trees established. We wished to distinguish sites that won't regenerate to trees because of changing climate from sites where trees could grow post fire if they had a seed source or were planted, thus supporting forest ecosystem services for society and nature, such as timber supply, habitat, watershed protection, and carbon storage.

**Results:** Our literature review showed that little to no post-fire tree regeneration was more common in low-elevation, dry forest types than in high-elevation forest types. However, depending on the region and species, low tree regeneration was also observed in high elevation, moist forests. Regeneration densities varied by species and seedling densities were attributed to distances to a seed source, water stress or precipitation, elevation, slope, aspect, and plant competition. Our findings provide land managers with two primary considerations to offset low tree regeneration densities. First, we supply a decision support tool of where to plant tree seedling in large high severity burned patches. Second, we recommend possibilities for mitigating and limiting large high severity burned patches to increase survival of trees to be sources of seed for natural regeneration.

**Conclusions:** Few or no tree seedlings are establishing on some areas of the 150+ forest fires sampled across western US, suggesting that forests may be replaced by shrublands and grasslands, especially where few seed source trees survived the wildfires. Key information gaps on how species will respond to continued climate change, repeated disturbances, and other site factors following wildfires currently limit our ability to determine future trends in forest regeneration. We provide a decision tree to assist managers in prioritizing post-fire reforestation. We emphasize prioritizing the interior of large burned patches and considering current and future climate in deciding what, when, and where to plant trees. Finally, managing fires and forests for more seed-source tree survival will reduce large, non-forested areas following wildfires where post-fire management may be necessary.

**Keywords:** alternate stable states, climate, distance to seed source, post-fire forest recovery, reforestation, tree regeneration, tree seedlings, wildfires

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## Resumen

**Antecedentes:** Los incendios, como muchos disturbios, pueden ser catalizadores para cambios en el ecosistema. Dadas las proyecciones del cambio climático, se predice una declinación en la regeneración de árboles y cambios en el ecosistema después de incendios severos. Revisamos la literatura científica para entender dónde y por qué pocos o ningún árbol se establece en la regeneración post-fuego. Deseábamos distinguir sitios que no regeneraban en árboles debido al cambio climático de aquellos sitios en que los árboles podrían crecer si tenían una fuente de semillas o fueran plantados en el post-fuego, sustentando la idea de proveer servicios ecosistémicos del bosque para la sociedad y la naturaleza, como productos forestales, hábitat, protección de cuencas, y almacenamiento de carbono.

**Resultados:** Nuestra revisión bibliográfica muestra que la escasa o nula regeneración arbórea post-fuego fue más común en tipos de bosques secos ubicados a bajas alturas que en bosques ubicados a mayores elevaciones. Sin embargo, dependiendo de la región y de la especie, una baja regeneración de árboles fue observada en lugares húmedos y a altas elevaciones. La densidad de la regeneración varió de acuerdo a la especie, y la densidad de plantines fue atribuida a la distancia de la fuente de semillas, el estrés hídrico o precipitación, la elevación, la pendiente, la exposición, y la competencia con otras plantas. Nuestros resultados proveen a los gestores de tierras con dos consideraciones primarias para compensar la baja densidad en la regeneración. Primero, presentamos una herramienta de ayuda sobre dónde plantar plantines en grandes parches quemados con alta severidad. Segundo, recomendamos la posibilidad de mitigar y limitar los parches de alta severidad para incrementar la supervivencia de árboles para que sirvan de fuentes de semilla para su regeneración natural.

**Conclusiones:** Pocos o ningún plantín se establecen en algunas de las áreas de los más de 150 bosques muestreados a través del oeste de los EEUU, sugiriendo que esos bosques pueden ser reemplazados por arbustales y pastizales, especialmente donde pocos árboles que actúan como fuentes de semillas sobreviven a los incendios. Existen vacíos de información que son clave para entender cómo las especies responderán a la continuidad del cambio climático, la repetición de disturbios y otros factores de sitio subsecuentes a los incendios y que limitan actualmente nuestra habilidad para determinar tendencias futuras en la regeneración de bosques. Proveemos de un árbol de decisiones para asistir a los gestores a priorizar la reforestación post-fuego. Enfatizamos la priorización de los grandes parches en el interior de grandes incendios y la consideración del cambio climático actual y futuro en la decisión de qué, cuándo y dónde plantar árboles. Finalmente, el manejo del fuego y los bosques para lograr que más árboles semilleros sobrevivan a los incendios va a reducir las grandes áreas que quedan sin árboles en el post-fuego, en las cuales el manejo post-fuego puede ser necesario.

## Introduction

Continuing climate change, droughts, and extreme weather (IPCC 2013), coupled with associated changes in wildfire activity (Westerling *et al.* 2006, Westerling *et al.* 2011, Abatzoglou and Williams 2016) are resulting in landscape ecosystem changes and shifts in community composition (Stevens-Rumann *et al.* 2018). Climate change is altering the mountainous ecosystems of the western US and affecting the people who depend on them for ecosystem services and livelihoods. With rapid biophysical changes already occurring in these forests, land managers are increasingly seeking to understand and mitigate the effects of a changing climate. Effective action depends on understanding regional and local implications of climate science and ecological effects (Blades *et al.* 2016), which can directly affect fire extent, tree mortality, and post-fire ecosystem recovery.

Legacies of prior disturbances and land use history, in addition to climate, play a prominent role in

disturbance severity and subsequent recovery following disturbances (Hessburg *et al.* 2005, Westerling *et al.* 2011). While ecosystem shifts are concerning in any ecosystem type, the transition from forests to grasslands and shrublands is often particularly alarming due to the loss of carbon storage capacity in forests versus grasslands or shrublands (Liang *et al.* 2018), habitat loss for many wildlife species (*e.g.*, Hobson and Schieck 1999), and the potential economic loss in timber industries (Thomas *et al.* 2017). In some settings, shifts to grassland or shrubland may be long-persisting as alternate stable states that do not transition back to forested ecosystems (*e.g.*, Savage and Mast 2005). Although some studies forecast a reduction of conifer-dominated ecosystems in the coming century due to a combination of climate and disturbances, these studies also point to locations where conifer regeneration may be abundant (Baker 2018, Serra-Diaz *et al.* 2018).

Forest ecosystem transitions are precipitated by both mortality of mature trees and reduced recruitment. Extensive mortality of mature trees due to wildfires, bark beetles, and drought is of growing concern. Severe wildfires contribute to millions of hectares of mature forest loss in the western US every year (NIFC 2018). While there is some debate about whether the proportion of area burned at high severity within large wildfires has increased in recent years (Dillon *et al.* 2011; Flannigan *et al.* 2013, van Mantgem *et al.* 2013, Parks *et al.* 2016a), area burned in large wildfires has increased over the past 30 years in the western US (Dennison *et al.* 2014). Further, mature tree mortality induced by drought stress and the compounding susceptibility to insects has contributed to reduction of forest cover worldwide (Allen *et al.* 2010, Hicke *et al.* 2012, Anderegg *et al.* 2015).

Conifer tree species in the western US exhibit many different life history strategies. Some have traits that aid in regeneration after high-severity fire, including bradspory, or serotiny, in which cones only open after heat is applied, thus protecting seed during a high-intensity fire and releasing viable seeds immediately following wildfires (Lotan 1967). Species like lodgepole pine (*Pinus contorta* Douglas ex Loudon) are often identified as serotinous; however, the proportion of serotinous cones and individuals is highly variable and largely unknown outside of the greater Yellowstone area (Lotan 1967). Populations of lodgepole pine outside of the Rocky Mountains may be primarily non-serotinous, depending on site and disturbance history (Lotan 1967, Alexander 1974). Most conifers in western North America rely on other seed dispersal and reproduction mechanisms. For example, species like whitebark pine (*Pinus albicaulis* Engelm.) and limber pine (*Pinus flexilis* James) can rely on dispersal by animals (Agee 1993). Many other species, including ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), rely on nearby seed trees for wind or gravity dispersal (Agee 1993). Surviving trees are critical sources of seed for tree replacement after fires, thus the severity and extent of mature tree mortality is critical, although less so for serotinous trees. For many species, living seed trees and the number and viability of their seeds plays a critical role in tree establishment. Drought and temperature stress impact the youngest life stages of many plants (Bell *et al.* 2014, Dobrowski *et al.* 2015, Petrie *et al.* 2016). Thus, even with available seed, germination and establishment may be controlled by climatic conditions (Petrie *et al.* 2016), and temperature and moisture requirements vary significantly by species (Petrie *et al.* 2016, Davis *et al.* 2018). In many ecosystems, site conditions such as aspect, slope, and microsite conditions can influence success, with fewer tree seedlings often found on harsh sites (*e.g.*, Bonnet *et al.* 2005).

However, it is unclear how seed source, climate, competition or facilitation, and micro-climates may interact to either promote or inhibit successful reestablishment post fire.

Managers commonly plant trees or plan for natural regeneration from local seed sources (Johnson *et al.* 2010). On federal and state lands in the US, policies require reforestation after logging and fires within areas that are actively managed for timber supply (*e.g.*, 16 U.S.C. § 475, 16 U.S.C. § 551; 81 FR 24785). On private lands, reforestation is typically required after a disturbance by state forest practices acts (*e.g.*, Idaho IDAPA 20.02.01, Washington Title 222 WAC). While some planting may be contested from a historical fire regime perspective or when regeneration is expected to be slow and episodic (*e.g.*, Owen *et al.* 2017, Baker 2018), managers of many public and private lands are mandated to regenerate by law and policy. Thus, there is a need to strategically target their limited money, personnel, and time where they will be effective.

In a regional study of the Rocky Mountains of the US, Stevens-Rumann *et al.* (2018) found decreases in tree regeneration in recent decades partly as a result of increasing temperatures and low moisture availability and long distances to seed sources. They detected a significant change in post-fire climate for fires that burned after 2000 in comparison to fires that burned between 1984 and 2000. However, Stevens-Rumann *et al.* (2018) did not cover a full range of forest types across their study areas, with only subalpine and upper montane forests represented in the northern Rockies, and this warranted an additional analysis of the literature. Here, we built upon this regional dataset with a literature review to address the following questions for all western US forests:

- 1) To what extent do recent studies of post-fire tree regeneration indicate patterns of low tree regeneration densities post fire?
- 2) What causes are attributed to low tree regeneration densities post fire?
- 3) What are the ecological and management implications for the future throughout the West, particularly where extensive mature tree mortality due to fire is coupled with low regeneration densities?

We conducted a systematic review of recently published literature that reported field data on natural tree regeneration following wildfires in the western US. We discuss the ecological and management implications for the future, particularly when a lack of regeneration is coupled with extensive mature tree mortality. We outline key information gaps and scientific uncertainties that currently limit our ability to determine trends in

forest regeneration and predict locations of future climate-induced ecosystem transitions. Finally, we discuss possible management actions that may offset the effects of low regeneration densities, and on which sites.

## Methods

We conducted a systematic search for published accounts of post-fire tree regeneration using the ISI Web of Science (<https://login.webofknowledge.com>) and Google Scholar (<https://scholar.google.com/>). We used different three-word combinations of these key words: “wildfire” and “forest” or “tree regeneration,” or “seedling” and “failure” or “lack of” or “alternate stable states” or “transition” in the searches on both ISI Web of Science and Google Scholar. In addition, we used Google Scholar to find more recent publications that had cited the publications found in our search. To identify potential explanatory factors for tree seedling density, we additionally searched for terms “distance to seed source,” or “climate,” or “repeated fire” in conjunction with “wildfire.” Only peer-reviewed papers published since 2000 that included field measurements of natural (not planted) post-fire tree seedling density in the western US were included in our analysis. Many researchers included statistical modeling, and a few had manipulative experiments or simulation modeling, but such papers without field observations were excluded because we wanted to understand observed tree regeneration patterns.

Data presented here are from studies that focused on natural regeneration. Additionally, we excluded post-fire studies that gave densities of seedlings but did not analyze factors potentially influencing the observed tree regeneration. We limited our inferences to only those studies or parts of studies that focused on areas not treated post fire. Forests worldwide are faced with similar concerns over low regeneration densities (e.g., Retana *et al.* 2002, Pausas *et al.* 2008, Paritsis *et al.* 2015, Morgan *et al.* 2018); however, we felt the potential influencing factors across the world would be many and thus were excluded from our review. While we focused primarily on conifer species, all tree species mentioned in each paper were considered. We focused on papers published since the year 2000 for several reasons. First, if regeneration densities are changing due to climate and increased area burned, as demonstrated in multiple studies (e.g., Littell *et al.* 2009), then we expected these effects to be evident in more recent literature. However, multiple wildfires included in studies presented here burned prior to 2000, with the earliest wildfires in the review dating from the 1940s. Second, while localized climate data dates back to 1979, the availability of these data and use in post-fire studies is only found in the literature in the last 5 to 10 years. While we included

papers in the discussion that focused on >100-year-old fires that employed dendrochronological methods for tree establishment, we intended to focus on patterns of recent regeneration in our review. Additionally, there are many potential disturbances that interact with wildfires to change post-wildfire recovery, such as wind events, pathogens, seed predation, human disturbances, etc. While papers that discussed these topics were included, we focused on the other driving factors of regeneration for this review as well as on the two most prevalent repeated disturbances in the literature: repeated wildfires and bark beetle-fire interactions.

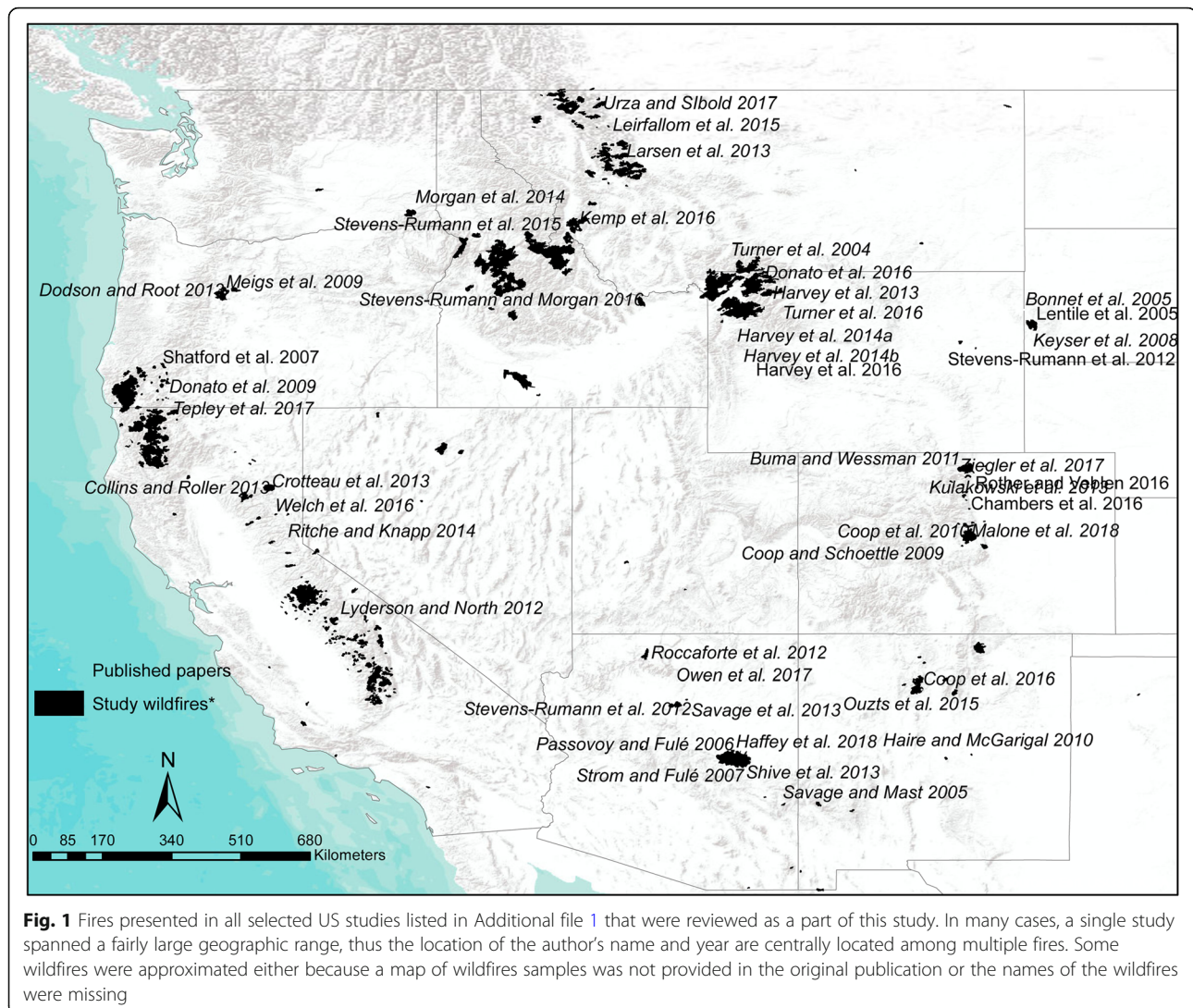
In our management recommendation, we excluded discussions of other post-fire and pre-fire management strategies besides wildfires and planting, as these other aspects of management were not addressed directly in this review. We did not incorporate any studies of regeneration after prescribed fire or forest treatments and did not synthesize data on salvage logging, mulching, or other post-fire management actions. Thus, we did not provide recommendations around these actions.

## Results

We found more than 200 publications in our search. After those not meeting our criteria were excluded, we included the remaining 49 in our synthesis. These publications documented tree seedling presence or density by species for 1 to 64 years following more than 150 wildfires in forests across the western US (Fig. 1).

Post-fire regeneration from 20 conifer tree species were measured in these studies, the most common being ponderosa pine, lodgepole pine, Douglas-fir, subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), and Englemann spruce (*Picea engelmannii* Parry ex Engelm.). Other conifers found in at least one study were twoneedle pinyon (*Pinus edulis* Engelm.), knobcone pine (*Pinus attenuata* Lemmon), sugar pine (*Pinus lambertiana* Douglas), Jeffrey pine (*Pinus jeffreyi* Balf.), whitebark pine, limber pine, bristlecone pine (*Pinus aristata* Engelm.), grand fir (*Abies grandis* [Douglas ex D. Don] Lindl.), white fir (*Abies concolor* [Gord. & Glend.] Lindl. ex Hildebr.), red fir (*Abies magnifica* A. Murray bis), western larch (*Larix occidentalis* Nutt.), incense-cedar (*Calocedrus decurrens* [Torr.] Florin), Rocky Mountain juniper (*Juniperus scopulorum* Sarg.), alligator juniper (*Juniperus deppeana* Steud.), and oneseed juniper (*Juniperus monosperma* [Engelm.] Sarg.). In addition, non-coniferous species that generally composed a small proportion of the observed regeneration except in certain locations included quaking aspen (*Populus tremuloides* Michx.), Gambel oak (*Quercus gambelii* Nutt.), Emory oak (*Quercus emoryi* Torr.), California black oak (*Quercus kelloggii* Newberry), canyon live oak (*Quercus chrysolepis* Liebm.), Pacific madrone (*Arbutus menziesii* Pursh), tanoak





**Fig. 1** Fires presented in all selected US studies listed in Additional file 1 that were reviewed as a part of this study. In many cases, a single study spanned a fairly large geographic range, thus the location of the author's name and year are centrally located among multiple fires. Some wildfires were approximated either because a map of wildfires samples was not provided in the original publication or the names of the wildfires were missing

(*Notholithocarpus densiflorus* [Hook. & Arn.] P.S. Manos, C.H. Cannon, & S.H. Oh), and bigleaf maple (*Acer macrophyllum* Pursh).

Tree seedling density was highly variable, with some plots within a given fire having an abundance of seedlings and other sites having few to none. The warmest and driest sites near lower timberline had the highest probability of none or very few seedlings. Researchers attributed the lack of post-fire tree regeneration success to multiple factors, including distance to seed source, burn severity, moisture stress, increased temperatures, repeated disturbances, topographic variables, and competing vegetation.

Areas with high mortality of mature trees had few tree seedlings. In the studies assessed here, seed availability was often inferred from either distance to a living tree seed source or burn severity. In 26 studies, researchers measured and provided statistical significance for

distance from plots or transects to living trees, although whether this was to a single living tree or distance to a low-severity burned or unburned patch with many trees varied among the studies (Table 1). In 24 of the 26 studies, tree regeneration density decreased significantly at distances of 40 to 400 meters from a living mature tree, regardless of which conifer species was dominant.

Multiple researchers analyzed tree seedling density by burn-severity class (low, moderate, and high severity) or some other ground-truthed version of severity (Table 2). For example, Coop and Schoettle (2009) used “partial burn” or less than 100% versus “complete burn” or 100% tree mortality, while Welch *et al.* (2016) used five severity classes. Additionally, multiple studies measured both severity and distance to seed source (*e.g.*, Coop *et al.* 2010, Rother and Veblen 2016). Proximity to potential seed source trees is often assessed using burn-severity classes, and these burn-severity categories and distance to seed

**Table 1** The US papers from 2005 to 2018 chosen for our literature review that measured and discussed the effect of distance to seed source on tree regeneration following wildfires. Papers, region, significant relationship, and distance are described. A plus sign (+) indicates a positive relationship between distance to seed source and tree regeneration, a minus sign (–) indicates a negative relationship, and a zero (0) indicates no relationship. The major findings describe the distance at which tree regeneration begins to decline, and the distance beyond which no regeneration was detected in parentheses, if identified in individual papers. All distances are in meters. In some cases, a distance was not specified, although a significant relationship was detected. Additionally in some cases, different metrics or descriptions were used and are included here

Study	US Region	Relationship between distance of seed source to seedling density	Major findings
Bonnet <i>et al.</i> 2005	Black Hills, South Dakota	–	50 m
Lentile <i>et al.</i> 2005	Black Hills, South Dakota	–	30 m
Shatford <i>et al.</i> 2007	Pacific Northwest	0	No difference detected between 50 m and 400 m from edge
Tepley <i>et al.</i> 2017	Pacific Northwest	–	Measured “propagule pressure:” the proportion of area within a 400 m radius circle (50 ha) with living trees
Collins and Roller 2013	Pacific Southwest	0	No difference detected
Ritchie and Knapp 2014	Pacific Southwest	–	60 m
Welch <i>et al.</i> 2016	Pacific Southwest	–	40 m
Haire and McGarigal 2010	Southwest	–	150 to 200 m
Owen <i>et al.</i> 2017	Southwest	–	Distance not specified
Haffey <i>et al.</i> 2018	Southwest	–	150 m (225 m)
Coop and Schoettle 2009	Southern Rocky Mountains	–	Negative relationship but seedlings present at all sites
Coop <i>et al.</i> 2010	Southern Rocky Mountains	–	50 to 100 m
Rother and Veblen 2016	Southern Rocky Mountains	–	50
Chambers <i>et al.</i> 2016	Southern Rocky Mountains	–	50 to 100 m
Ziegler <i>et al.</i> 2017	Southern Rocky Mountains	–	Distance not specified
Malone <i>et al.</i> 2018	Southern Rocky Mountains	–	30 m
Donato <i>et al.</i> 2016	Northern Rocky Mountains	– and +	100 m for dry forests; higher densities of <i>P. contorta</i> at farther distances
Harvey <i>et al.</i> 2016	Northern Rocky Mountains	–	150 to 330 m
Kemp <i>et al.</i> 2016	Northern Rocky Mountains	–	95 m
Leirfallom <i>et al.</i> 2015	Northern Rocky Mountains	–	Negative relationship but seedlings present at all sites
Urza and Sibold 2017	Northern Rocky Mountains	–	>100 m
Stevens-Rumann <i>et al.</i> 2015	Northern Rocky Mountains	–	Distance not specified
Stevens-Rumann and Morgan 2016	Northern Rocky Mountains	–	Distance not specified
Stevens-Rumann <i>et al.</i> 2018	Northern Rocky Mountains	–	200 m
Turner <i>et al.</i> 2004	Northern Rocky Mountains	–	“Distance to unburned forest was significant but explained only 3% ... of variation”
Turner <i>et al.</i> 2016	Northern Rocky Mountains	0	No difference detected

source can be highly correlated (Kemp *et al.* 2016). In several studies, tree regeneration was not significantly correlated with burn severity, but tree regeneration did vary with distance to seed source (Coop and Schoettle 2009; Rother and Veblen 2016). Most studies examined here found either no relationship between regeneration and burn severity or a significant decline in regeneration at high-severity burned sites. In contrast, Coop *et al.*

(2010) and Shive *et al.* (2013) found the highest tree regeneration densities at high-severity burned plots, although distance to a living tree was still important.

Numerous additional studies stated that distance to a living tree was measured but did not report if this metric was significant in predicting regeneration. For example, Ouzts *et al.* (2015) recorded distance to the nearest seed source up to 36 m away but no farther, and Harvey *et al.*

**Table 2** Literature that tested the effect of severity on tree regeneration density. Region, severity at which lower regeneration density was observed, and the major findings in relation to severity and its relationship to tree regeneration

Study	US Region	Severity with lower regeneration	Major findings
Keyser <i>et al.</i> 2008	Black Hills, South Dakota	High severity	Regeneration at high burn severity sites consistently lower than low to moderate severity.
Stevens-Rumann <i>et al.</i> 2012	Black Hills, South Dakota	>40% tree mortality	Only 13 out of 50 plots had any regeneration
Stevens-Rumann <i>et al.</i> 2012	Southwest	>60% tree mortality	Only 10 out of 60 plots had regeneration across all severities
Shive <i>et al.</i> 2013	Southwest	Low severity	Pine regeneration was highest in high-severity burned areas
Crotteau <i>et al.</i> 2013	Pacific Southwest	High severity	6 to 9 times lower densities in high severity sites. Mean density of 710 trees ha <sup>-1</sup> in high severity sites
Meigs <i>et al.</i> 2009	Pacific Northwest	High severity	In ponderosa pine forest high burn severity sites, no seedlings were observed. In mixed conifer forests, mean was below 500 trees ha <sup>-1</sup> compared to means above 5000 trees ha <sup>-1</sup> in low to moderate severity sites
Larson and Franklin 2005	Pacific Northwest	Low severity	Douglas-fir regeneration increased with burn severity but other species did not vary by severity and seedling abundance was high across all sites
Coop and Schoettle 2009	Southern Rocky Mountains	No effect of severity	Compared complete burn (100% canopy mortality) to partial burn (<100% canopy mortality): regeneration patterns varied by fire and species, no strong correlation to burn severity
Coop <i>et al.</i> 2010	Southern Rocky Mountains	No effect of severity	Complete burn (100% canopy mortality) had the most regeneration but declined at farther distances to high-severity edge compared partial burns (<100% tree mortality)
Rother and Veblen 2016	Southern Rocky Mountains	No effect of severity	Low regeneration rates across all severities, no consistent pattern
Harvey <i>et al.</i> 2013	Northern Rocky Mountains	High Severity	Crown and severe surface fire had a median density of 0 trees ha <sup>-1</sup> , while light surface fires had a median of 167 trees ha <sup>-1</sup>
Welch <i>et al.</i> 2016	Pacific Southwest	High severity, intermediate severity	Seedling density was lowest at high burn severity and highest at low-moderate and high-moderate severity

(2013) included distance to seed source in a regression tree, but neither study reported these results. Donato *et al.* (2009) stated the range of distance to seed sources measured, but did not present analysis on this variable. Similarly, Savage and Mast (2005), Shive *et al.* (2013), and Morgan *et al.* (2014) stated that patterns of tree regeneration were influenced by distance to seed source, but results of analysis on this factor were not presented.

Only six studies explicitly analyzed climate as a factor in post-fire tree regeneration. The significant climate metrics included moisture deficit of some kind as the most common influence on regeneration, followed by either annual or seasonal precipitation (Table 3). While all studies identified here found that water stress influenced regeneration, one study demonstrated a relationship to degree days for one species (Urza and Sibold 2017). Donato *et al.* (2016), Kemp *et al.* (2016), and Dodson and Root (2013) discussed potential site climates through topographic proxies and metrics like heat load index, forest type, or elevation-precipitation-temperature gradients, but did not analyze climate directly.

Repeated disturbances, topography, and competing vegetation also influenced tree regeneration. In the five

studies that examined tree seedling response to repeated wildfires, short intervals between wildfires (1 to 30 years) resulted in a decline in post-fire tree regeneration density compared to once-burned areas (Table 4). The four studies on the effect of bark beetle outbreaks and wildfires were less consistent across species and studies. Topographic factors including elevation, aspect, and slope, were common predictors in many of the studies assessed here, as were potential competition of shrubs, non-native grasses, and resprouting deciduous trees. At least 27 studies presented in this review found one of these factors to be significant (Additional file 1).

## Discussion

### Fires are catalysts for forest change

Several factors dominated in explaining tree regeneration patterns post fire. First, seed supply is required for seedling establishment unless planted; thus, proximity to living trees was important across many of the tree species in the studies presented here, including species that are serotinous, animal dispersed, and wind or gravity dispersed. Tree regeneration density decreased at distances of 40 to 400 meters from a living mature tree,

**Table 3** Literature that discussed the influence of various climate metrics on tree regeneration following wildfires. Study, region, significant climate metric evaluated, the time period over which climate was considered, and the relationship of said climate variable and tree regeneration along with additional information on major findings. A plus sign (+) indicates a positive relationship between climate metric and tree regeneration, a minus sign (–) indicates a negative relationship, and a zero (0) indicates no relationship. Specific species-level information is described when individual papers analyzed climate variables against individual species

Study	Region	Climate metric	Time period of metric	Relationship between climate variable and regeneration
Urza and Sibold 2017	Northern Rocky Mountains	Growing season precipitation, degree days	8 years post fire	+ Larch, Douglas-fir, Englemann spruce + for Douglas-fir only
Harvey <i>et al.</i> 2016	Northern Rocky Mountains	Drought severity	4 years post fire	– All species combined – Englemann spruce, subalpine fir 0 lodgepole pine, Douglas-fir, larch, aspen, whitebark pine
Stevens-Rumann <i>et al.</i> 2018 <sup>a</sup>	Rocky Mountains	Post-fire moisture deficit, average moisture deficit	3 years post fire, 30 year average climate	– pre 2000, 0 post 2000 + pre 2000, – post 2000
Tepley <i>et al.</i> 2017	Pacific Northwest	Mean moisture deficit	Post-fire deficit	– all species analyzed together
Savage <i>et al.</i> 2013	Southwest	Drought	Post-fire drought	– fire at the end of the drought had more regeneration than those fires from the middle of the drought
Welch <i>et al.</i> 2016	Pacific Southwest	Precipitation	Post-fire annual precipitation	+ for all forest types and mixed conifer

<sup>a</sup>In this one case, the influence of climate was analyzed separately in two different climatic periods and is described instead of individual species influenced

especially for ponderosa pine, Douglas-fir, and true firs across the western US. However, several studies of often animal-dispersed species such as whitebark pine and limber pine also experienced a decline in density at longer distances from seed trees. Both Coop and Schoettle (2009) and Leirfallom *et al.* (2015) found tree seedling densities declined with increasing distance from mature trees unaffected by white pine blister rust (*Cronartium ribicola* J.C. Fisch), although this decline was more

gradual than for species that only relied on wind or gravity dispersal. Studies that examined the relationship between lodgepole pine seedling density and distance to a living lodgepole pine found variable relationships. For example, Turner *et al.* (2004) found a small but significant negative relationship of seedling density to distance to live seed source, while Kemp *et al.* (2016) and Urza and Sibold (2017) and Turner *et al.* (2016) found no relationship. Donato *et al.* (2016) found a positive relationship

**Table 4** Literature that discussed the impact of interacting disturbances on tree regeneration. Studies, forest type, and described interacting disturbances identified. Fire-fire indicates that a study examined two wildfires that reburned the same area; bark beetle-fire describes studies that examined bark beetle outbreaks that preceded a wildfire. The influence of disturbances column explains the differences observed between areas that only experienced a wildfire and those that experienced either a previous bark beetle outbreak or a previous wildfire

Study	Forest type	Disturbances	Influence of disturbances
Coop <i>et al.</i> 2016	Ponderosa-mixed conifer	Fire-fire	Higher reburn severity promoted transition to non-forest cover types
Donato <i>et al.</i> 2009	Mixed conifer	Fire-fire	No reduction in regeneration
Harvey <i>et al.</i> 2014a	Lodgepole	Bark beetle-fire	No reduction in regeneration
Harvey <i>et al.</i> 2014b	Lodgepole	Bark beetle-fire	No reduction in regeneration
Harvey <i>et al.</i> 2013	Douglas-fir	Bark beetle-fire	Low tree regeneration in bark beetle and high severity fire areas
Larson <i>et al.</i> 2013	Dry mixed conifer	Fire-fire	Repeated fires killed regeneration from the first fire but restored a more historical species composition
Lydersen and North 2012	Ponderosa-mixed conifer	Fire-fire	Shrub cover increased and decreased regeneration
Stevens-Rumann <i>et al.</i> 2015	Dry mixed conifer	Bark beetle-fire	No reduction in regeneration due to both disturbances
Stevens-Rumann and Morgan 2016	Dry and moist mixed conifer	Fire-fire	Tree regeneration reductions in repeated high-severity fires



between distance to live seed source and relative abundance of lodgepole pine seedlings. However, this could be explained by the proximity to nearby burned, serotinous individuals and lack of other species regenerating at far distances from living trees, rather than a relationship to live lodgepole pine trees. To some degree, the lack of consistency in the importance of proximity of a burned location to live lodgepole pines may be due to the proportion of lodgepole pines that are serotinous, which was demonstrated through the differing predictive factors of serotinous versus non-serotinous lodgepole pine by Harvey *et al.* (2016). In this case, non-serotinous lodgepole pine was negatively correlated to distance while serotinous lodgepole pine was not (Harvey *et al.* 2016). Additionally, the distance at which regeneration declined appeared to vary by species, with seedling density declining at distances around 400 m from seed-source Douglas-fir trees in the Pacific Northwest (Donato *et al.* 2009), and as close as 40 to 100 m from seed-source ponderosa pines in the Black Hills in South Dakota, the southern Rocky Mountains in Colorado and Wyoming, and the Pacific Southwest (*e.g.*, Bonnet *et al.* 2005, Ritchie and Knapp 2014, Rother and Veblen 2016). To some degree, regional differences may be driven by different regenerating species, like patterns of regeneration in ponderosa pine versus Douglas-fir. However, many studies reported significance of regeneration across all species, not for individual species except for Kemp *et al.* (2016), Urza and Sibold (2017), Coop and Schoettle (2009), and Harvey *et al.* (2016) (See Additional file 1 for more details). Additionally, several studies only saw one regenerating species; thus, their findings were specific to only one species, such as Bonnet *et al.* (2005) in the Black Hills, which only observed ponderosa pine regeneration.

A burned site's distance to living trees to living trees is also simply a proxy for explaining the availability of seeds. However, the assumption that living nearby trees equals adequate available seed is not always accurate. For example, Leirfallom *et al.* (2015) demonstrated that it was the proximity to healthy, non-blister-rust affected, whitebark pine trees that was important, not just proximity to simply living trees. Similarly, ponderosa pine trees in the southwestern US and in the southern Rocky Mountains have episodic regeneration events (Savage *et al.* 1996). Thus, proximity to a living, mature tree does not always guarantee seed availability. More research is needed to identify locations where the lack of tree regeneration is due to lack of seed production or seed viability instead of proximity to trees.

Second, changing climatic conditions are influencing regeneration densities, as climate has for centuries. With the increasingly warm springs and summers in recent decades throughout the western US (IPCC 2013), conditions for seedling survival are changing. On the driest

sites, even a small increase in water deficit could negatively influence tree regeneration (Stevens-Rumann *et al.* 2018). On colder, more mesic sites, these changing climatic conditions could promote regeneration where previously limited by cold or snow (Stevens-Rumann *et al.* 2018). Water deficit, low precipitation, or drought reduced regeneration success in all studies. The correlation between increased regeneration and available moisture is supported by Petrie *et al.* (2017), who found this to be an important predictor of seedling success in greenhouse experiments. Additionally, in a multi-century analysis of tree establishment, Brown and Wu (2005) found strong links between seedling establishment and moister climatic conditions. However, in the case of Brown and Wu (2005), the pattern of establishment during cooler and wetter climatic periods correlated with periods of decreased fire activity; thus, the growth of individual trees to a fire-resistant age between wildfires may contribute to the observed cohort of tree establishment, as others have found (Meunier *et al.* 2014). Modeling exercises similarly found correlations between tree seedling response and both moisture gradients and temperature following wildfires (Hansen *et al.* 2018). Thus, changes in precipitation patterns may play a large role in the vulnerability of regenerating trees in a warmer climate, and abnormally moist years following wildfires may allow for germination and establishment in otherwise non-regenerating sites. The relationship between climate and regeneration is an aspect of post-fire seedling establishment that warrants extensive additional research.

Individual tree species respond differently to environmental stressors due to their varying environmental requirements and species characteristics (Dobrowski *et al.* 2015, Davis *et al.* 2019). In dry forests dominated by ponderosa pine and Douglas-fir trees, ponderosa pine appears to be more susceptible to regeneration failure (Davis *et al.* 2018), but current observed patterns could also be related to the longer seed dispersal distances for Douglas-fir. However, these studies focus on lower elevational ranges of these species; thus, it is important to consider how species ranges may expand as higher elevations and higher latitudes become more favorable to tree growth (Lenoir *et al.* 2008). In this review, only three studies explicitly tested for species shifts following wildfires (Buma and Wessman 2011, Kulakowski *et al.* 2013, Donato *et al.* 2016), and only one examined potential climate-induced range shifts following wildfires (Donato *et al.* 2016). Understanding how species ranges may expand, in addition to contract, will be critically important for forest management of burned areas in the coming decades.

As discussed previously, most studies presented here combined species for analyses even though it is well understood that species respond differently to

environmental and climatic conditions. This is further demonstrated by climate envelope modeling (e.g., Rehfeldt *et al.* 2014), which suggests that different species will have variable responses to climate change. Rehfeldt *et al.* (2014) predicted a 50% decline in the range of ponderosa pine by 2060. Alternatively, in higher elevation forests, most observed tree regeneration studies demonstrated consistent and often abundant regeneration of lodgepole pine, even where there were few seedlings of other tree species (e.g., Harvey *et al.* 2016). While documented declines in lodgepole pine regeneration have not been observed, there is modeling evidence that lodgepole pine may see substantial declines in the coming decades due to both an increase in fire frequency (Westerling *et al.* 2011) and continued changes in climatic conditions (Coops and Waring 2011). All of this speaks to the large degree of uncertainty around individual species responses to climate variability following wildfires.

Third, multiple disturbances such as bark beetles and fire and repeated fire are playing an increasingly important role in tree establishment. As the extent of wildfires increases, in part due to climate (Westerling *et al.* 2011; Dennison *et al.* 2014), so will the area repeatedly burned (Prichard *et al.* 2017). Similarly, interactions between wildfires, drought, insects, and pathogens are expected to increase (Hicke *et al.* 2016). Repeated wildfires or the combination of bark beetle infestation and wildfire may influence ecosystem transitions. Repeated high-severity wildfires in short succession may be precipitating vegetation changes (Table 4). This change is likely due to the repeated disturbances themselves, not increasing distance to seed source, as at least in several studies, distance to seed source did not vary between once burned and repeatedly disturbed areas (e.g., Stevens-Rumann and Morgan 2016). However, repeated wildfires at low to moderate severity that result in the survival of at least some overstory trees, especially in low elevation forests that would have historically burned at more frequent intervals, may be maintaining more open forests rather than precipitating a transition to non-forested ecosystems (Larson *et al.* 2013; Stevens-Rumann and Morgan 2016; Walker *et al.* 2018). In studies of tree seedling response after bark beetle outbreaks and wildfires, the findings are less consistent and these two disturbances, in many cases, do not seem to be decreasing tree regeneration (Harvey *et al.* 2014a, 2014b; Stevens-Rumann *et al.* 2015). Conversely, Harvey *et al.* (2013) did find significant declines in tree regeneration follow bark beetle outbreaks and high-severity wildfires in Douglas-fir-dominated systems. Given the relatively small number of studies on repeated disturbances and lack of agreement among studies, future research is needed, especially in the face of increasingly common overlap of disturbances in both time and space.

Fourth, tree regeneration was less successful post fire in particular site conditions, with the most common influences being elevation, slope, aspect, and competing vegetation. Steeper slopes and more westerly or southerly aspects often resulted in lower regeneration density compared to shallower slopes and northerly and easterly aspects (Lydersen and North 2012, Kemp *et al.* 2016; Ziegler *et al.* 2017). In some locations, highly competitive and potentially flammable non-forest vegetation may result in positive feedbacks by burning readily and thus continuing dominance by non-forest vegetation (Wilson and Agnew 1992, Donato *et al.* 2009). In many locations, forests are being replaced by non-forest vegetation, but the replacing vegetation varies. In California, the primary concern, especially in drier forest sites at low elevations, is that the chaparral shrubland vegetation replacing forests is highly flammable (e.g., Collins and Roller 2013). In the US northern Rocky Mountains, forests are more commonly replaced by grass or shrubs (e.g., Kemp *et al.* 2016), while in the southwestern US and some places in the southern Rocky Mountains, conifers are often being replaced by resprouting trees or shrubs (e.g., Haire and McGarigal 2010, Roccaforte *et al.* 2012). All these potential ecosystem transitions to grasslands or shrublands should be assessed with an understanding of the historical heterogeneity. In some places, wildfires may be restoring the historical vegetation structure where tree establishment only occurred as a result of fire suppression (Hessburg *et al.* 2005, Nagel and Taylor 2005). Thus, there is a need to identify where the lack of regeneration is creating new and novel conditions on a site versus where little or no regeneration is promoting historical heterogeneity. More research is needed in this area to promote sound management intervention in areas of concern.

Understanding the relative importance of the variables presented here will be critical for adaptive fire management in the future. Climate may drive changes in some forested systems, while the disturbance, topography, or competing vegetation may drive changes in other forests. Scientists and managers are implementing experiments to understand the contributing factors (e.g., Tercero-Bucardo *et al.* 2007, Rother *et al.* 2015, Petrie *et al.* 2017), but more analysis of species-specific vulnerabilities is needed to fully understand responses to climate, landscape settings, and biological interactions.

#### Limitations and research needs

Comprehensive understanding of the drivers of natural regeneration and thus areas where true regeneration “failures” occur is limited by three prominent limitations that warrant further research: (1) understanding spatial variability across burned landscapes, (2) quantifying temporal variability of regeneration patterns, and (3)

identifying the controlling mechanisms of regeneration success. First, while tree seedling density may be low in many burned areas, it is highly variable spatially and, as such, researchers should be careful to conclude that large, high-severity burned patches are not regenerating at all without sampling larger plots to characterize spatial variability of fire effects and tree regeneration. The plots used to sample tree regeneration were small across most studies (generally less than 600 m<sup>2</sup>). However, in studies using plot sizes of 4 ha, tree seedlings were always detected (Owen *et al.* 2017). Fully understanding spatial and temporal variability of fire effects and vegetation post fire is important to ecosystem function, yet we often do not capture this with a smaller plot size and short periods of study.

Second, time since fire has long been a concern for making inferences about ecosystem trajectory and recovery. Some long-term studies suggested continued recruitment through decades to even centuries following wildfires (MacKenzie *et al.* 2004, Tepley *et al.* 2013, Freund *et al.* 2014). While many of the sites studied here may continue to see tree regeneration in the coming decades, short-term tree regeneration patterns are often highly correlated with long-term regeneration patterns (*e.g.*, Coop *et al.* 2010). Thus, the patterns of regeneration in the first few years post fire will likely influence the trajectory of that ecosystem (Turner *et al.* 2016). Most of the studies only presented data for <10 years post fire, with some studies as short as 1-2 years post-fire (*e.g.*, Strom and Fule 2007, Larson *et al.* 2013), although some studies presented did span a large time since fire, of 25-64 years post fire (*e.g.*, Passovoy and Fule 2006, Haire and McGarigal 2010). Further, past regeneration patterns may be very different from future patterns given the increasingly unfavorable climate for tree regeneration, especially at lower elevational ranges. Thus, discussion of persistent non-forest vegetation shifts is more prevalent and the level of uncertainty around continued gradual regeneration through time is an ongoing concern. That said, some of these vegetation shifts may be offset by one or several consecutive moist or cool and moist years that could promote tree establishment and growth, even in a warmer climate (Serra-Diaz *et al.* 2018), thus there is need for additional research into the mechanisms controlling tree germination and regeneration.

Finally, the processes driving seedling establishment and survival in burned areas specifically may vary from unburned areas and greenhouse experiments (Petrie *et al.* 2017). The interaction among all potential influencing drivers in post-fire environments are complex, and measurements like distance of a site to living trees or fine resolution climate variables may not adequately explain the processes involved in germination and survival. Some

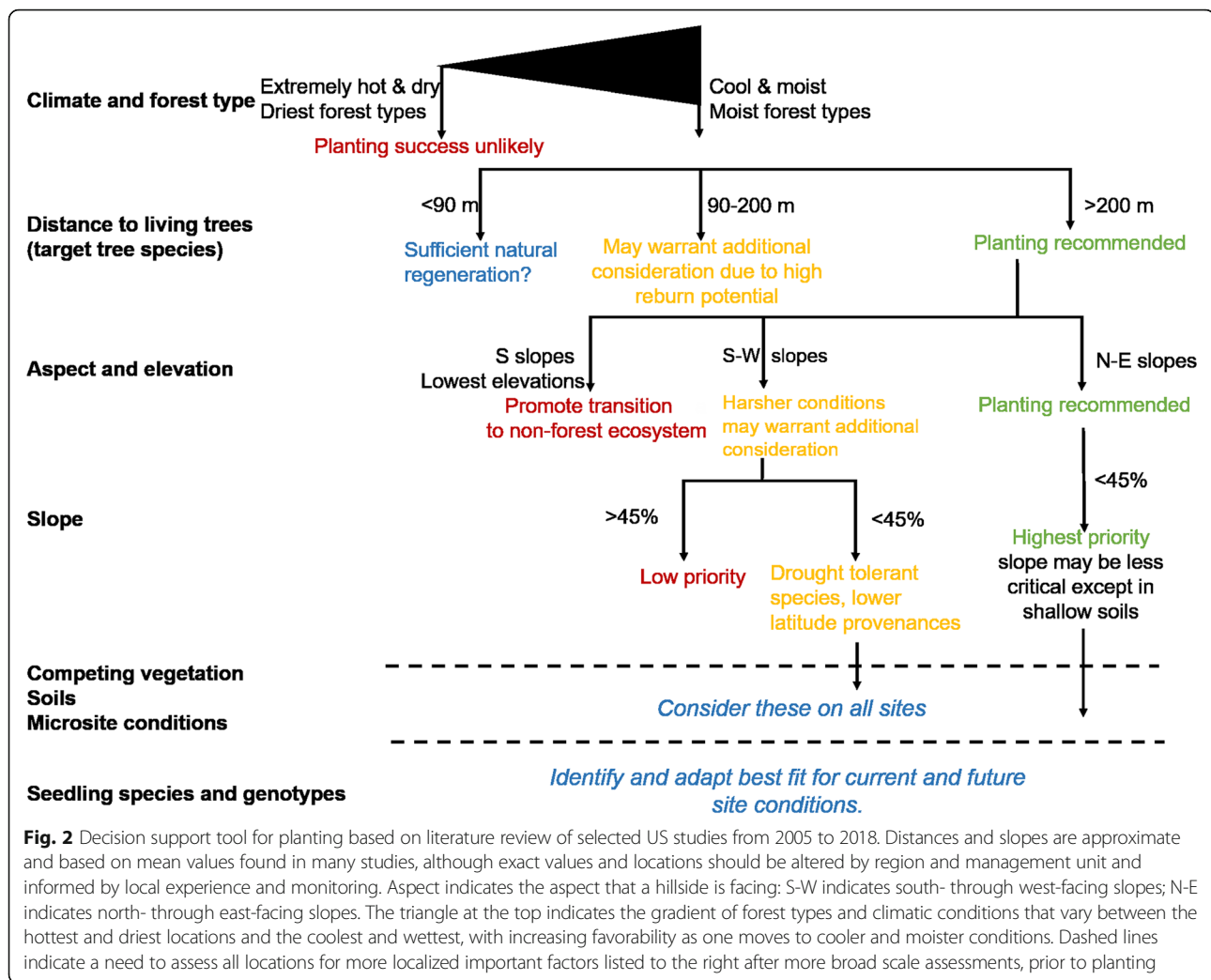
alternative explanations for a lack of regeneration that were not considered here but could be important include competing vegetation, other pre-fire disturbances not often described (*e.g.*, Buma and Wessman 2011, Leirfallom *et al.* 2015), highly variable cone production, seed viability that is linked to climate and many other factors (*e.g.*, Buechling *et al.* 2016), and slow regeneration rates that may be natural for some species and harsh sites. Authors of studies presented here often attributed slow regeneration to changing climate, but there are relatively few studies on physiology of cones, seeds, and seedlings in these settings. To truly determine how a lack of regeneration in the short term post fire corresponds to long-term persistence of non-forest communities, further considerations of these mechanistic influences, temporal variability, and spatial variability are necessary.

### Management in a world of more fires and less tree regeneration

Multiple management strategies can be employed to help forests adapt to more fires and more burned area in a changing climate. Specifically, we propose several management strategies to promote tree survival during fires and higher likelihood of tree regeneration success, especially of tree species that are not serotinous. We generally break these strategies into two categories that correspond to two of the dominant drivers of tree regeneration presented here: (1) how to adapt post-fire management strategies, such as planting, to changing climate, and (2) how to mitigate large high-severity burn patches and, thus, long distances to living tree seed sources.

### Planting in a changing climate

Strategies for managing landscapes after wildfire must consider climate suitability now and in the future. The many factors interacting to influence seedling germination and establishment warrant consideration prior to post-fire management. We made a decision tree (Fig. 2) based on the literature presented here and in consultation with managers. This decision tree framework can be used to guide planting and other management considerations within wildfire perimeters. We propose that, along with considerations of the forest plans, site objectives, and funding availability, current and future precipitation quantity and patterns and temperature are carefully evaluated along with forest type that can indicate general climatic conditions. While science may suggest that climate consideration or forest type should be the first factor in decision making, we acknowledge that management of burned landscapes is often influenced by more than science; thus, our decision tree begins once an area has been prioritized for potential reforestation. In some cases, forest plans and general guidelines for



site objectives should be refined to incorporate climate change more effectively, although this is beyond the scope of our decision tree.

As climate becomes increasingly unfavorable to tree establishment for many species within portions of their current distribution, we must identify areas that may be favorable for target species, given the current and future climate. As multiple studies presented here demonstrated, the climate on some sites may not be currently, or in the near future, compatible with the establishment and survival of those tree species present pre fire (e.g., Davis *et al.* 2019). Planting trees should be limited to prime locations for tree regeneration success, now and in the future climate, that are not expected to regenerate without management intervention. Thus, promoting productive and diverse non-forested ecosystems or new, novel forested ecosystems may be the best course of action in some locations. For example, many studies showed that those areas at the lowest elevations, or often in the hottest and driest forests were regenerating poorly

(e.g., Dodson and Root 2013, Donato *et al.* 2016; Stevens-Rumann *et al.* 2018), thus it may be beneficial to identify whether these sites could continue to support similar species assemblages before planting, and perhaps prioritize those sites that are slightly cooler and wetter over the harshest sites. Alternatively, planting diverse tree species or a single species from a genetically diverse pool may help overcome some of the site productivity limitations, especially if current individuals are no longer suitable but a forest ecosystem is still desired.

Our second broad-scale, science-based consideration is proximity to a seed source. As the literature presented here demonstrated, there are multiple locations where tree regeneration is likely to be abundant, such as within small high-severity burned patches or within 50 to 100 m of living trees; thus, these areas may not need to be replanted. Conversely, planting may be necessary to reforest in large, high-severity burned patches with long distances to surviving seed-source trees. Distance to living trees was an important predictor of post-fire tree seedling density; thus,



understanding the shape and size of high-severity burned patches is critical in understanding the potential for tree regeneration and when management intervention may be desired (Shive *et al.* 2018). Mapping high-severity burned patches through satellite imagery can begin to address which areas are large enough to warrant concern, and where competing vegetation may pose a threat to delayed planting success. In many cases, no planting may be recommended due to the size and shape of those large patches, even within large fires. Even in large patches, the irregular shape and unburned islands leave much burned area close to surviving trees that can be potential seed sources. For instance, Kemp *et al.* (2016) found that, on 21 large fires, >75% of the burned area was within 95 m of surviving trees. Thus, planting efforts should be focused on those largest, high-severity burned patches in which large areas within the patches are more than 100 to 400 m, depending on region and species, from a lesser burned edge or unburned island of substantive size (North *et al.* 2019).

We propose not planting trees close to the edge of high-severity burned patches to avoid areas that will likely experience high fuel accumulations through time (*e.g.*, Roccaforte *et al.* 2012; Eskelson and Monleon 2018) and thus experience higher potential for reburning (Prichard *et al.* 2017). Prior fires can limit fire extent or burn severity for ~5 to 20 years, depending on region, forest type, and individual fire events (Parks *et al.* 2015; Parks *et al.* 2016b). Thus, providing a buffer and potential containment area within a high-severity burn perimeter will decrease the likelihood of burning planted seedlings. With the increasing likelihood of reburns, managers should be conscious of where and how subsequent fires may burn and how tree seedlings may contribute to the fuel loading. We propose planting only within the interior of large, high-severity burned patches to avoid loss of money and effort invested in planting tree seedlings.

After these first two broad-scale considerations of climate and seed source availability, we focus on those finer-scale topographic or topo-climate variables that are important for regeneration success across the western US. Elevation, aspect, and slope all play roles in identifying suitable locations for planting. We provide general guidelines for these different metrics, but local knowledge and adaptations will be necessary. For example, Kemp *et al.* (2016), Donato *et al.* (2016), and many others demonstrated that less regeneration was naturally occurring at the lowest elevation sites on south- to southwest-facing slopes, thus indicating that these sites may be outside of their climatic tolerance. Conversely, a south-facing slope at a high elevation location could promote regeneration at the upper elevational range of a particular species. Slope may be more important in combination with soil

properties. Shallow soils on steep slopes may not promote regeneration establishment, but in deep, rich soils, perhaps the slope percentage is of less concern.

Finally, multiple studies found local site conditions to be important and should always be considered prior to planting. Identifying if and where competing vegetation may either deter natural regeneration or compete against planted seedlings may alter planting timelines. For instance, promoting immediate post-fire planting in areas of fast-growing, resprouting species may be more important in some areas, while in other areas where competing vegetation is less of a concern, allowing a couple of years to observe natural regeneration densities may be warranted before planting. Soil types and soil depths may influence the density or species planted, and a plethora of microsite conditions, such as the presence of nurse structures, may be important considerations (Haffey *et al.* 2018). All of these are very site specific and may even vary across a treatment unit, thus requiring manager discretion, drawing on local experience.

#### Using fire to promote natural regeneration

Hessburg *et al.* (2015) outlined seven principles for managing landscapes strategically. They emphasized the need for thinking about where to do what treatments, including doing nothing in some locations. Increasing landscape-level treatments, including thinning, fuels treatments, prescribed fire, or managed wildfires, could curtail the area that burns under extreme conditions, and thus increase the potential for survival of trees that could provide seed sources for regeneration. Currently, multiple researchers and managers are suggesting increasing strategic planning pre fire that focuses on limiting risk to firefighters, managing the very high costs of fire suppression, and developing a preemptive strategic plan for managing wildfires (Thompson and Calkin 2011, Schoennagel *et al.* 2017). Managing fires often includes aggressive fire suppression that will likely continue when human values are at risk. However, in places where risk to human values is low and ecological need is high, we join others in advocating for less aggressive suppression actions (Schoennagel *et al.* 2017, Halofsky *et al.* 2018). Likely, this means delaying, herding, and otherwise managing ongoing fires to foster survival of seed source trees and desirable patch size distribution (Hessburg *et al.* 2015). The National Cohesive Fire Management Strategy (USDA and USDI 2018), which is supported by federal, state, and other managers, calls for fire suppression when possible and desired, as well as using fire as part of natural resource management. Part of adapting to a future of more frequent and larger fires will be appreciating when wildfires are doing “good work” to further vegetation management goals.

With respect to post-fire tree regeneration, the broader goals of these managed wildfires include fostering survival of more adult trees to rain seed through time, and creating less severe, patchier fire effects. Both effects are more likely when fires burn under less extreme conditions—the very conditions in which fire suppression is most effective. Increasing the proportion of “fire refugia,” unburned or low-severity burned sites, could provide more ecological services (Kolden *et al.* 2012, Meddens *et al.* 2018), and while the promotion of fire refugia is important under any burning condition, less extreme weather conditions promote the creation and maintenance of “fire refugia” (Krawchuk *et al.* 2016). Some forest openings, especially when smaller in size, may be ecologically beneficial and increase the heterogeneity of landscapes.

Ultimately, these approaches blend together for, in most areas, fires will occur in the future and what we do post fire will affect the forest conditions prior to the next fire and how that next fire will burn. Decisions need to be strategic for, in years of widespread fire, there are more areas to plant than there are trees, and there are many sites that will likely not support similar forests to those found pre fire. All management strategies, including no action, have consequences that can be evaluated to inform management decisions.

## Conclusions

Management actions that could offset the effects of low tree regeneration densities in the first years following a wildfire on some sites include prescribed burning and managing fires to burn more area under less extreme conditions to favor more seed source trees surviving, and planting post fire in locations where seedlings are most likely to survive in terms of microsite and site conditions and risk of future fires. Triage among sites is needed to strategically differentiate those sites for which management actions are most likely to be worth the effort and cost. For instance, post-fire tree seedling densities are high on many mesic sites, and on many sites close to seed source trees where regeneration may eventually occur, while others are so warm and dry that even with intensive effort, neither planted nor naturally regenerated trees are likely to survive (Stevens-Rumann *et al.* 2018). Baker (2018) aptly points out that some sites will regenerate slowly without intervention and management actions may not always be warranted. Fire suppression has, in many ecosystems across the western US, increased tree density, forest continuity, and homogeneity, and allowed encroachment of many trees into non-forested ecosystems (*e.g.*, Gruell 2001, Nagel and Taylor 2005). As a result, some loss of forest area may restore historical landscape heterogeneity of different ecosystem types. Thus, while we have focused on the

lack of tree regeneration and possible pathways for restoring forest ecosystems, in some cases promoting a non-forested ecosystem may be recommended even if the site is climatically suitable for forests.

While reactive treatments will no doubt occur, proactive management informed by assessment of forest vulnerability is sorely needed. Such an approach could mean that we prescribe more fires and manage more wildfires to foster future resilience (Schoennagel *et al.* 2017). However, with the projection for larger fires and longer fire seasons, vulnerability of forests for which disturbance-induced tree mortality overlaps with and contributes to lack of tree regeneration, we will also have to accept that some forests will be replaced by shrublands, woodlands, and grasslands as we adapt to a future with more fire.

## Additional file

**Additional file 1:** All US studies from 2005 to 2018 that were included in the literature review, showing region, time since fire, and significant variables found to influence tree regeneration. (DOCX 22 kb)

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## Availability of data and materials

No unique data were created in the writing of this manuscript, so no additional data are available.

## Authors' contributions

CSSR carried out the search and synthesis. PM and CSSR wrote and edited the manuscript, participated in the interpretation of the results, and read and approved the final manuscript.

## Ethics approval and consent to participate

Not applicable.

## Consent for publication

Consent for publication not applicable as we did not use data from individual people.

## Competing interests

The authors declare that they have no competing interests.

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