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Tamm Review: Reforestation for resilience in dry western U.S. forests



Malcolm P. North^{a,k,*}, Jens T. Stevens^{b,c}, David F. Greene^d, Michelle Coppoletta^e, Eric E. Knapp^f, Andrew M. Latimer^a, Christina M. Restaino^g, Ryan E. Tompkins^h, Kevin R. Welch^a, Rob A. York^b, Derek J.N. Young^a, Jodi N. Axelson^b, Tom N. Buckley^a, Becky L. Estesⁱ, Rachel N. Hager^j, Jonathan W. Long^k, Marc D. Meyer^l, Steven M. Ostoja^m, Hugh D. Safford^{n,o}, Kristen L. Shive^b, Carmen L. Tubbesing^b, Heather Vice^a, Dana Walsh^p, Chhaya M. Werner^b, Peter Wyrsch^b

- ^a Dept of Plant Sciences, University of California, Davis, CA 95616, United States
- ^b Environmental Science, Policy, and Management Dept., University of California, Berkeley, CA 94720, United States
- ^c New Mexico Landscapes Field Station, U. S. Geological Survey, Santa Fe, NM 87508, United States
- ^d Dept. of Forestry and Wildland Resources, Humboldt State University, Arcata, CA 95521, United States
- ^e USDA Forest Service, Sierra Cascade Regional Ecology Program, Quincy, CA 95971, United States
- f USDA Forest Service, PSW Research Station, Redding, CA 96002, United States
- g Tahoe Regional Planning Agency, Stateline, NV 89449, United States
- h USDA Forest Service, Plumas N.F., Quincy, CA 95971, United States
- ⁱ USDA Forest Service, Central Sierra Regional Ecology Program, Placerville, CA 95667, United States
- ^j Dept. of Watershed Sciences, Utah State University, Logan, UT 84321, United States
- k USDA Forest Service, PSW Research Station, Davis, CA 95618, United States
- ¹ USDA Forest Service, Southern Sierra Regional Ecology Program, Bishop, CA 93514, United States
- m USDA California Climate Hub, Agricultural Research Service, University of California, Davis, CA 95616, United States
- ⁿ USDA Forest Service, Regional Ecology Program, Vallejo, CA 94592, United States
- Operatment of Environmental Science and Policy, University of California, Davis, CA 95618, United States
- P USDA Forest Service, Eldorado N.F., Georgetown, CA 95634, United States

ARTICLE INFO

Keywords: Climate change Drought Fire Spatial heterogeneity Tree mortality Tree regeneration Young plantations

ABSTRACT

The increasing frequency and severity of fire and drought events have negatively impacted the capacity and success of reforestation efforts in many dry, western U.S. forests. Challenges to reforestation include the cost and safety concerns of replanting large areas of standing dead trees, and high seedling and sapling mortality rates due to water stress, competing vegetation, and repeat fires that burn young plantations. Standard reforestation practices have emphasized establishing dense conifer cover with gridded planting, sometimes called 'pines in lines', followed by shrub control and pre-commercial thinning. Resources for such intensive management are increasingly limited, reducing the capacity for young plantations to develop early resilience to fire and drought. This paper summarizes recent research on the conditions under which current standard reforestation practices in the western U.S. may need adjustment, and suggests how these practices might be modified to improve their success. In particular we examine where and when plantations with regular tree spacing elevate the risk of future mortality, and how planting density, spatial arrangement, and species composition might be modified to increase seedling and sapling survival through recurring drought and fire events. Within large areas of contiguous mortality, we suggest a "three zone" approach to reforestation following a major disturbance that includes; (a) working with natural recruitment within a peripheral zone near live tree seed sources; (b) in a second zone, beyond effective seed dispersal range but in accessible areas, planting a combination of clustered and regularly spaced seedlings that varies with microsite water availability and potential fire behavior; and (c) a final zone defined by remote, steep terrain that in practice limits reforestation efforts to the establishment of founder stands. We also emphasize the early use of prescribed fire to build resilience in developing stands subject to increasingly common wildfires and drought events. Finally, we highlight limits to our current understanding of how young stands may respond and develop under these proposed planting and silvicultural practices, and identify areas where new research could help refine them.

E-mail address: mnorth@ucdavis.edu (M.P. North).

^{*} Corresponding author.

1. Introduction

Recent increases in wildfire and drought-related mortality have created significant reforestation challenges for managers. For example, in California the annual area burned since 2000 (228,000 ha) is double the annual area burned over the previous three decades (FRAP, 2018). Equally problematic for managers, the increase in area burned has been accompanied by a dramatic increase in the proportion of burns experiencing crown fire (e.g. in yellow pine/mixed conifer forests the high severity fraction has increased from an historical range of 4-13% to 32% (Miller and Safford, 2012; Safford and Stevens, 2017; FRAP, 2018)). Large, stand-replacing fires lead to sizeable areas without nearby seed sources for non-serotinous tree species and thus natural regeneration is frequently inadequate, especially > 200 m from a live tree seed source (Greene and Johnson, 1996; Welch et al., 2016; Stevens et al., 2017). In addition, droughts such as California's 2012-2016 event that killed an estimated 129 million trees in the Sierra Nevada, can result in watersheds where near-complete overstory tree mortality may limit natural regeneration.

It is not just the extent of tree loss, however, that is challenging management capacity. If the frequency and severity of wildfire (Keyser and Westerling, 2017) and drought (Adams et al., 2009; Allen et al., 2010; Williams et al., 2013; Griffin and Anchukaitis, 2014) events increase, as most climate change models suggest (Restaino and Safford, 2018), then regeneration practices must also promote increased drought and fire resilience in young stands. For example, California's 2013 Rim Fire re-burned many areas that had been planted at 300 + trees per acre (tpa; 740 + trees per hectare [tph]) after the 1987 Stanislaus complex wildfire. Most of these young plantations supported rapid fire spread and high fire intensity, resulting in 100% mortality (Lydersen et al., 2014, 2017). Even in areas that escape re-burning for decades, mortality has increased with the frequency and severity of western U.S. drought, with the rate of mortality correlated with stand density (Young et al., 2017; Stevens-Rumann et al., 2018).

Many of the standard reforestation practices arose from controlled field trials focused on testing different regular spacing densities and subsequent silvicultural treatments such as thinning, fertilization, and control of competing vegetation. On public lands, a shrinking work force and tighter budgets often reduce or eliminate second-entry practices, a trend that is expected to continue (Landram, 1996). This means initial arrangement and density need to be carefully considered, as opportunities for 'course correction' with silvicultural tools are becoming more limited. Regular spacing at high density fails to produce both the spatial pattern that recent research has suggested is associated with greater fire and drought resilience, and the diversified structure that is optimal for wildlife habitat and species diversity (Larson and Churchill, 2012).

Many of the ideas we propose have been tried informally in various combinations and contexts by silviculturists, but few examples are available in the literature to provide guidance and spur improvements. Experience has accordingly remained site-specific so that we lack general guidelines. Nonetheless, recent work increasingly supports a critical role for variable forest structure from the scale of individual trees up to the forest landscape (North et al., 2009b, Hessburg et al., 2015, 2016). There is also a focus on modifying silvicultural practices to incorporate ecosystem function into improving forest restoration (Stanturf et al., 2014). We believe these principles suggest concrete ways to harness ecological processes to pull young stands in the direction of higher resilience as well as providing habitat for a broader array of species. In this paper we focus on yellow pine (Pinus ponderosa and P. jeffreyi) and mixed-conifer forests on federal lands in California's Sierra Nevada. However, the changes in reforestation practices we propose are appropriate for dry western forests of any ownership that historically had a frequent, low-moderate severity fire regime.

In this paper we first identify the conditions under which standard reforestation practices may result in high mortality, and then examine how planting practices, particularly with regard to spacing and density, could be modified to increase seedling survival and build early drought and fire resilience. Finally, we address likely criticisms of this approach and summarize where new research could help optimize planting strategies.

2. Reforestation challenges

2.1. Current reforestation practices

Reforestation on U.S. Forest Service lands is guided by the National Forest Management Act, which directs that forest lands that have been "cut-over or otherwise denuded or deforested" be reforested, and that harvested areas must be reforested within 5 years of harvest (NFMA, 1976 [Section 6 E ii]). Areas are planted when silviculturists determine that natural processes will not achieve the preferred stocking, species composition, growth rates or forest structure within a desired time-frame. Timing is an important variable as costs and control of competing vegetation generally increase with time since disturbance (McDonald and Fiddler, 1993; Smith et al., 1997).

Steps in the reforestation process may include salvage logging (removal of standing dead timber, both for sale to fund subsequent reforestation steps, and for worker safety), site preparation (which includes segregation or removal of slash and exposure of mineral soil for ease of planting), planting of seedling stock (generally conifers), competition control for enhancing both seedling survival and growth, and, later, pre-commercial or commercial thinning. The specific treatments often vary depending on aridity, forest type, understory vegetation, and social acceptance of specific practices (i.e. tilling for site prep, use of herbicides, etc. (Schubert and Adams, 1971, Helms and Tappeiner, 1996)).

Historically, planting programs in western U.S. forests were focused on reforesting harvested areas, old burns, and non-stocked areas considered capable of supporting forest. Early reforestation efforts were plagued with low survival due to a variety of factors including poor stock, and thus high densities (435–680 tpa; 1075–1483 tph) were considered necessary (Schubert and Adams, 1971). Despite improvements in nursery practices (planting stock and seedling handling) and onsite practices (site preparation and management of competing vegetation), reforestation has continued to focus on establishing regularly-spaced trees (125–300 tpa [309–741 tph]) depending on site class and forest type) (Fig. 1). This planting strategy is designed for full site occupancy (i.e. a closed canopy forest) and the capacity to produce an intermediate commercial harvest (USDA Forest Service, 1989).

Once trees are established, follow-up treatments are often required to promote the growth and survival of planted trees (i.e. "release") in the first five years. In areas where planted trees are more widely spaced, drought stress can be exacerbated by the rapid growth of shrubs and grasses in the high-light environment between trees and increase competition for nutrients and soil moisture, (Lanini and Radosevich, 1986; Riegel et al., 1992; McDonald and Fiddler, 2010; Bohlman et al., 2016). Competing vegetation is reduced manually, mechanically, or with herbicides.

By contrast, trees initially planted at high densities may experience less competition from shrubs and grasses as crowns interlock early and reduce light to the understory (Rubilar et al., 2018). As trees mature, however, intertree competition reduces growth rates and increases the probability of density-dependent mortality. Thus additional follow-up treatments are often required, such as pre-commercial thinning and mastication (Stephens and York, 2017) to reduce intertree competition and to adjust species composition and tree spatial patterns (Long, 1985).

This intensive approach to reforestation can be cost prohibitive. Despite the need for follow-up treatments, over the past 20 years there has been a substantial decline in the number of hectares treated on National Forest lands. On these lands in the western U.S. (Regions 1-6),



Fig. 1. Different tree planting patterns compared to an 'ICO' stand structure. Upper left is area burned by the 2007 Moonlight Fire seven years after the fire. The left side of the road is private land regularly planted with ponderosa pine and treated with herbicide. The right side of the road, U.S. Forest Service land, was left unsalvaged and unplanted. The upper right photo is a cluster planted area ten years after the 2006 Boulder Fire. Lower left is a 50-year old ponderosa pine plantation nearby but outside the Moonlight and Boulder burns. The lower right photo shows the 'ICO' pattern produced by an active fire regime in an unmanaged Jeffrey pine stand in the Sierra San Pedro del Martir, Baja, Mexico.

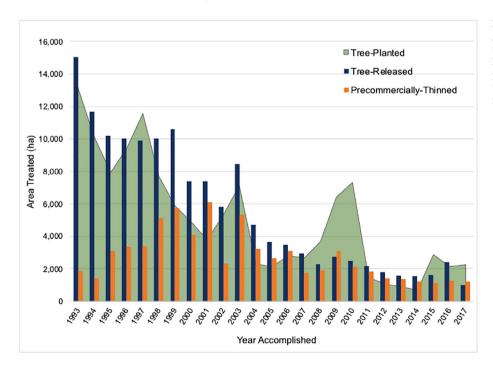


Fig. 2. Hectares of trees planted (green-shaded graph), released (blue bars), and pre-commercially thinned (orange bars) over the last 25 years on U.S. National Forests in the Sierra Nevada. Data compiled from the FACTS dataset. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

comparing 1997-2001 to 2013-2017, the average annual area 'released' has decreased by 40.6% (16,834 to 10,008 ha) (www.fs.fed.us/forest-management/vegetation-management/reforest-tsi.shtml). Average annual fire suppression costs on National Forest Lands for the same two

periods increased by 228% (\$748M to \$1,702M standardized to \$2017) (www.nifc.gov/fireInfo/fireInfo_statistics.html). For California, analysis of data from the Forest Service Activity Tracking System (FACTS) found the percentage of area planted after salvage logging declined

from approximately 60% in the late 1980s to approximately 25% currently (Ursell and Young, 2017). Analyzing the same data but focusing only on the Sierra Nevada region (USDA, 2018), the planted area decreased by 30% while the area of plantations treated for competition declined by 70% when comparing the most recent decade (2008–2017) with the previous decade (1998–2007) (Fig. 2). In addition, the area pre-commercially thinned declined by 58% over the same time period. On 26% of the area in plantations, neither competition reduction nor thinning treatments were done. Over half (57%) of plantations established between 1993 and 2016 have never been precommercially thinned and 38% have received no release from competition. Factors contributing to this decline include reductions in the federal workforce and loss of professional expertise, but ultimately, much of the cause is the decrease in the non-fire suppression share of the Forest Service budget.

2.2. Drivers of successful conifer regeneration

Conifer regeneration following disturbance is dependent upon species' life-history traits, seedbed quality, granivory rate, climate (particularly precipitation trends over both short and long time periods), and competition for light and soil moisture with non-conifer vegetation (Dobrowski et al., 2015). However, the first-order control on natural regeneration of non-sprouting conifers (the great majority of western conifer species) is seed availability.

In California, for example, there are many serotinous species, but none are wide-spread except in the chaparral belt, a testament perhaps to the very different pre-settlement fire regimes of chaparral – mostly low frequency crown fires - and montane conifer forest - mostly high frequency surface fires (Keeley and Safford, 2016)). Further, none of the tree species have fire-resistant seeds stored in the soil seed bank. Thus, following stand-replacing fire, non-sprouting conifers must recolonize from live-tree edges or small patches of unburned "islands" (Greene and Johnson, 2000; Goforth and Minnich, 2008; Donato et al., 2009; Haire and McGarigal, 2010; Welch et al., 2016; Shive et al., 2018). The welldocumented trend of a greater proportion of fires burning at high severity in the western United States has created larger contiguous, severely burned patches with few, if any remnant seed trees (Cansler and McKenzie, 2014; Miller and Quayle, 2015; Harvey et al., 2016; Stevens et al., 2017; Steel et al., 2018). Adequate seed availability for reforesting with wind-dispersed conifers is generally limited to 200 m from a living seed source (Greene and Johnson, 2000), while distances across large patches of stand-replacing fires can easily exceed a kilometer. Consequently, non-serotinous species will poorly reforest the bulk of a large, severe fire, an expectation broady confirmed by empirical studies of recent fires (Collins and Roller, 2013; Stevens et al., 2017). Recent instances of high tree mortality across large areas affected by drought and insects raises concern that dispersal limitation could also be a factor in regenerating stands affected by these non-pyric disturbances.

Synchrony between precipitation events, seed production and dispersal after disturbance is critical to successful natural regeneration (Brown and Wu, 2005; Peters et al., 2005). In a climate where summer drought is the norm, the temporal pattern of spring and summer rain in the first few years following fire is especially important because young seedlings (especially germinants with their lack of bark and small initial root system) are extremely sensitive to moisture stress (Gray et al., 2005; Puhlick et al., 2012; Savage et al., 2013; Petrie et al., 2016). In addition to the temporal variability of post-fire weather conditions, most conifers species are also known to mast, producing large seed crops only a few times each decade (USDA Forest Service, 1990; Greene and Johnson, 2004). Low seed production in non-mast years will limit natural regeneration just as effectively as distance (e.g. Peters et al., 2005). Once established, seedlings must survive competition for water from non-conifer vegetation (Section 2.3) and subsequent disturbances and climate stress to reach maturity.

When natural forest regeneration is expected to be poor, due to

failure to clear any of these barriers, managers may plant to speed forest recovery, modify the mix of species, capture site resources, and achieve a preferred spacing. While post-fire weather and climate patterns also influence the growth and survival of planted seedlings, their effects may be less intense, as planted seedlings ≥ 1 yr old begin with a much more extensive root system than natural recruits (Millar and Libby, 1989). However, while initially buffered, even planted conifer regeneration is still susceptible to extreme climate variation, competition, and subsequent disturbance.

Managers are primarily concerned that competing vegetation reduces regeneration growth rates, lengthens the time required for trees to reach a size resistant to surface fires, and favors conifer species that are more shade-tolerant yet sensitive to fire and drought, such as white fir (*Abies concolor*) and incense cedar (*Calocedrus decurrens*) (McDonald and Fiddler, 2010).

Montane shrubs that either resprout or germinate from a long-lived seedbank are common to many forested environments (Knapp et al., 2012), but this phenomenon is particularly well-developed in and around the California Floristic Province and other Mediterranean-climate regions (Keeley et al., 2011; Knapp et al., 2012). These shrubs whose germination is often strongly cued by fire - respond vigorously to the high-light environment following canopy disturbance, with the sprouting species typically outpacing conifer seedling growth. Although some shrubs may briefly facilitate early survival of tree seedlings in the first summer because shading reduces desiccation (Conard and Radosevich, 1982a; Gómez-Aparicio et al., 2004, 2005; Holmgren et al., 2012), for established (or planted) tree seedlings, initial growth has been shown to be substantially slowed by shrub competition until the conifer overtops the shrub canopy (Conard and Radosevich, 1982a; Oliver, 1984; Lanini and Radosevich, 1986; Peterson et al., 1988; Oliver, 1990; Erickson and Harrington, 2006; Zhang et al., 2013, 2017; Lauvaux et al., 2016). Shrubs that are then overtopped and die may actually enhance soil fertility, increasing subsequent tree growth (Oakley et al., 2006; Zhang et al., 2006). In lower productivity or xeric sites, this process can proceed very slowly (Conard and Radosevich, 1982b; Powers and Reynolds, 1996; Zhang et al., 2006). On such lowproductivity sites, competition for soil moisture may last until conifer saplings roots extend below shrub roots (Plamboeck et al., 2007, 2008).

High shrub abundance not only competes with young conifers but also serves as potential fuel or as a heat sink depending on environmental conditions at the time of burning (Zhang et al., 2006, Knapp et al., 2013). Montane shrubs can be a cause of higher-intensity fire, producing flame lengths that readily kill smaller trees. Most montane shrub fields burn at high-severity under severe fire weather conditions, especially when live fuel moisture is at seasonal lows (Coppoletta et al., 2016). However, depending on burn conditions and time of year, shrubs can also be a heat sink that reduces fire severity (Pellizzaro et al., 2007; Knapp et al., 2009). At times with higher live fuel moisture and lacking wind, shrubs and resprouting hardwoods often actually impede fire spread. Many montane shrubs rapidly take up near surface soil moisture produced by melting snow or growing season precipitation, making them more difficult to combust under early to mid-season conditions. Low shrub flammability in moderate fire conditions is evidenced by lower historical fire return intervals in chaparral patches compared to neighboring forest (Nagel and Taylor, 2005). This potential benefit of shrubs is rarely realized because most contemporary wildfires burn under extreme fuel and weather conditions when dessicated shrubs amplify fire intensity. Some shrub species, however, can reduce intensity even under these extreme conditions. For example, prostrate ceanothus (Ceanothus prostratus) and pinemat manzanita (Arctostaphylos nevadensis) can slow fire spread and create fire refugia, due to their low stature and relative lack of dead material, thereby facilitating tree seedling establishment (Show and Kotok, 1924).

Many of the more aggressive shrub species colonizing the post highseverity fire environment are very shade sensitive (Safford and Stevens, 2017). In the historical mixed-conifer forest, dense shrubs were mostly relegated to gaps or areas with very low tree basal area, which together covered perhaps 10–30% of stands (Knapp et al., 2013, Collins et al., 2015, Safford and Stevens, 2017). In addition to high-light microsites, shrubs also occupied more xeric locations within stands such as shallow soil microsites (Meyer et al., 2007b), where their superior water use efficiency provides an advantage over conifers (Field et al., 1983). At historical abundances, shrubs provided important habitat for wildlife, without unduly sacrificing the growth potential of young trees or contributing to fuel conditions likely to lead to stand replacement in the event of a wildfire. Allowing some shrub cover in regenerating forests, away from tree seedlings, particularly in more xeric, high-light microsites, may increase the resilience and habitat diversity of reforested areas.

Where present, hardwood trees are more challenging for managers because conifers may not be able to overtop them even after several decades. Many species of hardwoods reliably resprout following high-severity fires, and the stored carbohydrates in the root system give them an early advantage in height growth compared to sexually-recruited conifers or even planted stock (Cocking et al., 2014). At the same time, hardwoods have the potential to facilitate growth of conifer trees by moderating microclimates and constraining growth of understory plants with stronger competitive effects on conifers (Löf et al., 2014). Groves of oaks, aspens, and other hardwoods help to diversify wildlife habitat and often serve as natural fuel breaks, so their inclusion within conifer forests may advance landscape heterogeneity and resilience (Long et al., 2016). In some locations, it may be both financially and ecologically beneficial to accept some degree of hardwood dominance in a post-fire landscape.

3. Reforesting for greater resilience

A common theme in the recent North American forestry literature is that harvesting and regeneration should attempt to emulate the natural disturbance regime (e.g. Bergeron et al., 2002; Long, 2008; North and Keeton, 2008). For the Sierra Nevada, however, reforestation practices cannot simply emulate patterns of historical tree regeneration as humans have substantially altered disturbance regimes and forest conditions (Stephens et al., 2015; van Wagtendonk et al., 2018) and future climatic conditions are expected to differ markedly from historical ones. The few studies of tree regeneration patterns prior to fire suppression (Sudworth, 1900; Leiberg, 1902; Greeley, 1907) and contemporary reference sites (Stephens and Gill, 2005; Taylor, 2010), indicate that seedling densities were highly heterogeneous, with high density patches commonly found in forest gaps. Green saplings are often too moist to burn, but over time, repeated fire entry would reduce density in these regeneration clumps until the remaining trees were large enough to survive surface fire (Weaver, 1947; Cooper, 1960, 1961; White, 1985; Stephens et al., 2008; Taylor, 2010). It would be difficult and inefficient for current silviculture practices to mimic this temporal pattern given current unmanaged fire patterns (i.e., infrequent but high intensity) and the limited nursery stock available for reforesting large severe burns. Modern reforestation could foster greater resilience using mature forests as a blueprint for desired spatial structure, and then develop planting and budget-limited follow-up treatments that will promote desired stand conditions over time (ex. Four Forest Restoration Project, www.fs.usda.gov/4fri).

In general, lower stocking density and a more spatially heterogeneous planting pattern may be more resilient to fire and more adaptive to a summer-dry climate than regularly-spaced, densely planted conifers. Fire severity and tree mortality are typically higher in young plantations than surrounding forest, especially when plantations have not received fuel treatments (Weatherspoon and Skinner, 1995; Lyons-Tinsley and Peterson, 2012; Zald and Dunn, 2018). Water stress increases with density (Greenwood and Weisberg, 2008; van Mantgem et al., 2016; Young et al., 2017) and serious weakening or mortality of trees by mountain-pine beetles and other saprophagous insects is

associated with moisture-stress (Sartwell, 1971; Fettig et al., 2007). Planting strategies need to account for early fire and drought stress while enhancing the ability of conifers to compete with other vegetation. The primary challenge is to move from the initial stage of stand development, consisting of small fire-sensitive trees mixed with shrubs and other competing vegetation – a structural configuration susceptible to reburning at stand-replacing severity (Coppoletta et al., 2016) – to one where trees are large enough and densities are low enough, and fuels and competing vegetation are sufficiently heterogeneous, that the stand can withstand subsequent fires and droughts (Stevens et al., 2014).

Facilitating such a transition is challenging. Planting tree seedlings at high densities may more rapidly shade out competing shrubs but such stands are also more susceptible to stand-replacing fire and competitive effects (Zald and Dunn, 2018). To reduce this risk and accelerate tree growth, high-density developing stands require periodic thinning, which is often precluded by current budgets. Conversely, while lower planting densities may reduce or delay intertree competition and obviate the need for pre-commercial thinning, the high light environment will favor shrub and hardwood growth. A middle ground between these two strategies might include varying planting densities, including clusters with relatively narrow spacing, where growing trees more rapidly shade out competing vegetation, intermixed with unplanted areas or areas with widely spaced individual trees, and spotty shrub control to generate fuel and structural heterogeneity.

3.1. Zones for different reforestation strategies

We suggest dividing a recent burn or extensive drought-killed area into three categories: (1) the areas adjacent to green trees where natural recruitment is likely; (2) the zone further out where the dispersal constraint ensures that natural regeneration will range from zero to sparse; and (3) a zone which lumps all stands that might otherwise be in the second category but are too costly to plant for reasons of remoteness or topography (Fig. 3).

A number of recent tools have been developed to aid the identification of areas that are unlikely to support sufficient conifer regeneration to meet management goals (zone 1). For example, Welch et al. (2016) used an extensive Forest Service postfire inventory dataset to build a graphical tool identifying field locations likely to be above or below a predetermined stocking threshold, based on easily-measured variables (e.g., slope, aspect, live basal area in the stand, distance to nearest living seed tree). Shive et al. (2018) used the same dataset to develop a spatially-explicit predictive tool for forecasting postfire forest regeneration. The tool predicts spatial variability in seed availability based on prefire live basal area adjusted by burn severity. After scaling by 30-yr mean annual precipitation, the tool generates a map of predicted seedling densities. Alternatively, Greene and Johnson (1996) developed and tested a micrometeorological model of dispersal with default values for the wind parameters such that a manager need only input the tree height and the characteristic terminal velocity (fall rate) of the seeds. Seed terminal velocity data for most commercially valuable species are readily available (or can be calculated using the mean seed mass: Greene and Johnson, 1993).

Where these sorts of tools are used, sites where seedling regeneration is likely to be inadequate can be quickly identified. In the absence of such tools, general guidance is available. For example, within approximately 200 m of a green edge (our first zone), the roughly negative exponential decline in seed density with distance (Greene and Johnson, 1996; Clark et al., 1999) means that a well-stocked source population should provide sufficient natural regeneration within five years so that planting may be foregone or consist merely of spot planting to reach a desired density or species composition. Given the low abundance of serotinous species in the western U.S., well-stocked areas at greater distances into the burn could only occur if the fire was late in the summer when the seeds had finished maturation and thus these species



Fig. 3. A partially salvaged area two years after the 2014 Eiler Fire near Burney, California. Zone 1, outlined in green, indicates areas likely to receive seed from adjacent islands of green trees. Zone 2, in the remaining area beyond most natural recruitment, are the areas readily accessible for reforestation. Two areas within this zone, A and B separated by the blue dashed line, indicate gentler, more uniform topography (A) and more variable, steeper sloped conditions (B), each of which could have a different planting strategy discussed in the text. The unsalvaged, snag area in the center could be planted if safety allows (facilitating future forest habitat connectivity) or left to provide wildlife habitat for post-fire specialists. Zone 3, outlined in red in the distant center of the photo, is a steep slope, distant from

access roads that might be planted with founder stands (groups of seedlings in mesic, sheltered microsites less likely to burn or become drought stressed).

can behave as if they were serotinous (Michaletz et al, 2013). For interplanting this zone when natural recruitment is sparse, managers may choose to create a mix of species by planting more fire- and drought-tolerant species such as pines in areas that have recruited mainly 'fir' (e.g., Abies and Douglas-fir) and incense cedar (Calocedrus decurrents) from nearby green trees (Zald et al., 2008).

Beyond the zone of adequate seed deposition, the interior of large mortality patches may be divided into two zones based upon access and terrain. Easier access and flatter terrain mean that both salvage of dead trees and planting can be economically viable. Scattered or concentrated groups of snags may be retained for wildlife habitat and planting can occur among them if completed before snags begin to fall (generally 5-15 years; Innes et al., 2006; Ritchie et al., 2013) compromising safety (Fig. 3). To enhance the horizontal heterogeneity of stand structure, variable replanting densities might correspond to different microsite conditions, with higher densities and cluster planting in more mesic locations, and reduced density and shifting seedling locations to avoid shrubs in more xeric conditions, such as areas with shallow soils. Within this zone, microsites may vary from being relatively homogenous in flatter more uniform areas (zone 2A in Fig. 3) to highly variable (zone 2B Fig. 3) suggesting two different planting approaches discussed below (Section 3.2).

The third zone is the area beyond live-tree seed dispersal where access and terrain make both salvage of dead trees and replanting difficult and unlikely. Steeper slopes (generally > 35%) or sites further than 500 m from an existing road typically make salvage infeasible and replanting a low priority. In addition, mill capacity in many parts of California for federal land timber is so small that it limits the potential for salvage mostly to burned stands that are readily accessible (Lydersen et al., 2014). Without any salvage, large fuels (> 1000 h) accumulate once snags fall over, increasing the intensity of any reburn and increasing the likelihood of seedling and sapling mortality except those in wetter fire refugia (Stephens et al., 2018). In this third zone, standard planting practices may no longer be economically feasible. Silviculturists might consider an approach using founder stands (i.e., small groups of trees strategically planted to seed the surrounding area). This approach is similar to applied nucleation (Corbin and Holl, 2012), a restoration method used in tropical forests in which small patches of shrubs and/or trees are established to serve as focal areas for recovery. Nuclei can modify harsh microclimates, stabilize soil, and provide habitat for the birds and small mammals that aid seed dispersal for some species (Del Moral and Bliss, 1993). In temperate dry western coniferous forests, founder stands could be planted in mesic, less fireprone locations (i.e., concavities, slope breaks, lower slope positions) where developing trees are most buffered from drought stress and less likely to experience high-intensity fire. To reduce fuels and shrub cover, and to provide germination sites, managers may need to strategically remove shrubs (i.e., grubbing) or broadcast burn the area adjacent to

the founder stand. Burning might be carried out when fuel moisture and weather conditions greatly reduce the risk of founder stand mortality.

The decision not to plant some areas should be made with ecological objectives in mind. Indeed, avoiding planting on steep slopes for logistical reasons may align with past conditions, as steep slopes often historically supported shrubs (Nagel and Taylor, 2005) and sprouting hardwoods adapted to high-severity fires (Taylor and Skinner, 2003), especially in warm, wind-aligned locations. Conifer reforestation may be ill-conceived in wet meadows and riparian areas, even if accessible, if fire suppression has facilitated conifer encroachment into such areas. Consequently, fire that kills conifer stands in these areas may be regarded as restorative (Cocking et al., 2014, Boisramé et al., 2017b).

3.2. Planting in clusters vs. Regular spacing

Resilience of a stand to stresses such as drought and fire is influenced by tree spatial pattern (Larson and Churchill, 2012, Churchill et al., 2013; Owen et al., 2017; Ziegler et al., 2017). Frequent-fire forests historically had a spatial pattern characterized by three general components: individual scattered trees in a matrix of shrubs and hardwoods, clumps of trees, and openings ("ICO"). This ICO pattern has been found in fire-dependent forests throughout western North America (Larson and Churchill, 2012; Lydersen et al., 2013; Fry et al., 2014; Clyatt et al., 2016) and analysis of tree rings has documented trees in stands with this pattern surviving repeated exposure to fire and water stress. While climate change models vary in their specific predictions, all agree that fire and drought are likely to increase in frequency and severity (Williams et al., 2013; Allen et al., 2015; Millar and Stephenson, 2015; Abatzoglou and Williams, 2016). Plantations are now more likely to be exposed to these stresses while young, when trees have thinner bark, less crown-to-ground separation, and smaller root networks for capturing soil moisture. Re-planting efforts that produce an early ICO pattern may be particularly important in locations likely to experience frequent fire and drought.

There are several proposed mechanisms by which spatial heterogeneity in tree density engenders lower fire severity: it breaks up crown continuity, creates highly variable surface fuel loads, limits torching to clumps with ladder fuels, and creates mini-fire breaks in openings (Miller and Urban, 2000; Knapp et al., 2006; Symons et al., 2008; Bigelow and North, 2012; Kennedy and Johnson, 2014; Lydersen et al., 2015; Parsons et al., 2017; Ziegler et al., 2017). Further, ICO patterns typically have lower mean densities than evenly-spaced plantations, and lower density in general has been associated with greater water availability (Skov et al., 2004; Troendle et al., 2010). Within this pattern, tree clumps may experience more water stress than scattered individual trees, although two factors may moderate water limitations. Trees in clumps are likely to have roots extending laterally into adjacent openings increasing their water capture area, and the fungal network

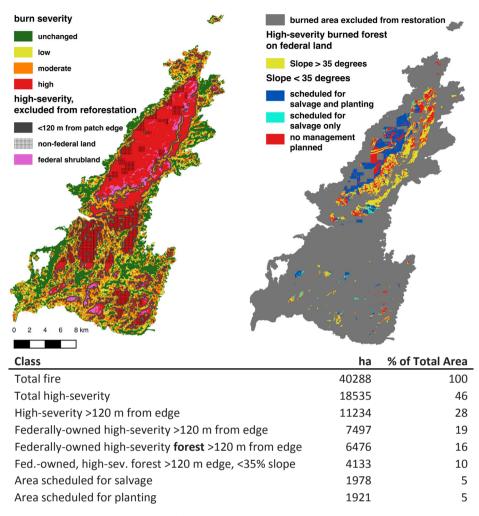


Fig. 4. Outline of the 2014 King Fire, 60 km east of Sacramento, California. This type of extreme 'megafire' is becoming more common in the western U.S. (46% of the King fire burned at high severity, with a central patch > 10,000 ha). Thresholds for unchanged, low, moderate, and high severity are from Miller and Thode (2007). The table below the figure shows the size (ha) of the fire footprint and in each row the area remaining that fits each criterion. For practical purposes on such a large fire, the Forest Service used a GIS analysis to divide the fire area into zones with different planting strategies.

amongst trees in a close group can increase nutrient and water uptake (Warren et al., 2008; Teste and Simard, 2008; Bingham and Simard, 2011). Fundamentally, the gradient of densities in an ICO pattern provide a broader range of responses to stresses compared to regularly-spaced planting where all trees have similar local neighborhood densities (Churchill et al., 2013).

3.2.1. Implementing resilient reforestation

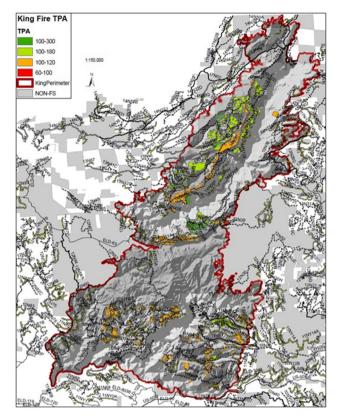
Within the active reforestation zone (e.g., Zone 2 in Fig. 3), the goal is to foster a variable spatial pattern where, whenever possible, clump location and tree density is aligned with water availability and topographic influences on fire behavior. Tree clumps would be associated with concavities, slope positions, and soil conditions with greater available water and water holding capacity, and in areas of potential fire refugia (i.e., lower slopes, slope breaks, and wet zones). As an example, we outline how some elements of this approach were used by one of us (Walsh) to develop a reforestation strategy for the large, high-severity burn patches within the recent King Fire (Fig. 4).

First the King Fire was categorized by fire severity, distance from green tree edge, ownership, and slope to identify potential areas for salvage and planting, a process similar to the three-zone approach discussed above. Within the areas scheduled for planting, further subzones were identified with different replanting strategies and standlevel target densities identified in the replanting contracts (Fig. 5).

These discrete subzones were identified using topography and edaphic conditions that are associated with differences in mature forest basal area and density (Lydersen and North, 2012; Kane et al., 2015a). The GIS-based Landscape Management Unit tool (North et al., 2012), which parses a landscape into different units based on slope position, aspect and slope steepness, was used to delineate areas with different reforestation targets. In each unit, an overall desired stand density for 100 years in the future was identified, and then the planting density was increased to account for expected mortality estimated with a stand development model, the Forest Vegetation Simulator (Fig. 5).

Within each of these subzones, targets for cluster spacing were identified, along with desired density per cluster and species composition using several stand reconstruction studies for yellow pine and mixed-conifer forest (Churchill et al., 2013; Lydersen et al., 2013; Fry et al., 2014). While variability in spacing, trees per cluster and composition in response to microtopography may be the eventual goal, current contract procedures require identifying a desired value for each of these along with a range of allowed variability. The experience with the aftermath of the King Fire was that currently, planting crews need a set inter-cluster spacing (e.g., 9 m or 30 ft) with an allowable adjustment to that distance (e.g., \pm 20% [1.8 m or 6 ft]).

Planting individual trees between tree clumps is also important because the availability of light and soil moisture will maximize their growth. A planting strategy that uses both cluster and regularly spaced



Zone	Condition	Long-term average desired stocking, trees per acre (tpa) (@100 years)	Average stocking at time of planting based on future treatments and expected mortality
Strategic Fire Mgmt. Zone and WUI	Low site, lava outcrops, chaparral and oak dominated areas on ridges and south slopes	0-40 tpa	These areas are not proposed for planting.
	Conifer dominated desired future condition with a likely seed source for a desirable species composition and arrangement	40-70 tpa	
	Conifer dominated desired future condition with a seed source, but not likely to provide a seed source of a desirable species composition and arrangement within the next decade based on desired future stocking	40-70 tpa	50-84 tpa
	Conditions other than above without a seed source	40-80 tpa	50-96 tpa
Conifer Resilience Areas	Conifer dominated desired future condition with a seed source, but not likely to provide a seed source of a desirable species composition and arrangement within the next decade based on desired future stocking	60-130 tpa	72-156 tpa
	Lower slopes	134-250 tpa	161-300 tpa
	Mid slope	80-120 tpa	96-144 tpa
	Upperslope	70-100 tpa	84-120 tpa

Fig. 5. A map of the planting areas within the King Fire, color-coded into Landscape Management Units with different target overall densities (TPA, trees per acre). The table below the figure indicates the different areas and the initial target (far right column) and final desired (second to right column) stocking.

planting may engender a more resilient forest spatial pattern by creating a range of densities resulting from different inter-tree spacing within clusters and between clusters and individual tree seedlings.

In highly dissected areas with distinct microsite variability (Fig. 3, Zone 2-B) planting might focus on first identifying and planting clusters in mesic microsites. In steeper areas, the best microsites are easier to identify and adjusting the planting pattern to topography is crucial for

cluster seedling survival. After clusters are planted, the remainder of the area can be regularly planted, again with some location flexibility. Fig. 6 provides an example of this approach and how such a stand might develop over 80 years.

3.3. Prescribed burning in young stands

In mature stands, the most effective means of building forest resilience to wildfire is with prescribed fire (Agee and Skinner, 2005). Surface fuels are a principal driver of fire behavior, and mechanical treatments for thinning or competition control often increase surface fuel loading unless they are specifically targeted to reduce these fuels. In contrast, prescribed fire is focused on surface and ladder fuel reduction, reducing crown fire potential and the stem densities associated with greater water stress. If prescribed fire in young stands also produces these beneficial structural changes as they have in mature forests, then developing stands can build resilience earlier and to a greater extent than with either mechanical-only or no-treatment options. Factors affecting fire behavior in young conifer stands, however, are markedly different than in mature stands (Weatherspoon and Skinner, 1995; Lyons-Tinsley and Peterson, 2012), and applying standard burning prescriptions developed for mature stands may not be successful. Despite these uncertainties, research has consistently found that, given fire's ubiquitous and recurrent role in shaping stand dynamics in dry, western forests prior to fire suppression, it is an important tool for building forest resilience (e.g. Steel et al., 2015; Keeley and Safford, 2016; Safford and Stevens, 2017).

While the application of prescribed burning in young conifer stands has traditionally been associated with a risk of high stand mortality (Smith et al., 1997), emerging research suggests prescribed fire can effectively treat young stands with relatively low levels of stand mortality while supporting other management objectives, including: (1) reduction of surface fuels (Lyons-Tinsley and Peterson, 2012; Stevens et al., 2014); (2) maintenance of evolutionary selection for fire-resistant trees; (3) introduction of stand heterogeneity (Kobziar et al., 2009); (4) cost-effectiveness compared to mechanical treatments (Kobziar et al., 2009); (5) reducing activity fuel following mechanical treatments such as mastication (Reiner et al., 2012; Bellows et al., 2016); and (6) stand density management (York et al., 2013) (Fig. 7). Early fire introduction is well-aligned with the historical natural fire regime of yellow pine and mixed-conifer forests, where short fire-return intervals (i.e., 5-10 and 10-20 years, respectively) made fire in young stands a common occurence (Collins and Stephens, 2010; Safford and Stevens, 2017).

Structurally, young stands are defined by their low stature which, along with thin bark, makes trees vulnerable to heat from surface fires (van Mantgem and Schwartz, 2004). This vulnerability means managers must carefully weigh when to begin burning developing stands. We know of several examples of prescribed burns in young ponderosa pine and mixed-conifer stands ranging from 13 to 40 years old (Peterson et al., 2007; Kobziar et al., 2009; Knapp et al., 2011; Reiner et al., 2012; Bellows et al., 2016). Collectively, the studies underscore the need for managers to accept variable outcomes in fire-related mortality. Of the empirical studies, mortality on these sites ranged from 0 to 66% but most results were in the range 5-25%. While these mortality rates are high, if they succeed at making the less dense stand subsequently more resilient to fire or drought, then the long-term loss to fire may well be acceptable compared to conventional practice in an increasingly fireprone landscape. The particular structure and composition at different stand ages, and therefore the fire effects, will be related to early stand management practices such as planting, vegetation control, and thinning. An important distinction to make is the presence or absence of fuel from preceding mature stands. In these experimental studies, site preparation treatments that reduced large residual surface fuels were done prior to planting. Where site preparation has not occurred, prescribed fire will likely lead to higher mortality.

The studies described here also conform to a traditional model of

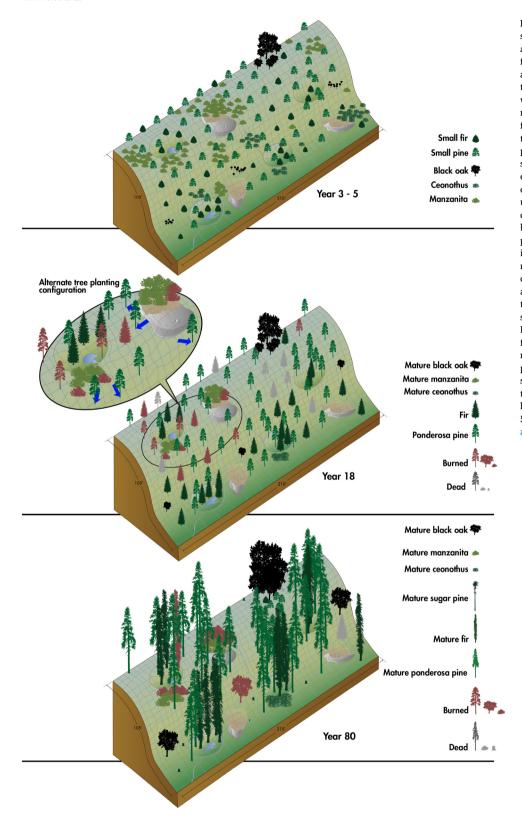


Fig. 6. Schematic of the initial planting and stand development for a dissected, more fire and drought prone 0.2 ha (0.5 ac, 105 by 210 ft) slope of mixed-conifer forest where favorable cluster microsites are more easily identified. (A) Initial planting schematic (usually within 1-5 years following disturbance). First more mesic microsites (concavities in the figure) are identified and planted with clusters of trees and then the remaining area is planted with individual trees on a regularlyspaced grid (here 4.6 m or 15' by 15'). In this example only 60 of 115 (i.e., if fully planted on a 4.6 m spacing) potential trees are regularly planted, and 22 are planted in four clusters at mesic microsites. (B) After the first burn (15 years after planting). In this hypothetical example, of the 82 original conifers, eight have died over the last period and nine were killed by the prescribed fire, reducing live tree density to 65 on the 0.2 ha (0.5 ac). The prescribed fire, designed to maintain tree and shrub separation, has also killed some shrubs. (C) After 77 years of growth. Fire has been applied every 15 years to reduce fuels and shrub cover. In this example, 22 more trees have been killed by drought and prescribed fire, leaving a mature forest density of 40 conifer and three oak live trees (212 tree/ha or 86 trees/ac), within the estimated historical mixed conifer density range of 59-329 tree/ha (24-133 trees/ac) (Safford and Stevens, 2017).

grid-planting focused on ponderosa pine. The exception is Bellows et al. (2016), which used mixed-species stands. An advantage of using mixed species is their variable fire tolerance. Although young trees are generally characterized by thin bark, there is much variation in thickness among species and individuals within species. At dbh < 10 cm (< 4 in) (which equates to $\sim 10-25$ years of age on most sites, or the typical age at which young trees would have experienced fire before fire

suppression), the average ponderosa or Jeffrey pine supports bark that is twice the thickness of white fir or Douglas-fir, and this is a major driver of differential sapling survival through fires in young stands and perhaps the primary reason that yellow pine was ubiquitous in presettlement forests (Safford and Stevens, 2017).

New stand establishment practices, such as reduced/no site preparation and widely-spaced clumps of planted seedlings (Section 3.2)

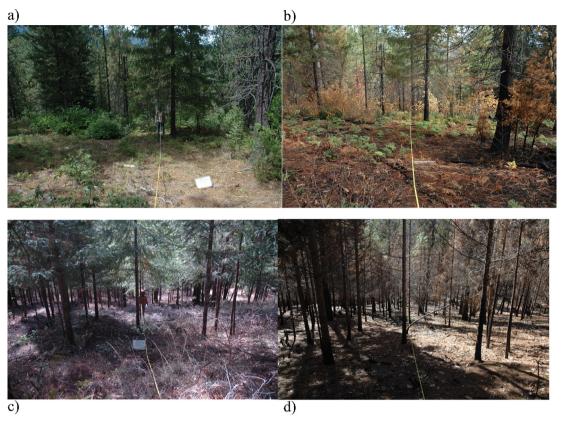


Fig. 7. Examples of prescribed burning in young stands on the Shasta-Trinity National Forest. The upper pair are before (a) and after (b) photos from a mixed-conifer plantation that was masticated and burned (in spring) 33 years after planting, showing reduction in surface fuels and removal of some understory stems. The lower pair are before (c) and after (d) photos from a plantation with considerable added tree density due to natural regeneration, that was masticated, branch pruned, and burned (in fall) 25 years after planting. In the latter case, the prescribed fire was effectively a pre-commercial thinning, reducing stand density closer to desired levels and also generating within-stand spatial heterogeneity.

will need to approach young stand burning as true management experiments. Dense stands of seedlings following fire (e.g. Moghaddas et al., 2008) in small canopy openings (Collins et al., 2009) were likely a common structure in Sierra Nevada forests prior to suppression. Young stand resilience to fire may therefore be related to this high-density structure, suggesting reforestation practices consider promoting variable (including high) density patches of seedlings that are subsequently thinned with prescribed fire. In addition, application of fire when stands are young and locally dense will preferentially cull thinbarked species and individuals and lead to a more fire-resistant gene pool in the long run.

As a treatment option, mastication has been compared to burning. While Kobziar et al. (2009) caution against mastication because of model predictions of higher wildfire mortality compared to prescribed burns in 30 year old stands, Bellows et al. (2016) observed low prescribed fire-related mortality in both masticated and un-masticated 13 year old stands burned in the fall. Experimental removal of masticated fuel around the base of young trees improved survival following prescribed burns in a 25-year old ponderosa pine stand (Reiner et al., 2012), but did not improve survival in a 40-year old ponderosa pine stand (Knapp et al., 2011), nor in a 13-14 year old mixed-species stand (Bellows et al., 2016). The variability suggests it was not masticated fuel, per se, that was the determining factor for survival. As Knapp et al. (2011) point out, controlling crown scorch is key when trees are relatively short, making ignition patterns (i.e., using a backing fire in young stands) a critical determinant of actual survival during prescribed burns.

On the whole, studies thus far suggest that mechanical treatments are not necessary to facilitate young stand burning (Knapp et al., 2011; Bellows et al., 2016). However, mastications and/or thinning may

enable earlier burning than would otherwise be possible with low surface fuels and high canopy densities. This may especially be the case if burning windows are pushed later in the fall or into the spring, when fuel moisture is higher and a lower canopy density coupled with greater fine surface fuels may be necessary for adequate fire spread.

3.4. Current and changing site suitability

Current reforestation guidelines consider any site that was forested pre-fire as a good candidate for active reforestation (Anonymous, 1991). With changing climate and disturbance regimes, however, it is important to consider current and future site suitability when prioritizing limited resources for reforestation. For several reasons climatic conditions may already be marginal for a species that was on-site prior to a fire. First, increases in temperature documented over the last several decades may have shifted formerly suitable sites into more marginal ones (Bell et al., 2013). Since mature trees can withstand a wider range of environmental conditions than seedlings (Grubb, 1977; Dobrowski et al., 2015), species may be present at sites as adults that their seedlings are now unable to tolerate (Safford et al., 2012). In these areas, natural regeneration would likely be very weak, and local reforestation with the same species may be undesirable. Second, more than a century of fire suppression has allowed for expansion of forest into more marginal sites where it was historically excluded (Fites-Kaufman et al., 2007). This expansion was likely driven by episodic regeneration in years with a coincidence of a mast crop and unusually favorable summer precipitation (North et al., 2005), despite such sites having higher moisture stress over the long term. Forest mortality in such marginal sites is especially high during droughts and after disturbances.

Identifying areas that are likely already marginal would include assessment of local site moisture stress, a key variable influencing the suitability of a given site for supporting trees (Stephenson, 1998; Lutz et al., 2010). Recent drought events have been associated with elevated tree mortality (van Mantgem et al., 2009; Allen et al., 2010; Paz-Kagan et al., 2017), particularly at sites with high moisture stress and where high basal area results in intense competition for water (Young et al., 2017). Although it is impossible to know what the weather conditions will be like the first few years after fire (or after planting), identifying sites with high long-term moisture stress over recent past periods can help detect less suitable sites. For example, in the Sierra Nevada of California, Young et al. (2017) found higher drought mortality in areas where 30-year mean annual climatic water deficit values exceeded 800 mm, and Shive et al. (2018) observed reduced probabilities of finding conifer regeneration where 30-year mean annual precipitation was less than 1200 mm.

In addition to current site suitability, future site suitability should also be considered. Because sites that are already dry appear to be the most sensitive to adult tree mortality and poor natural regeneration, replanting trees in such sites may be unwise, particularly if droughts become hotter and more frequent as climate projections suggest (Wang et al., 2017). Therefore, areas that are most likely to become unsuitable in the next few decades (i.e., "marginal" forested areas with low mean annual precipitation and high mean annual temperatures) could be identified by examining climate datasets from sources such as PRISM (PRISM Climate Group, 2018) and Climate Engine (Huntington et al., 2017). Climatic drivers should be considered simultaneously with topographic and soil characteristics to assess overall site suitability. Although topography and soil are indirectly assessed in broad-scale models of climatic water deficit (e.g., the Basin Characterization Model; Flint et al., 2013), more focused local factors should also be considered (e.g. avoiding planting on steep, south facing slopes, areas with shallow soils and areas on ecotonal edges; Section 3.1). These considerations can be factored into selecting appropriate tree seed sources using the web-based seedlot selection tool (http://seedlotselectiontool.org/sst/).

Nursery-grown tree seedling stock, which have side-stepped the high mortality rate that occurs from deposited seed to second-summer seedling (Ledig and Kitzmiller, 1992), may be more tolerant of extreme conditions than natural recruits and thus able to establish in more climatically marginal sites. The extent to which this is the case is not well understood. However, even if planting allows managers to re-establish forests in sites where natural seedlings would not survive, doing so may be undesirable if it leads to establishment of stands that are in disequilibrium with their environment, having little potential to persist for additional generations through natural recruitment (Millar and Libby, 1989).

In sites that are considered too marginal for traditional reforestation with local species and seed stock, there are several options for post-fire management. First, these areas could be allowed to shift toward other vegetation types (i.e. montane chaparral or native grassland) or to naturally transition to forests with different species composition (i.e. ecotonal edges where, for example, gray pine [Pinus sabiniana] or hardwood species may seed in from lower elevations). Second, managers could consider assisted migration (McLachlan et al., 2007) of species thought to be better adapted to future climates. Given the potential drawbacks of moving species outside their ranges and the long lag between an experimental planting and the measured growth and mortality of adults, this novel management strategy is not of immediate use to managers (Ricciardi and Simberloff, 2009, Sax et al., 2009). Third, managers may be able to take advantage of the strong local adaptation to environmental conditions often observed among populations even within a given species (Savolainen et al., 2007). For example, by selectively planting seedling stock collected from lower-elevation sites (and thus potentially better drought-adapted source populations), managers may facilitate movement of tree genotypes to the sites where these genotypes will be best adapted as climate warms.

This practice, known as "assisted gene flow" (Aitken and Whitlock, 2013; Aitken and Bemmels, 2016), offers substantial potential for maintenance of resilient forests under climate change, but as with the purposeful movement of species, it has not been thoroughly tested and also carries risks (Bucharova, 2017).

3.5. Potential ecological benefits

Modifying reforestation practices to promote lower-density, structurally heterogeneous stands will have the primary ecological benefit of increasing resistance (minimizing forest loss) and/or resilience (recovering quickly from forest loss) of forest stands to recurring disturbance as they develop and mature. In essence, such modified reforestation practices will achieve ecological benefits primarily by setting forest stands on a course to have a low over-all density but variable structure as they grow, reducing potential large-scale losses from fire, drought, and pests or pathogens.

Fine-scale heterogeneity in forests is self-reinforcing, as subsequent fires are likely to create or expand small openings (Coppoletta et al., 2016). Heterogeneous and complex forest structure have highly variable microclimates at the stand scale (Ma et al., 2010; Norris et al., 2012), with different temperature and moisture niches leading to high understory plant diversity (Wayman and North, 2007; Stevens et al., 2015). These microclimates may be key for facilitating species persistence on the landscape under climate change (De Frenne et al., 2013).

Promoting reforestation practices that result in variable forest structure at the stand scale is also important for creating a diversity of wildlife habitat (Hessburg et al., 2016). Because animal species have different habitat requirements, responses to increased forest heterogeneity will be species-specific. In some areas, however, avian species richness in the Sierra Nevada has been found to increase with stand openness (Stevens et al., 2016), and more heterogeneous stands appear to have higher avian richness than more evenly-spaced stands (White et al., 2013). Some species such as the spotted owl (Strix occidentalis) and the northern flying squirrel (Glaucomys sabrinus) that require denser forest cover may experience a decrease in habitat quality in lower-density stands (Meyer et al., 2007a; Stephens et al., 2014), but variability in stand density across the landscape may buffer these standscale effects (Sollman et al., 2016) and, in any case, these species persisted in the past with density heterogeneity. Reforestation efforts that allow for clusters of trees at the stand-scale with gaps surrounding them (Churchill et al., 2013) could reduce tree mortality from fire in some of these clusters, and aid in the retention of tall tree cover, which is important for California spotted owl habitat (North et al., 2017). Furthermore, some denser patches within variable stands may still torch during fire and create snag habitat for post-fire specialists (Hessburg et al., 2016). Such variability in post-fire structure has also been linked with increased small mammal diversity (Meyer et al., 2005; Roberts

Plant diversity in frequent-fire forests is also closely tied to fire regimes and heterogeneous stand structures that approximate pre-settlement conditions. In forests historically characterized by low and moderate severity fires, postfire patterns in plant diversity are generally hump-shaped along the fire severity gradient, with higher numbers of species found in areas burned at low and low-moderate severity and lower numbers in unburned sites and sites burned at high severity (Stevens et al., 2015; DeSiervo et al., 2015). This is hypothetically attributed to (1) the larger pool of species adapted to regenerating after low severity fire versus a very small pool adapted to regenerate after high-severity fire, which was historically rare in these forests (Keeley and Safford, 2016); and (2) greater forest patchiness and habitat heterogeneity created by moderate ("mixed") severity fire, which permits coexistence of species adapted to both mesic and xeric habitats (Stevens et al., 2015).

Lower densities of trees at a watershed scale are associated with decreases in evapotranspiration and increases in streamflow (Bales

et al., 2011; Boisramé et al., 2017a; Hallema et al., 2018). Lower densities of trees at the margins of wet meadows are particularly important for increasing local soil moisture storage through dry periods (Boisramé et al., 2017b), while forest gaps increase snow accumulation in higher elevation forests (Varhola et al., 2010; Lundquist et al., 2013; Stevens, 2017). However, the lack of shade in large gaps created by high-severity fire can accelerate snowpack loss, particularly in low snow years, suggesting that a variable forest with numerous smaller gaps (of ~ 0.5 ha, or with diameters less than roughly twice the average tree height) surrounded by forest cover may create optimal conditions for snowpack retention (Kittreadge, 1953; Stevens, 2017).

Reforestation strategies that promote lower and variable densities can increase the potential for long-term carbon storage because retaining live tree biomass through multiple disturbance is an important carbon pool and long-lived sink (North and Hurteau, 2011; Winford and Gaither, 2012). Forests that are less dense but with more large trees not only hold more carbon than high-density stands comprised of many smaller trees (Hurteau and North, 2009; 2010), their resilience to mortality from stress and disturbance increases the stability of the carbon reserve (North et al., 2009a; Soung-Ryoul et al., 2009; Earles et al., 2014; Hurteau et al., 2016). These forest conditions, whether realized through thinning, fire, or low density reforestation, produce sustainable carbon sinks critical to realizing goals such as the California Forest Carbon Plan (North et al., 2016, Forest Climate Action, 2018).

4. Criticisms and research questions

There are many reasons to be skeptical of the novel proposition advanced here. In particular, while the ICO pattern may have resilience benefits in mature stands, it is largely untested as a pattern that can increase the probability of survival during early stand development. 'Natural' stands probably did not develop ICO patterns until several burns over 50–60 years reduced thickets of regeneration into smaller tree clumps, scattered individuals and opening. Early and frequent use of prescribed fire may help build young stand resilience, but it cannot fully replace the absence of an active fire regime. Like many silvicultural systems working in an environment with altered disturbance regimes, the proposed reforestation is an effort to engineer a desired mature stand structure when simply mimicking historical seral development is not an option.

Silviculturists using current practices may argue that it will be difficult to determine where tree clusters should be planted and their seedlings will grow slower because of higher local density. Regular spacing 'samples' the soil and increases the likelihood that trees find the best spots to thrive in. Wide spacing leads to faster seedling growth rates that develop thicker bark and taller trees, a 'backbone' that will become more fire resistant. This approach first creates a forest foundation followed by release treatments and commercial thinnings that can adjust spatial pattern and structure to build mature stand resilience.

We suggest, however, that favorable microsites for cluster planting can be identified focusing on how local topography affects water availability and fire behavior. A combination of regular and cluster planting will still provide rapid tree growth while also creating a range of densities, increasing variability in resource competition, fuel loads, and habitat conditions. Competing vegetation will be reduced in tree clusters through shading and more extensively throughout the stand with cost-effective prescribed burning that builds fire resilience. Initial planting pattern and frequent burning foster stand development and spatial pattern that is more congruent with topographic, edaphic, and disturbance influences on forest resilience without depending on costly future treatments or hoped for commercial thinning to adjust the developing forest. Given that a mature ICO pattern is unlikely to result from regular planting patterns and limited silviculture budgets, there is much to be gained by researching and incorporating variable spatial patterns early in the reforestation process.

Any researcher unfamiliar with forestry's agronomic roots, would be

dumbfounded at the number of studies testing different planting permutations of regular spacing, tree species, and site quality, and yet the near absence of studies testing variable or adaptive planting patterns. In the absence of uniform spacing, tree seedling survival and growth will be more variable and complex. Studies are needed that identify influential factors such as identifying key microsite conditions and their interaction with local tree density. Although initially challenging, in the end such information could bring reforestation practices more in sync with edaphic and abiotic conditions rather then imposing a uniform pattern best suited to crop production.

Clearly, the effect of prescribed burning on direct mortality in juvenile plantations and volunteer stands and on their subsequent capacity to better withstand wildfire needs far more study. Burning in young stands is a new frontier for both scientists and managers. Of critical importance are experiments which explore the factors of early stand management (site preparation, planting density, vegetation control) in influencing subsequent prescribed fire behavior. Evaluations of alternative schedules of burning that are variable in season, timing of first entry, and frequency of re-entry would also be helpful. Research that identifies likely mortality levels under different ignition patterns and burning conditions would help with developing targets and implementation. Many managers will resist putting prescribed fire in young stands given the effort and money that went into planting an area. Clearly, only a large number of successful field tests can help allay this hesitation.

With any new reforestation system there are legitimate concerns about costs relative to current practice. A thorough economic analysis of different reforestation methods using a lifecyle approach is needed because there are several unknowns that make cost predictions difficult. There are potentially higher upfront costs with our proposed planting scheme compared to conventional forestry because it will be slower for planting crews to learn and more difficult to check for compliance. Longer term savings, however, are likely as prescribed fire is used in place of other controls of competing vegetation (i.e., grubbing, mastication and herbicides) and pre-commercial thinning. Prescribed burn costs vary with site conditions, but are often roughly half the cost per acre of these more labor-intensive treatments.

Large LiDAR data sets (Kane et al., 2014, 2015b), together with multispectral photogrammetry (Näsi et al., 2015) and historical stem maps (North et al., 2007; Taylor, 2010; Knapp et al., 2013; Lydersen et al., 2013), now allow us to describe distinctive patterns of tree size structure, composition, and spatial arrangement in forests, including those few areas where active fire regimes have been allowed to shape conditions (Jeronimo et al., 2018). A critical area needing more study is the development of metrics that formally quantify spatial patterns (cf. Parker et al., 2006; Roccaforte et al., 2015) in contemporary young stands and then relate these patterns to growth rates, free-to-grow status, and water balance. How do structural features such as density, species composition, and structural heterogeneity influence bark beetle population growth rates and transitions from endemic to epidemic behavior (Bentz et al., 2010)? Particularly important is a better understanding of how these features in forest structure influence habitat use in forest dependent wildlife species?

The paucity of empirical knowledge of physiological response to drought and elevated atmospheric CO_2 for many tree species and their competitors hinders an informed choice of species and planting density by managers. A key goal is to generate site-specific maps of drought mortality risk by characterizing physiological drought death thresholds in situ. This needs to be done across the major mixed-conifer tree species and using regional-scale climate models to quantify probabilities of drought severity and duration at different time horizons. Direct measurement of tree water use can help in understanding how climate and stand structure interact to determine tree- and stand-level evapotranspiration (Buckley et al., 2012), as well as snowpack accumulation and water yield, which tend to be greater in the low and variable-density forests associated with frequent fire regimes (Stevens, 2017;

Bales et al., 2011).

In planning restoration treatments, one critical question is the probability that a planted stand will burn before it reaches a size and structure sufficient to resist fire. Fire severity maps in the West are now available for several decades, an interval long enough that fire frequency models (e.g. Johnson and Gutsell, 1994) could estimate contemporary probabilities of burning by a particular age. Nonparametric models may be helpful as they allow conditional fire probability to vary with factors such as tree density and land ownership (e.g. Wilson et al., 2010; Starrs et al., 2018).

5. Summary

Changes in wildfire severity, patch size and climate variability challenge reforestation practitioners to explore new methods for replanting large areas of dead trees. Establishing dense conifer cover with regularly spaced planting may reduce competing vegetation, but the uniform spacing and high density can fail to build adaptive capacity into the developing forest. For dry western coniferous forests, we have proposed adjusting several planting strategies in response to these changes, particularly focused on building fire and drought resilience early in regenerating forests, varying spacing to foster a future clump and gap distribution, and reducing density and water competition.

Spatial pattern matters. Planting all seedlings on a regular spacing does not have an ecological analog, fails to account for microsite variability, and creates a uniform density lacking a gradient of resource competition. Ultimately, such a strategy depends heavily on costly additional treatments to create more natural patterns. Tree density should vary and be congruent with local water availability and microand macro-topography. Tree seedlings need not control all of the replanting area to become established, and ceding some space to other vegetation such as shrubs and hardwoods diversifies fuel and habitat conditions, and may enhance drought resilience. Furthermore changing climate conditions suggest managers may need to identify 'marginal' locations where trying to re-establish current species composition from local genetic stock may no longer be viable. Changing disturbance and climatic conditions continue to alter the forest regeneration niche. Reforestation strategies that foster greater heterogeneity in fuels, vegetation, and planting patterns can increase resilience in regenerating forests.

Acknowledgments

This manuscript grew out of a reforestation and climate change workshop sponsored by the USDA Climate Change Hub at the University of California at Davis, United States.. We thank Steve Oerding, IET Academic Technology Service, University of California, Davis for providing Figure 6. McIntire-Stennis funding supported one of the co-authors (DFG). We also appreciate critiques by Joe Sherlock and Ramiro Rojas, USFS Region 5 silviculturists, and two anonymous reviewers which greatly improved the manuscript.

References

- Abatzoglou, J.T., Williams, A.P., 2016. The impact of anthropogenic climate change on wildfire across western US forests. Proc. Natl. Acad. Sci. 1113, 11770–11775.
- Adams, H.D., Guardiola-Claramonte, M., Barron-Gafford, G.A., Villegas, J.C., Breshears, D.D., Zou, C.B., Troch, P.A., Huxman, T.E., 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proc. Natl. Acad. Sci. 106 (17), 7063–7066.
- Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuels reduction treatments. For Ecol. Manage. 211, 83–96.
- Aitken, S.N., Bemmels, J.B., 2016. Time to get moving: assisted gene flow of forest trees. Evol. Appl. 9, 271–290.
- Aitken, S.N., Whitlock, M.C., 2013. Assisted gene flow to facilitate local adaptation to climate change. Annu. Rev. Ecol. Evol. Syst. 44, 367–388.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., (Ted) Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality

- reveals emerging climate change risks for forests. For. Ecol. Manage. 259, 660–684. Allen, C.D., Breshears, D.D., McDowell, N.G., 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6. art129.
- Reforestation handbook. FSH 2409.266. USDA Forest Service, Region 5.
- Bales, R.C., Hopmans, J.W., O'Geen, A.T., Meadows, M., Hartsough, P.C., Kirchner, P., Hunsaker, C.T., Beaudette, D., 2011. Soil moisture response to snowmelt and rainfall in a sierra nevada mixed-conifer forest. Vadose Zone J. 10 (3), 786–799.
- Bell, D.M., Bradford, J.B., Lauenroth, W.K., 2013. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. Global Ecol. Biogeography 168–180.
- Bellows, R.S., Thomson, A.C., Helmstedt, K.J., York, R.A., Potts, M.D., 2016. Damage and mortality patterns in young mixed conifer plantations following prescribed fires in the Sierra Nevada, California. For. Ecol. Manage. 376, 193–204.
- Bentz, B.J., Régnière, J., Fettig, C.J., Hansen, E.M., Hayes, J.L., Hicke, J.A., Kelsey, R.G., Negrón, J.F., Seybold, S.J., 2010. Climate change and bark beetles of the Western United States and Canada: direct and indirect effects. Bioscience 60, 602–613.
- Bergeron, Y., Leduc, A., Harvey, B.D., Gauthier, S., 2002. Natural fire regime: a guide for sustainable management of the Canadian boreal forest. Silva fennica 36, 81–95.
- Bigelow, S.W., North, M.P., 2012. Microclimate effects of fuels-reduction and group-selection silviculture: Implications for fire behavior in Sierran mixed-conifer forests. For. Ecol. Manage. 264, 51–59.
- Bingham, M.A., Simard, S.W., 2011. Do mycorrhizal network benefits to survival and growth of interior Douglas-fir seedlings increase with soil moisture stress? Ecol. Evol. 1, 306–316.
- Bohlman, G.N., North, M., Safford, H.D., 2016. Shrub removal in reforested post-fire areas increases native plant species richness. For. Ecol. Manage. 374, 195–210.
- Boisramé, G., Thompson, S., Collins, B., Stephens, S., 2017a. Managed wildfire effects on forest resilience and water in the Sierra Nevada. Ecosystems 20, 717–732.
- Boisramé, G.F.S., Thompson, S.E., Kelly, M., Cavalli, J., Wilkin, K.M., Stephens, S.L., 2017b. Vegetation change during 40 years of repeated managed wildfires in the Sierra Nevada, California. For. Ecol. Manage. 402, 241–252.
- Brown, P.M., Wu, R., 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. Ecology 86, 3030–3038.
- Bucharova, A., 2017. Assisted migration within species range ignores biotic interactions and lacks evidence. Restor. Ecol. 25, 14–18.
- Buckley, T.N., Turnbull, T.L., Adams, M.A., 2012. Simple models for stomatal conductance derived from a process model: cross-validation against sap flux data. Plant, Cell Environ. 35, 1647–1662.
- Cansler, C.A., McKenzie, D., 2014. Climate, fire size, and biophysical setting control fire severity and spatial pattern in the northern Cascade Range, USA. Ecol. Appl. 24, 1037–1056.
- Churchill, D.J., Larson, A.J., Dahlgreen, M.C., Franklin, J.F., Hessburg, P.F., Lutz, J.A., 2013. Restoring forest resilience: from reference spatial patterns to silvicultural prescriptions and monitoring. For. Ecol. Manage. 291, 442–457.
- Clark, J.S., Silman, M., Kern, R., 1999. Seed dispersal near and far: patterns across temperate and tropical forests. Ecology 80, 1475–1494.
- Clyatt, K.A., Crotteau, J.S., Schaedel, M.S., Wiggins, H.L., Kelley, H., Churchill, D.J., Larson, A.J., 2016. Historical spatial patterns and comtemporary tree mortality in dry mixed-conifer forests. For. Ecol. Manage. 361, 23–37.
- Cocking, M.I., Varner, J.M., Knapp, E.E., 2014. Long-term effects of fire severity on oakconifer dynamics in the southern Cascades. Ecol. Appl. 24 (1), 94–107.
- Collins, B.M., Lydersen, J.M., Everett, R.G., Fry, D.L., Stephens, S.L., 2015. Novel characterization of landscape-level variability in historical vegetation structure. Ecol. Appl. 25, 1167–1174.
- Collins, B.M., Miller, J.D., Thode, A.E., Kelly, M., van Wagtendonk, J.W., Stephens, S.L., 2009. Interactions among wildland fires in a long-established Sierra Nevada natural fire area. Ecosystems 12, 114–128.
- Collins, B.M., Roller, G.B., 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. Landscape Ecol. 28, 1801–1813.
- Collins, B.C., Stephens, S.L., 2010. Stand-replacing patches within a 'mixed severity' fire regime: quantitative characterization using recent fires in a long-established natural fire area. Landscape Ecol. 25, 927–939.
- Conard, S.G., Radosevich, S.R., 1982a. Growth responses of white fir to decreased shading and root competition by montane chaparral shrubs. Forest Science 28, 309–320.
- Conard, S.G., Radosevich, S.R., 1982b. Post-fire succession in white fire (Abies concolor) vegetation of the northern Sierra Nevada. Madrono 29, 42–56.
- Cooper, C.F., 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. Ecol. Monogr. 30, 129–164.
- Cooper, C.F., 1961. Pattern in ponderosa pine forests. Ecology 42, 493-499.
- Coppoletta, M., Merriam, K.E., Collins, B.M., 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. Ecol. Appl. 26, 686–699.
- Corbin, J.D., Holl, K.D., 2012. Applied nucleation as a forest restoration strategy. For. Ecol. Manage. 265, 37–46.
- De Frenne, P., Rodríguez-Sánchez, F., Coomes, D.A., et al., 2013. Microclimate moderates plant responses to macroclimate warming. Proc. Natl. Acad. Sci. 110, 18561–18565.
- Del Moral, R., Bliss, L., 1993. Mechanisms of primary succession: Insights from the eruption of Mount St. Helens. In: Begon, M., Fitter, H.H. (Eds.), Advances in Ecological Research. Aceadmeic Press, San Diego, CA, pp. 1–66.
- DeSiervo, M.H., Jules, E., Safford, H.D., 2015. Disturbance response across a productivity gradient: postfire vegetation in serpentine and non-serpentine forests. Ecosphere 6 (4) Article 60.
- Dobrowski, S.Z., Swanson, A.K., Abatzoglou, J.T., Holden, Z.A., Safford, H.D., Schwartz, M.K., Gavin, D.G., 2015. Forest structure and species traits mediate projected recruitment declines in western US tree species. Glob. Ecol. Biogeogr. 24, 917–927.
- Donato, D.C., Fontaine, J.B., Campbell, J.L., Robinson, W.D., Kauffman, J.B., Law, B.E., 2009. Conifer regeneration in stand-replacement portions of a large mixed-severity wildfire in the Klamath-Siskiyou Mountains. Can. J. Forest Res. 39, 823–838.
- Earles, M., North, M., Hurteau, M., 2014. Wildfire and drought dynamics destabilize carbon stores of fire-suppressed forests. Ecol. Appl. 24, 732–740.

- Erickson, H.E., Harrington, C.A., 2006. Conifer-Ceanothus interactions influence tree growth before and after shrub removal in a forest plantation in the western Cascade Mountains, USA. For. Ecol. Manage. 229, 183-194.
- Fettig, C.J., Klepzig, K.D., Billings, R.F., Munson, A.S., Nebeker, T.E., Negron, J.F., Nowak, J.T., 2007. The effectiveness of vegetation management practices for prevention and control of bark beetle infestations in coniferous forests of the western and southern United States. For. Ecol. Manage. 238, 24-53.
- Field, C., Merino, J., Mooney, H.A., 1983. Compromises between water-use efficiency and nitrogen-use efficiency in five species of California evergreens. Oecologia 60, 384_389
- Fites-Kaufman, J.A., Rundel, P., Stephenson, N., Weixelman, D.A., 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. In: Barbour, M., Keeler-Wolf, T., Schoenherr, A.A. (Eds.), Terrestrial Vegetation of California. University of California Press, pp. 456-501.
- Flint, L.E., Flint, A.L., Thorne, J.H., Boynton, R., 2013. Fine-scale hydrologic modeling for regional landscape applications: the California Basin Characterization Model development and performance. Ecological Processes 2, 25.
 Forest Climate Action Team, 2018. California Forest Carbon Plan: Managing Our Forest
- Landscapes in a Changing Climate. Sacramento, CA, pp. 178.
- FRAP. 2018. California's Forest and Rangelands: 2018 Assessment. California Depart. of Forestry and Fire Protection. < http://frap.fire.ca.gov/assessment/index >
- Fry, D.L., Stephens, S.L., Collins, B.M., North, M.P., Franco-Vizcaino, E., Gill, S.J., 2014. Contrasting spatial patterns in active-fire and fire-suppressed Mediterranean climate old-growth, mixed conifer forests. PLoS ONE. https://doi.org/10.1371/journal.pone.
- Goforth, B.R., Minnich, R.A., 2008. Densification, stand-replacement wildfire, and extirpation of mixed conifer forest in Cuvamaca Rancho State Park, southern California. For. Ecol. Manage. 256, 36-45.
- Gómez-Aparicio, L., Gómez, J.M., Zamora, R., Boettinger, J.L., 2005. Canopy vs. soil effects of shrubs facilitating tree seedlings in Mediterranean montane ecosystems. J. Veg. Sci. 16, 191–198.
- Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., Baraza, E., 2004.

 Applying plant facilitation to forest restoration: A meta-analysis of the use of shrubs as nurse plants. Ecologocial Appl. 14, 1128–1138.
- Gray, A., Zald, H., Kern, R., North, M., 2005. Stand conditions associated with tree regeneration in Sierran mixed-conifer forests. Forest Sci. 5, 198-210.
- Greeley, W.B., 1907. A rough system of management for reserve lands in the western Sierras. Proc. Soc. Am. Foresters 2, 103-114.
- Greene, D.F., Johnson, E.A., 1993. Seed mass and dispersal capacity in wind-dispersed diaspores. Oikos 67, 69–74.
- Greene, D.F., Johnson, E.A., 1996. Wind dispersal of seeds from a forest into a clearing. Ecology 77, 595-609.
- Greene, D.F., Johnson, E.A., 2000. Tree recruitment from burn edges. Can. J. For. Res. 30,
- 1264-1274. Greene, D.F., Johnson, E.A., 2004. Modelling the temporal variation in North American
- tree seed production. Can. J. For. Res. 34, 65-75. Greenwood, D.L., Weisberg, P.J., 2008. Density-dependent tree mortality in pinyon-ju-
- niper woodlands. For. Ecol. Manage. 255, 2129–2137. Griffin, D., Anchukaitis, K.J., 2014. How unusual is the 2012–2014 California drought? Geophys. Res. Lett. 41, 9017-9023.
- Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107-145.
- Haire, S.L., McGarigal, K., 2010. Effects of landscape patterns of fire severity on regenerating ponderosa pine forests (*Pinus ponderosa*) in New Mexico and Arizona, USA. Landscape Ecol. 25, 1055–1069.
- Hallema, D.W., Sun, G., Caldwell, P.V., Norman, S.P., Cohen, E.C., Liu, Y., Bladon, K.D., McNulty, S.G., 2018. Burned forests impact water supplies. Nat. Commun. 9, 1307. https://doi.org/10.1038/s41467-018-03735-6.
- Harvey, B.J., Donato, D.C., Turner, M.G., 2016. Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984-2010). Landscape Ecol. 31, 2367–2383.
- Helms, J.A., Tappeiner, J.C., 1996. Silvicultural systems for the Sierra Nevada. Sierra Nevada Ecsosystem Project: Final report to Congress. University of California Centers for Water and Wildland Resources, Davis.
- Hessburg, P.F., Churchill, D.J., Larson, A.J., Jaugo, R.D., Miller, C., Spies, T.A., North, M.P., Povak, N.A., Belote, R.T., Singleton, P.H., Gaines, W.L., Keane, R.E., Aplet, G.H., Stephens, S.L., Morgan, P., Bisson, P.A., Rieman, B.E., Salter, R.B., Reeves, G.H., 2015. Restoring fire-prone inland Pacific landscapes: seven core principles. Landscape Ecol. 30, 1805-1835.
- Hessburg, P.F., Spies, T.A., Perry, D.A., Skinner, C.N., Taylor, A.H., Brown, P.M., Stephens, S.L., Larson, A.J., Churchill, D.J., Povak, N.A., Singleton, P.H., McComb, B., Zielinski, W.J., Collins, B.M., Salter, R.B., Keane, J.J., Franklin, J.F., Riegel, G., 2016. Tamm Review: Management of mixed-severity fire regime foress in Oregon, Washington and Northern California. Forest Ecology and Management 366, 221-250.
- Holmgren, M., Gómez-Aparicio, L., Quero, J.L., Valladares, F., 2012. Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. Oecologia 169, 293-305.
- Huntington, J.L., Hegewisch, K.C., Daudert, B., Morton, C.G., Abatzoglou, J.T., McEvoy, D.J., Erickson, T., 2017. Climate engine: cloud computing and visualization of climate and remote sensing data for advanced natural resource monitoring and process understanding. Bull. Am. Meteorol. Soc. 98, 2397-2410.
- Hurteau, M.D., Liang, S., Martin, K.L., North, M.P., Koch, G.W., Hungate, B.A., 2016. Restoring forest structure and process stabilizes forest carbon in wildfire-prone southwestern ponderosa pine forests. Ecol. Appl. 26, 382–391.
- Hurteau, M., North, M., 2009. Fuel treatment effects on tree-based forest carbon storage and emissions under modeled wildfire scenarios. Front. Ecol. Environ. 7, 409-414.
- Hurteau, M., North, M., 2010. Carbon recovery rates following different wildfire risk mitigation treatments. For. Ecol. Manage. 260, 930-937.
- Innes, J., North, M., Williamson, N., 2006. Effect of thinning and prescribed fire restoration treatments on woody debris and snag dynamics in a Sierran old-growth

- mixed-conifer forest. Can. J. For. Res. 36, 3183-3193.
- Jeronimo, S.M., Kane, V.R., Churchill, D.J., McGaughey, R.J., Franklin, J.F., 2018. Applying LiDAR individual tree detection to management of structurally diverse forest landscapes, J. Forest, 116, 336-346.
- Johnson, A., Gutsell, S.L., 1994. Fire frequency models, methods and interpretations. Adv. Ecological Res. 25.
- Kane, V.R., Cansler, C.A., Povak, N.A., Kane, J.T., McGaughey, R.J., Lutz, J.A., Churchill, D.J., North, M.P., 2015a. Mixed severity fire effects within the Rim fire: Relative importance of local climate, fire weather, topography and forest structure. For. Ecol. Manage. 358, 62-79.
- Kane, V.R., Lutz, J.A., Cansler, C.A., Povak, N.A., Churchill, D.J., Smith, D.F., Kane, J.T., North, M.P., 2015b. Water balance and topography predict fire and forest structure patterns. For. Ecol. Manage. 338, 1-13.
- Kane, V.R., North, M.P., Lutz, J.A., Churchill, D.J., Roberts, S.L., Smith, D.F., McGaughey, R.J., Kane, J.T., Brooks, M.L., 2014. Assessing fire effects on forest spatial structure using a fusion of Landsat and airborne LiDAR data in Yosemite National Park. Remote Sens. Environ. 151, 89-101.
- Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G., Rundel, P.W., 2011. Fire in Mediterranean Ecosystems: Ecology, Evolution and Management. Cambridge University Press.
- Keeley, J.E., Safford, H.D., 2016. Fire as an ecosystem process. In: Mooney, H., Zavaleta, E. (Eds.), Ecosystems of California. University of California Press Oakland, California.
- Kennedy, M.C., Johnson, M.C., 2014. Fuel treatment prescriptions alter spatial patterns of fire severity around the wildland-urban interface during the Wallow Fire, Arizona, USA. For. Ecol. Manage. 318 122-13.
- Keyser, A., Westerling, A.L., 2017. Climate drives inter-annual variability in probability of high severity fire occurrence in the western United States. Environ. Res. Lett. 12,
- J. Kittreadge Kittreadge, J. 1953. Influences of forests on snow in the ponderosa, sugar pine, fir zone of the Central Sierra Nevada.
- Knapp, E.E., Estes, B.L., Skinner, C.N., 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. PSW-GTR-224. Albany, CA, pp. 80.
- Knapp, E.E., Skinner, C.N., North, M.P., Estes, B.L., 2013. Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed conifer forest. For. Ecol. Manage. 310, 903-914.
- Knapp, E.E., Weatherspoon, C.P., Skinner, C.N., 2012. Shrub seed banks in mixed conifer forests of northern California and the role of fire in regulating abundance. Fire Ecology 8, 32-48.
- Knapp, E.E., Schwilk, D.W., Kane, J.M., Keeley, J.E., 2006. Role of burning season on initial understory vegetation response to prescribed fire in a mixed conifer forest. Can. J. For. Res. 37, 11–22.
- Knapp, E.E., Varner, J.M., Busse, M.D., Skinner, C.N., Shestak, C.J., 2011. Behaviour and effects of prescribed fire in masticated fuelbeds. Int. J. Wildland Fire 20, 932-945.
- Kobziar, L.N., McBride, J.R., Stephens, S.L., 2009. The efficacy of fire and fuels reduction treatments in a Sierra Nevada pine plantation. Int. J. Wildland Fire 18, 791–801.
- Landram, M., 1996. Status of reforestation on National Forest Lands within the Sierra Nevada Ecosystem Project Study Area In Sierra Nevada Ecosystem Project: Final report to Congress, vol. III, Assessments and scientific basis for management options. University of California, Davis, Centers for Water and Wildland Resources.
- Lanini, W.T., Radosevich, S.R., 1986. Response of three conifer species to site preparation and shrub control. Forest Sci. 32, 61-77
- Larson, A.J., Churchill, D., 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments, For, Ecol. Manage, 267, 74-92.
- Lauvaux, C.A., Skinner, C.N., Taylor, A.H., 2016. High severity fire and mixed conifer forest-chaparral dynamics in the southern Cascade Range, USA. For. Ecol. Manage. 363, 74–85.
- Ledig, F.T., Kitzmiller, J.H., 1992. Genetic strategies for reforestation in the face of global climate change. For. Ecol. Manage. 50, 153-169.
- Leiberg, J.B., 1902. Forest conditions in the northern Sierra Nevada, California. U.S. Geological Survey Professional Paper 8. Washington, DC: U.S. Government Printing Office, pp. 194.
- Löf, M., Bolte, A., Jacobs, D.F., Jensen, A.M., 2014. Nurse trees as a forest restoration tool for mixed plantations: effects on competing vegetation and performance in target tree species. Restor. Ecol. 22, 758-765.
- Long, J.N., 1985. A practical approach to density management. Forestry Chronicle 61, 88-89.
- Long, J.N., 2008. Emulating natural disturbance regimes as a basis for forest management: a North American view. For. Ecol. Manage. 257, 1868–1873.
- Long, J.W., Anderson, M.K., Quinn-Davidson, L., Goode, R.W., Lake, F.K., Skinner, C.N., 2016. Restoring California black oak ecosystems to promote tribal values and wildlife. USDA Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-252.
- Lundquist, J.D., Dicerson-Lange, S.E., Lutz, J.A., Cristea, N.C., 2013. Lower forest density enhances snow retention in regions with warmer winters: A global framework developed from plot-scale observations and modeling. Water Resour. Res. 49, 6356-6370.
- Lutz, J.A., van Wagtendonk, J.W., Franklin, J.F., 2010. Climatic water deficit, tree species ranges, and climate change in Yosemite National Park. J. Biogeogr. 37, 936-950.
- Lydersen, J.M., Collins, B.M., Brooks, M.L., Matchett, J.R., Shive, K.L., Povak, N.A., Kane, V.R., Smith, D.F., 2017. Evidence of fuels management and fire weather influencing fire severity in an extreme fire event. Ecol. Appl. 27, 2013–2030. Lydersen, J.M., Collins, B.M., Knapp, E.E., Roller, G.B., Stephens, S.L., 2015. Relating fuel
- loads to overstorey structure and composition in a fire-excluded Sierra Nevada mixed conifer forest. Int. J. Wildland Fire 24, 484-494.
- Lydersen, J., North, M., 2012. Topographic variation in structure of mixed-conifer forests under an active-fire regime. Ecosystems 15, 1-13.
- Lydersen, J., North, M., Collins, B., 2014. Severity of an uncharacteristically large wildfire, the Rim Fire, in forests with relatively restored frequent fire regimes. For. Ecol.

- Manage. 328, 326-334.
- Lydersen, J.M., North, M.P., Knapp, E.E., Collins, B.M., 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: reference conditions and long-term changes following fire suppression and logging. For. Ecol. Manage. 304, 370–382.
- Lyons-Tinsley, C., Peterson, D., 2012. Surface fuel treatments in young, regenerating stands affect wildfire severity in a mixed conifer forest, eastside Cascade Range, Washington, USA. For. Ecol. Manage. 270, 117-125.
- Ma, S., Concilio, A., Oakley, B., North, M., Chen, J., 2010. Spatial variability in microclimate in a mixed-conifer forest before and after thinning and burning treatments. For. Ecol. Manage. 259, 904-915.
- McDonald, P.M., Fiddler, G.O., 1993. Feasibility of alternatives to herbicides in young conifer plantations in California. Can. J. For. Res. 23, 2015–2022.
- McDonald, P.M., Fiddler, G.O., 2010. Twenty-five years of managing vegetation in conifer plantations in northern and central California: results, application, principles, and challenges. Gen. Tech. Rep. PSW-GTR-231. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, pp. 87.
- McLachlan, J.S., Hellmann, J.J., Schwartz, M.W., 2007. A framework for debate of assisted migration in an era of climate change. Conserv. Biol. 21, 297–302.
 Meyer, M., Kelt, D., North, M., 2007a. Microhabit associations of northern flying squirrels
- in burned and thinned stands of the Sierra Nevada. Am. Midl. Nat. 157, 202-211.
- Meyer, M., North, M., Gray, A., Zald, H., 2007b. Influence of soil thickness on stand characteristics in a Sierra Nevada mixed-conifer forest. Plant Soil 294, 113-123.
- Meyer, M.D., North, M.P., Kelt, D.A., 2005. Short-term effects of fire and forest thinning on truffle abundance and consumption by Neotamias speciosus in the southern Sierra
- Nevada of California. Can. J. For. Res. 35, 1061–1070. Michaletz, S., Johnson, E.A., Mell, W.E., Greene, D.F., 2013. Timing of fire relative to seed development may allow non-serotinous species to recolonize from the aerial seedbanks of fire-killed trees. Biogeosciences 10, 5061-5078.
- Millar, C.I., Stephenson, N.L., 2015. Temperate forest health in an era of emerging megadisturbance. Science 349, 823-826.
- Millar, C.I., Libby, W.J., 1989. Disneyland or native ecosystem: genetics and the re-
- storationist. Ecological Restoration 7, 18–24.
 Miller, J.D., Thode, A.E., 2007. Quantifying burn severity in a heterogeneous landscape with a relative version of the delta Normalized Burn Ratio (dNBR). Remote Sens. Environ. 109, 66-80.
- Miller, C., Urban, D.L., 2000. Connectivity of forest fuels and surface fire regimes. Landscape Ecol. 15, 145-154.
- Miller, J.D., Quayle, B., 2015. Calibration and validation of immediate post-fire satellite derived data to three severity metrics. Fire Ecol. 11, 12-30.
- Miller, J.D., Safford, H., 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and southern Cascades, California, USA. Fire Ecol. 8, 41-57.
- Moghaddas, J.J., York, R.A., Stephens, S.L., 2008. Initial response of conifer and California black oak seedlings following fuel reduction activities in a Sierra Nevada mixed conifer forest. For. Ecol. Manage. 255, 3141-3150.
- Nagel, T.A., Taylor, A.H., 2005. Fire and persistence of montane chaparral in mixed conifer forest landscapes in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. J. Torrey Bot. Soc. 132, 442-457.
- Näsi, R., Honkavaara, E., Lyytikäinen-Saarenmaa, P., Blomqvist, M., Litkey, P., Hakala, T., Viljanen, N., Kantola, T., Tanhuanpää, T., Holopainen, M., 2015. Using UAV-based photogrammetry and hyperspectral imaging for mapping bark beetle damage at treelevel. Remote Sensing 7, 15467-15493.
- NFMA, 1976. National Forest Management Act of 1976. 16 U.S.C. 1600.
- Norris, C., Hobson, P., Ibisch, P.L., 2012. Microclimate and vegetation function as in-
- dicators of forest thermodynamic efficiency. J. Appl. Ecol. 49, 562–570.

 North, M., Boynton, R.M., Stine, P.A., Shipley, K.F., Underwood, E.C., Roth, N.E., Viers, J.

 H., Quinn, J.F., 2012. Geographic information system landscape analysis using GTR 220 concepts. Pages 107-115 In: North, M., (Ed.), Managing Sierra Nevada Forests, General Technical Report PSW-GTR-237, USDA Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 184.
- North, M., Collins, B., Safford, H., Stephenson, N., 2016. Montane Forests. Pages 553-578 In: Mooney, H., Zavelta, E., (Eds.), Ecosystems of California, U.C. Press, Berkeley, CA, pp. 984.
- North, M.P., Hurteau, M.D., 2011. High-severity wildfire effects on carbon stocks and emissions in fuels treated and untreated forest. For. Ecol. Manage. 261, 1115-1120.
- North, M., Hurteau, M., Fiegener, R., Barbour, M., 2005. Influence of fire and El Niño on tree recruitment varies by species in Sierran mixed conifer. Forest Sci. 51 (3), 187-197.
- North, M., Hurteau, M., Innes, J., 2009a. Fire suppression and fuels treatment effects on mixed-conifer carbon stocks and emissions. Ecol. Appl. 19, 1385–1396.
 North, M.P., Kane, J.T., Kane, V.R., Asner, G.P., Berigan, W., Churchill, D.J., Conway, S.,
- Gutiérrez, R.J., Jeronimo, S., Keane, J., Koltunov, A., Mark, T., Moskal, M., Munton, T., Peery, Z., Ramirez, C., Sollmann, R., White, A.M., Whitmore, S., 2017. Cover of tall trees best predicts California spotted owl habitat. For. Ecol. Manage. 405, 166-178.
- North, M., Keeton, W., 2008. Emulating natural disturbance regimes: an emerging approach for sustainable forest management. In: Lafortezza, R., Chen, J., Sanesi, G., Crow, T. (Eds.), Landscape Ecology: Sustainable Management of Forest Landscapes.
- Springer-Verlag Press, pp. 341–372 Chapter 17.
 North, M., Innes, J., Zald, H., 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. Can. J. For. Res. 37, 331-342
- North, M., Stine, P., Hara, K.O., Zielinski, W., Stephens, S., 2009b. An Ecosystem Management Strategy for Sierran Mixed- Conifer Forests. General Technical Report PSW-GTR-220, pp. 49.
- Oakley, B., North, M., Franklin, J., 2006. Facilitative and competitive effects of a N-fixing shrub on white fir saplings. For. Ecol. Manage. 233, 100-107.
- Oliver, W.W., 1984. Brush reduces growth of thinned ponderosa pine in northern California. USDA Forest Service, Pacific Southwest Research Station, Research Paper PSW-RP-172.
- Oliver, W.W., 1990. Spacing and shrub competition influence 20-year development of

- planted ponderosa pine. West. J. Appl. For. 5, 79-82.
- Owen, S.M.C.H., Sanchez Sieg, A.J., Meador, P.Z., Fule, J.M., Iniguez, L.S., Fornwalt Baggett, P.J., Battaglia, M.A., 2017. Spatial patterns of ponderosa pine regeneration in high-severity burn patches. For. Ecol. Manage. 405, 124–149.
- Parker, T.J., Clancy, K.M., Mathiasen, R.L., 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agric. For. Entomol. 8, 167-189.
- Parsons, R.A., Linn, R.R., Pimont, F., Hoffman, C., Sauer, J., Winterkamp, J., Sieg, C.H., Jolly, W.M., 2017. Numerical investigation of aggregated fuel spatial pattern impacts on fire behavior. Land 6, 43.
- Paz-Kagan, T., Brodrick, P.G., Vaughn, N.R., Das, A.J., Stephenson, N.L., Nydick, K.R., Asner, G.P., 2017. What mediates tree mortality during drought in the southern Sierra Nevada? Ecol. Appl. 27, 2443-2457.
- Pellizzaro, G., Duce, P., Ventura, A., Zara, P., 2007. Seasonal variations of live moisture content and ignitability of the Mediterranean Basin. Int. J. Wildland Fire 16, 633-641.
- Peters, V.S., Macdonald, S.E., Dale, M.R.T., 2005. The interaction between masting and fire is key to white spruce regeneration. Ecology 86, 1744–1750.

 Peterson, D.W., Hessburg, P.F., Salter, B., James, K.M., Dahlgreen, M.C., Barnes, J.A.
- 2007. Reintroducing fire in regeneration dry forests following stand-replacing wildfire. In: Powers, R.F. (tech. ed.), Restoring fire-adapted ecosystems: Proceedings of the 2005 National Silviculture Workshop. USDA Forest Service, PSW-GTR-203, Albany, CA, pp. 79-86.
- Peterson, T.D., Newton, M., Zedaker, S.M., 1988. Influence of Ceanothus velutinus and associated forbs on water stress and stemwood production of Douglas fir. Forest Sci. 34 333-343
- Petrie, M.D., Wildeman, A.M., Bradford, J.B., Hubbard, R.M., Lauenroth, W.K., 2016. A review of precipitation and temperature control on seedling emergence and establishment for ponderosa and lodgepole pine forest regeneration. For. Ecol. Manage. 361, 328-338,
- Plamboeck, A.H., Dawson, T.E., Egerton-Warburton, L.M., North, M.P., Bruns, T.D., Querejeta, J.I., 2007. Water transfer via ectomycorrhizal fungal hyphae to conifer seedlings. Mycorrhiza 17, 439-447.
- Plamboeck, A.H., North, M.P., Dawson, T.E., 2008. Conifer seedlings survival under closed canopy and manzanita patches in the Sierra Nevada. Madrono 55, 193–203.
- Powers, R.F., Reynolds, P.E., 1996. Ten-year responses of ponderosa pine plantations to repeated vegetation and nutrient control along an environmental gradient. Can. J. For. Res. 29, 1027-1038.
- PRISM Climate Group. 2018. Oregon State University, < http://prism.oregonstate.
- Puhlick, J.J., Laughlin, D.C., Moore, M.M., 2012. Factors influencing ponderosa pine regeneration in the southwestern USA. For. Ecol. Manage. 264, 10–19.
- Reiner, A.L., Vaillant, N.M., Dailey, S.N., 2012. Mastication and prescribed fire influences on the tree mortality and predicted fire behavior in ponderosa pine. West. J. Appl. For. 27, 36-41.
- Restaino, C.R., Safford, H.D., 2018. Fire and climate change. In: Van Wagtendonk, J., Sugihara, N.G., Stephens, S.L., Thode, A.E., Shaffer, K.E., Fites-Kaufman, J. (Eds.) Fire in California's ecosystems, second ed. University of California Press, Berkeley, CA Chapter 26.
- Ricciardi, A., Simberloff, D., 2009. Assisted colonization is not a viable conservation strategy. Trends Ecol. Evol. 24, 248-253.
- Riegel, G.M., Miller, R.F., Krueger, W.C., 1992. Competition for resources between understory vegetation and overstory Pinus ponderosa in northeastern Oregon. Ecol. Appl. 2, 71-85.
- Ritchie, M.W., Knapp, E.E., Skinner, C.N., 2013. Snag longevity and surface fuel accumulation following post-fire logging in a ponderosa pine dominated forest. For. Ecol. Manage. 287, 113-122.
- Roberts, S.L., Kelt, D.A., van Wagtendonk, J.W., Miles, A.K., Meyer, M.D., 2015. Effects of fire on small mammal communities in frequent-fire forests in California. J. Mammal. 96, 107-119.
- Roccaforte, J.P., Huffman, D.W., Fule, P.Z., Covington, W.W., Chancellor, W.W., Stoddard, M.T., Crouse, J.E., 2015. Forest structure and fuels dynamics following ponderosa pine restorations treatments, White Mountains, Arizona, USA. For. Ecol. Manage. 337, 174–185.
- Rubilar, R.A., Allen, H.L., Fox, T.R., Cook, R.L., Albaugh, T.J., Campoe, O.C., 2018 Advances in silviculture of intensively managed plantations. Curr. For. Rep. 4, 23-34.
- Safford, H.D., North, M.P., Meyer, M.D., 2012. Climate change and the relevance of historical forest conditions. Pages 23-45 In: North, M., (Ed.) Managing Sierra Nevada Forests, General Technical Report PSW-GTR-237. USDA Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 184.
- Safford, H.D., Stevens, J.T., 2017. Natural Range of Variation (NRV) for yellow pine and mixed conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. USDA Forest Service, Pacific Southwest Research Station. General Technical Report PSW-GTR-256, Albany, CA.
- Sartwell, C. 1971. Thinning ponderosa pine to prevent outbreaks of mountain pine beetle. In: Precommercial thinning of coastal and intermountain forests in the Pacific Northwest, Proceedings of a short course. Wasington State University, Pullman, pp. 41-52
- Savage, M., Mast, J.N., Feddema, J.J., 2013. Double whammy: high-severity fire and drought in ponderosa pine forests of the Southwest. Can. J. For. Res. 43, 570-583. Savolainen, O., Pyhäjärvi, T., Knürr, T., 2007. Gene flow and local adaptation in trees.
- Annu. Rev. Ecol. Evol. Syst. 38, 595-619. Sax, D.F., Smith, K.F., Thompson, A.R., 2009. Managed relocation: a nuanced evaluation is needed. Trends Ecol. Evol. 24, 472–473.
- Schubert, G.H., Adams, R.S., 1971. Reforestation Practices for Conifers in California. State of California Resources Agency, Department of Conservation, Division of Forestry, Sacramento, pp. 1971.
- Shive, K.L., Preisler, H.K., Welch, K.R., Safford, H.D., Butz, R.J., O'Hara, K.L., Stephens, S.L., 2018. From the stand-scale to the landscape-scale: predicting the spatial patterns of forest regeneration after disturbance. Ecol. Appl. https://doi.org/10.1002/eap.

- Show, S.B., Kotok, E.I., 1924. The role of fire in the California pine forests. USDA Bulletin No. 1294
- Skov, K.R., Kolb, T.E., Wallin, K.F., 2004. Tree size and drought affect ponderosa pine physiological response to thinning and burning treatments. Forest Sci. 50, 81–91.
- Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, M.S., 1997. The Practice of Silviculture: Applied Forest Ecology, ninth ed. Wiley and Son Inc, New York City, NY.
- Sollman, R., White, A.M., Tarbill, G.L., Manley, P.N., Knapp, E.E., 2016. Landscape hetergoneity compensates for fuel reduction treatment effects on Northern flying squirrel populations. For. Ecol. Manage. 373, 100-107.
- Soung-Ryoul, R., Concilio, A., Chen, J., North, M., Ma, S., 2009. Prescribed burning and mechanical thinning effects on belowground conditions and soil respiration in a mixed-conifer forest, California. For. Ecol. Manage. 257, 1324-1332.
- Stanturf, J.A., Palik, B.J., Dumroese, R.K., 2014. Contemporary forest restoration: A review emphasizing function. For. Ecol. Manage. 331, 292-323.
- Starrs, C.F., Butsic, V., Stephens, C., Stewart, W., 2018. The impact of land ownership, firefighting, and reserve status on fire probability in California. Environ. Res. Lett. 13, 034025
- Steel, Z.L., Safford, H.D., Viers, J.H., 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. Ecosphere 6, art8.
- Steel, Z.L., Koontz, M.J., Safford, H.D., 2018. The changing landscape of wildfire: burn pattern trends and implications for California's yellow pine and mixed conifer forests. Landscape Ecol. https://doi.org/10.1007/s10980-018-0665-5.
- Stephens, S.L., Bigelow, S.W., Burnett, R.D., Collins, B.M., Gallagher, C.V., Keane, J., Kelt, D.A., North, M.P., Roberts, S.J., Stine, P.A., Van Vuren, D.H., 2014. California spotted owl, songbird, and small mammal responses to landscape fuel treatments. Bioscience 64, 893-906.
- Stephens, S.L., Collins, B.M., Fettig, C.J., Finney, M.A., Hoffman, C.M., Knapp, E.E., North, M.P., Safford, H., Wayman, R.B., 2018. Drought, tree mortality, and wildfire in forests adapted to frequent fire. Bioscience 68, 77-88.
- Stephens, S.L., Fry, D., Franco-Vizcano, E., 2008. Wildfire and spatial patterns in forests in Northwestern Mexico: The United States wishes it had similar fire problems. Ecol. Soc. 13 (2) art. 10.
- Stephens, S.L., Gill, S.J., 2005. Forest structure and mortality in an old-growth Jeffrey pine-mixed conifer forest in north-western Mexico. For. Ecol. Manage. 205, 15–28.
- Stephens, S.L., Lydersen, J.M., Collins, B.M., Fry, D.L., Meyer, M.D., 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. Ecosphere 6, 1-63.
- Stephens, C.W., York, R.A., 2017. An evaluation of stand age as a factor of mastication efficiency and effectiveness in the central Sierra Nevada, California. Northwest Sci. 91, 389-398,
- Stephenson, N., 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. J. Biogeogr. 25, 855-870.
- Stevens, J.T., Collins, B.M., Long, J.W., North, M.P., Prichard, S.J., Tarnay, L.W., White, A.M., 2016. Evaluating potential trade-offs among fuel treatment strategies in mixedconifer forests of the Sierra Nevada. Ecosphere 7 (9), e01445. https://doi.org/10. 1002/ecs2.1445.
- Stevens, J.T., Safford, H.D., Harrison, S., Latimer, A.M., 2015. Forest disturbance accel-
- erates thermophilization of understory plant communities. J. Ecol. 103, 1253–1263. Stevens, J.T., Safford, H.D., Latimer, A.M., 2014. Wildfire-contingent effects of fuel treatments can promote ecological resilience in seasonally dry conifer forests. Can. J. For. Res. 44, 843-854.
- Stevens, J.T., Collins, B.M., Miller, J.D., North, M.P., Stephens, S.L., 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. For, Ecol. Manage 406, 28-36,
- Stevens, J.T., 2017. Scale-dependent effects of post-fire canopy cover on snowpack depth in montane coniferous forests. Ecol. Appl. 27, 1888-1900.
- Stevens-Rumann, C.S., Kemp, K.B., Higuera, P.E., Harvey, B.J., Rother, M.T., Donato, D.C., Morgan, P., Veblen, T.T., 2018. Evidence for declining forest resilience to wildfires under climate change. Ecol. Lett. 21, 243-252.
- Sudworth, G.B., 1900. Stanislaus and Lake Tahoe Forest Reserves, California and adjacent territory. Ann. Rep. U.S Geol. Surv. 21, 505–561.
 Symons, J.N., Fairbanks, D.H., Skinner, C.N., 2008. Influences of stand structure and fuel
- treatments on wildfire severity at Blacks Mountain Experimental Forest, northeastern California. California Geographer 48, 61–68.
- Taylor, A.H., 2010. Fire disturbance and forest structure in an old-growth Pinus ponderosa forest, southern Cascades, USA. J. Veg. Sci. 21, 561-572.
- Taylor, A.H., Skinner, C.N., 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains, Ecol. Appl. 13, 704-719.
- Teste, F.P., Simard, S.W., 2008. Mycorrhizal networks and distance from mature trees alter patterns of competition and facilitation in dry Douglas-fir forests. Oecologia
- Troendle, C.A., MacDonald, L., Luce, C.H., Larsen, I.J., 2010. Fuel management and water yield. In: Cumulative Watershed Effects of Fuel Management in the Western United States. In: Elliot, W.J., Miller, I.S., Audin, L., (Eds.), General Technical Report RMRS-GTR-231. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: Fort Collins, CO.
- Ursell, T., Young, D., 2017. Evaluating the prevalence of management activities in postfire plantations on National Forests in California. Unpublished report.
- USDA, 1989. Region 5 Silvicultural Practices Handbook. Forest Service Handbook 2409.

- 26, Chapter 40, Reforestation.
- USDA, 1990. Silvics of North America Volume 1: Conifers, United States Department of Agriculture (USDA), Forest Service.
- USDA, 2018. Forest Service Activity Tracking System (FACTS). National Resource Manager, USDA Forest Service. Accessed on May 2, 2018. Information online: http:// data.fs.usda.gov/geodata/edw/datasets.php.
- van Mantgem, P., Caprio, A.C., Stephenson, N.L., Das, A.J., 2016. Does prescribed fire promote resistance to drought in low elevation forests of the Sierra Nevada, California, USA? Fire Ecol. 12, 13–25.
- van Mantgem, P., Schwartz, M., 2004. An experimental demonstration of stem damage as a predictor of fire-caused mortality for ponderosa pine. Can. J. For. Res. 34, 1343-1347.
- van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fule, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., Veblen, T.T., 2009. Widespread increase of tree mortality rates in the western United States. Science 323, 521-524
- van Wagtendonk, J.W., Fites-Kaufman, J.A., Safford, H.D., North, M.P., Collins, B.M., 2018. Sierra Nevada Bioregion. In: van Wagtendonk, J.W., Sugihara, N.G., Stephens, S.L., Thode, A.E., Shaffer, K.E., Fites-Kaufman, J.A. (Eds.), Fire in California's Ecosystems, second ed. U.C. Press, Oakland, CA, pp. 249-278.
- Varhola, A., Coops, N.C., Weiler, M., Moore, R.D., 2010. Forest canopy effects on snow accumulation and ablation: An integrative review of empirical results. J. Hydrol. 392, 219–233.
- Wang, S.Y.S., Yoon, J.H., Becker, E., Gillies, R., 2017. California from drought to deluge.
- Nat. Clim. Change 7, 465–468. Warren, J.M., Brooks, J.R., Meinzer, F.C., Eberhart, J.L., 2008. Hydraulic redistribution of water from Pinus ponderosa trees to seedlings: evidence for an ectomycorrhizal pathway. New Phytol. 178, 382-394.
- Wayman, R., North, M., 2007. Initial response of a mixed-conifer understory plant community to burning and thinning restoration treatments. For. Ecol. Manage. 239, 32-44.
- Weatherspoon, C.P., Skinner, C.N., 1995. An assessment of factors associated with damage to tree crowns from the 1987 wildfires in Northern California. Forest Sci. 41, 430-451.
- Weaver, H., 1947. Fire- nature's thinning agent in ponderosa pine stands. J. Forest. 49,
- Welch, K.R., Safford, H.D., Young, T.P., 2016. Predicting conifer establishment post wildfire in mixed conifer forests of the North American Mediterranean-climate zone. Ecosphere 7 e01609-n/a.
- White, A.M., Zipkin, E.F., Manley, P.N., Schlesinger, M.D., 2013. Simulating avian species and forage group responses to fuel reduction treatments in coniferous forests. For. Ecol. Manage. 304, 261-274.
- White, A.S., 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. Ecology 66, 589-594.
- Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangodagamage, C., Cai, M., McDowell, N.G., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nat. Clim. Change 3, 292-297
- Wilson, A.M., Latimer, A.M., Gelfand, A.E., DeKlerk, H., Silander Jr., J.A., 2010. A hierarchical Bayesian model of wildfire in a Mediterranean biodiversity hotspot: implications of weather variability and global circulation. Ecol. Model. 221,
- Winford, E.M., Gaither Jr., J.C., 2012. Carbon outcomes from fuels treatment and bioenergy production in a Sierra Nevada forest. For. Ecol. Manage. 282. 1-9. York, R.A., O'Hara, K.L., Battles, J.J., 2013. Density effects on giant sequoia
- (Sequoiadendron giganteum) growth through 22 years: Implications for restoration and plantation management. West. J. Appl. For. 28, 30-36.
- Young, D.J.N., Stevens, J.T., Earles, J.M., Moore, J., Ellis, A., Jirka, A.L., Latimer, A.M., 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. Ecol. Lett. 20, 78–86.
- Zald, H.S.J., Dunn, C.J., 2018. Severe fire weather and intensive forest management increase fire severity in a multi-ownership landscape. Ecological Applications in press.
- Zald, H., Gray, A., North, M., Kern, R., 2008. Initial regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest, USA. For. Ecol. Manage. 256, 168-179.
- Zhang, J., Busse, M.D., Young, D.H., Fiddler, G.O., Sherlock, J.W., TenPas, J.D., 2017. Aboveground biomass responses to organic matter removal, soil compaction, and competing vegetation control on 20-year mixed conifer plantation in California. For. Ecol. Manage. 401, 341-353.
- Zhang, J., Oliver, W.W., Busse, M.D., 2006. Growth and development of ponderosa pine on sites of contrasting productivities: relative importance of stand density and shrub competition effects. Can. J. For. Res. 36, 2426-2438.
- Zhang, J., Powers, R.F., Oliver, W.W., Young, D.H., 2013. Response of ponderosa pine plantations to competing vegetation control in Northern California, USA: a meta analysis. Forestry 86, 3–11.
- Ziegler, J.P., Hoffman, C., Battaglia, M., Mell, W., 2017. Spatially explicit measurements of forest structure and fire behavior following restoration treatments in dry forests. For. Ecol. Manage. 386, 1-12.