

Changing climate and disturbance effects on southwestern US forests

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ABSTRACT

Changing climate and its interaction with disturbances is reshaping forests of the western United States and southwestern forests are experiencing these changes at an accelerated pace. Southwestern forests are fire prone and a legacy of fire exclusion from past land use and management have homogenized many frequent fire forests, increasing the chance that disturbances reinforce landscape homogeneity. Widespread disturbances, especially those that cause a vegetation type change from forest to non-forest, are and will continue to influence the provision of ecosystem services upon which society depends. Here we review our current understanding of changing climate and disturbance and how they will influence southwestern United States forests (defined as California, Nevada, Arizona and New Mexico). We synthesize the literature on climate-driven changes in disturbance and how disturbance combined with changing climate will alter forest structure, forest cover, and species composition. We then synthesize management options for improving forest resilience and present them in the context of the resist-accept-direct framework for managing in a changing climate. Managing for more resilient southwestern forests will require a more nimble approach to forest management than is currently practiced in the southwestern US. Our current process of years-long planning for a document that charts the course for several decades of management action is ill-suited to the rate of change that southwestern forests are undergoing. Effective management will require truly adaptive management, with frequent monitoring that informs decision-making and some level of experimentation with management approaches as a hedge against the uncertainty facing southwestern forests.

1. Introduction

In the southwestern US, climate change is interacting with insects, diseases, wildfire, and other disturbances to restructure forests. As climate change causes increasing aridification, disturbance is acting as a catalyst for change across the region and this portends a future with substantial forest cover contraction (Williams et al., 2013). These disturbances are occurring in forests that have been structured by land-use and land management activities that have increased structural homogeneity and forest cover continuity; a legacy of land-use and management that is commonplace throughout the western US (Lydersen et al., 2013, Huffman et al., 2020, Hagmann et al., 2021). Understanding how

the interacting effects of climate change and disturbance will impact forests across the southwestern US is essential for developing management approaches that can decrease the probability of forest cover loss, slow the rate of change, and manage the vegetation transition to increase the likelihood that intact functioning ecosystems persist and continue to provide ecosystem services.

Southwestern forests are critical for a range of both ecologically and societally relevant functions including the provision of habitat, recreational opportunity, and water, among many others (Broxton et al., 2020, Sánchez et al., 2021, Jones and Tingley, 2022). The importance of these functions and the role of forests in providing them vary spatially across the Southwest. For example, the Sierra Nevada of California experiences

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more precipitation relative to other locations in the Southwest, resulting in higher rates of tree growth and an increased volume of water available for downstream communities and agricultural production. Whereas in the Rio Grande watershed, upper forested watersheds receive less precipitation than the Sierra Nevada and much of the watershed is an arid environment, supporting less agricultural production. Regardless of the geographic location in the southwestern region (defined as California, Nevada, Arizona, and New Mexico following Hurteau et al., 2014), fire seasons that occur annually are common and changing climate and climate-driven increases in disturbance are altering forested ecosystems and impacting the services they provide.

Here we provide a synthesis of how changing climate and increasing wildfire and insect outbreaks are interacting with a legacy of land use and land management, which presents challenges to southwestern forest persistence and function. We build from and expand upon prior work (e. g. Hurteau et al., 2014) to include recent research that captures the accelerating rate of change that is impacting southwestern forests. We summarize past land-use, management, and fire history of many southwestern forests. We then review insects and fungi as drivers of forest structure, followed by a discussion of wildlife in southwestern forests, which are often drivers of management decision-making. We synthesize how changing climate and climate-driven increases in disturbance will directly affect forests and how forest change will alter water and carbon dynamics. We end with a discussion of the current understanding of how forest management can use the potential for change and the mechanisms of change to inform management options to facilitate ecosystem function under changing climate.

2. Past land-use and management

Forest types in the southwestern US range from oak and piñon-juniper woodlands at lower elevations to pine-dominated and mixed-conifer forests at mid-elevations to spruce and fir-dominated forests at higher elevations (Fig. 1). Historically, fire regimes varied across this elevation range and included natural caused and intentional human fire-use by indigenous groups (Fig. 1, Van de Water and Safford, 2011, Kitchen, 2012, Taylor et al., 2016, Guiterman et al., 2019, Syphard and Keeley, 2020). In low-elevation woodlands, fires were small and infrequent (Baker and Shinneman, 2004, Miller and Heyerdahl, 2008, Huffman et al., 2008, Bauer and Weisberg, 2009). In mid-elevation forests across the Southwest, high-frequency fire was commonplace, with Mean Fire Return Intervals (MFRI) ranging from several years to several decades (Table 1). The fire regimes in these frequent fire forests were augmented by indigenous groups with intentional burning which, in some areas, increased fire frequency and decreased fire size (Liebmann et al., 2016, Swetnam et al., 2016, Hankins, 2024, Boerigter et al., 2024). There is also evidence to suggest that fuel wood gathering occurred at a scale that would have introduced a fuel limitation to fire spread in some more densely populated areas (Roos et al., 2021, Knight et al., 2022). The high frequency of primarily surface fire created heterogeneous forest structure, with local scale variability consisting of individual trees, tree clusters, and openings as is common in many fire-maintained forests (Churchill et al., 2013).

Where fire was historically more frequent, grazing and logging altered vegetation structure, and generally caused a reduction in fire frequency (Covington et al., 1997, Fulé et al. 1997, Moore et al., 2004, Haggmann et al., 2021). At higher elevations, where fire is typically more climatically limited, human land-use and fire-exclusion had less impact

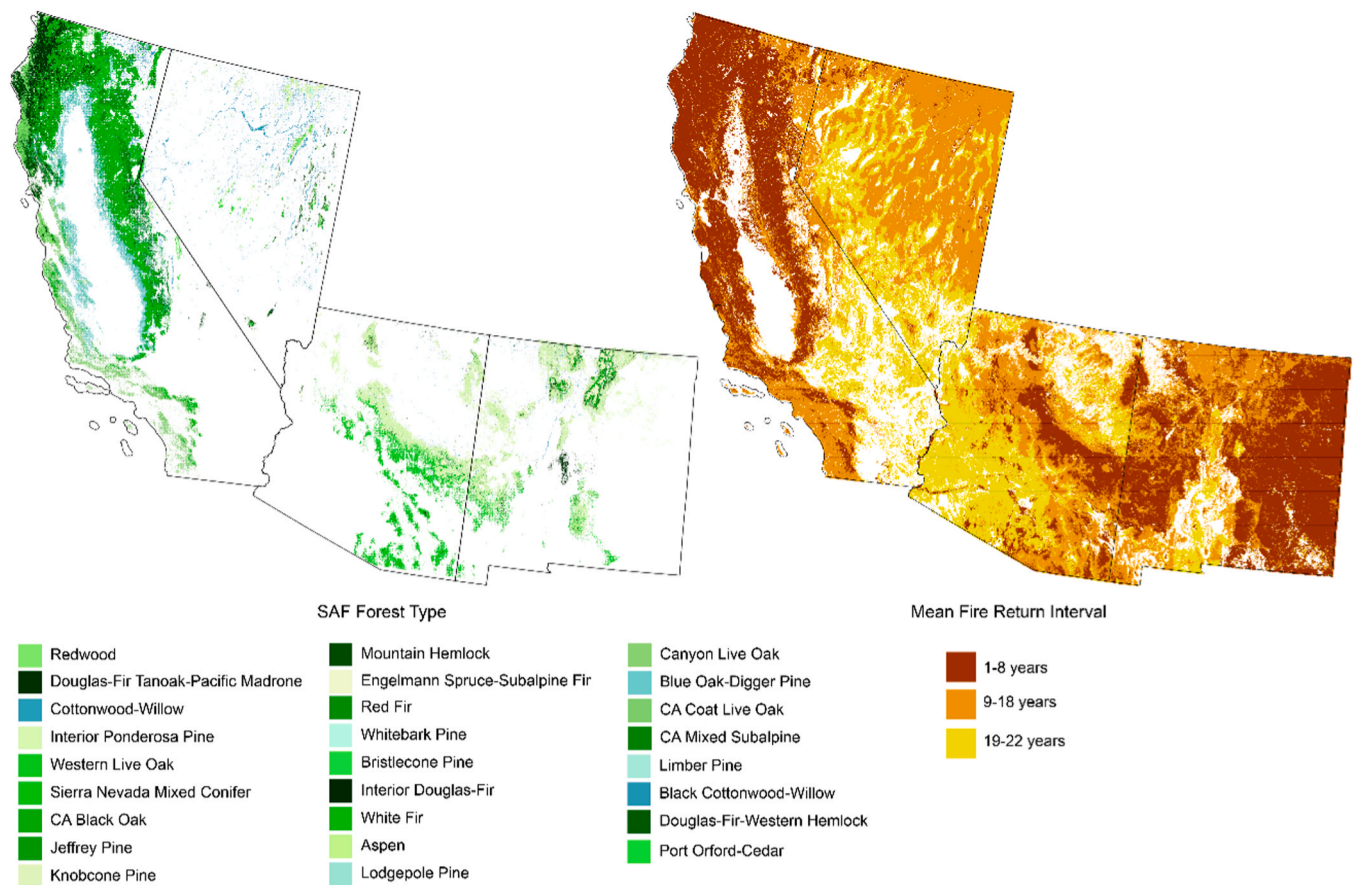


Fig. 1. Forest types (left) and historic mean fire return interval (right) for the southwestern US. Forest cover data are from LANDFIRE existing vegetation type and historic mean fire return interval from LANDFIRE mean fire return interval data products.

Table 1

Examples of fire frequency as measured by mean fire return interval (MFRI) by forest type and location for historically frequent fire forests. MFRI all scars in every year a fire scar is recorded. MFRI 25 % is calculated based on 25 % of sampled trees recording a given fire. NR = not reported.

Forest Type	MFRI all scars (years)	MFRI 25 % of trees scarred (years)	Location	Authors
Ponderosa pine	4.3	20.8	Santa Fe National Forest, New Mexico	(Margolis and Balmat, 2009)
Mixed-conifer	12.4	31.6	Santa Fe National Forest, New Mexico	(Margolis and Balmat, 2009)
Ponderosa pine/mixed-conifer	2.2	25.5	Saguaro National Park Wilderness, Arizona	(Farris et al. 2010)
Ponderosa pine	6.9	9.5	Grandview, Grand Canyon National Park, Arizona	(Fulé et al. 2003)
Ponderosa pine	3.2	9.2	Powell Plateau, Grand Canyon National Park, Arizona	(Fulé et al. 2003)
Ponderosa pine	3.7	6.4	Fire point, Grand Canyon National Park, Arizona	(Fulé et al. 2003)
Ponderosa pine	4.0	7.8	Rainbow Plateau, Grand Canyon National Park, Arizona	(Fulé et al. 2003)
Mixed-conifer	5.5	9.0	Swamp Ridge, Grand Canyon National Park, Arizona	(Fulé et al. 2003)
Ponderosa pine/piñon-juniper	4	NR	Mount Irish Range, Nevada	(Biondi et al. 2011)
Mixed-conifer	4.0	9.1	General Creek Watershed, Lake Tahoe Basin, California	(Beatty and Taylor, 2008)
Red fir	15.7	NR	Swain Mountain, California	(Taylor, 1993)
Giant Sequoia/mixed-conifer	3.3	34.8	Giant Forest, Sequoia National Park, California	(Swetnam et al. 2009)
Jeffrey pine/mixed-conifer	2.2	71	Sagehen Experimental Forest, California	(Vaillant and Stephens, 2009)
Mixed-conifer	11.4	NR	Teakettle Experimental Forest, California	(North et al. 2005)

(Hessburg et al., 2019). Fire suppression began in earnest in the early 1900s, following extensive grazing which had already interrupted frequent fire regimes (Savage and Swetnam, 1990). This ongoing fire exclusion has increased tree density and surface fuel loads beyond what was common prior to European-American settlement (Moore et al., 2004, Hanberry, 2014, Stephens et al., 2015). At the stand scale (i.e. 10 s to 100 ha), increased tree density and surface fuel loads have increased the risk of mortality, especially in low- and mid-elevation forests where fire was historically more frequent. Higher-density forests, with some exceptions for shade tolerant species, are typically more susceptible to mortality from drought and insects (Kane et al., 2014, Flake and Weisberg, 2019, Bradford et al., 2022). For example, during the 2012–2015 drought in the southern Sierra Nevada, 45 % of mortality was due to high tree density (Goulden and Bales, 2019). These same conditions also increase the risk of high-severity wildfire in forest types that historically experienced frequent low and mixed-severity fire regimes (Prichard et al., 2021). Importantly, infilling by trees across large landscapes has increased the homogeneity of fuel conditions, which support larger

disturbances.

3. Insects and fungi as drivers of forest structure and species distributions

Forest insects and fungi, including fungal pathogens, influence forests by altering the age and structure of trees, providing food sources for other insects and animals, breaking down plant material, and contributing to the overall structural diversity of forest ecosystems. Most insects and fungal pathogens in the Southwest are native where they typically occur at endemic levels, often causing little overall damage at a landscape scale. Generally, damage occurs at a small scale either via defoliation of parts of trees from larval or adult feeding from numerous insect groups (*Lepidoptera*, *Coleoptera*, *Hymenoptera*, *Diptera*) or from phloem feeding by bark beetles (*Coleoptera*: *Curculionidae*, *Scolytinae*) or wood-boring beetles (*Coleoptera*: *Buprestidae*, *Cerambycidae*). Phloem feeding bark beetles can cause growth loss by reducing the photosynthetic capacity of trees and can lead to increased susceptibility to secondary mortality agents and, in extreme cases, mortality. Woodboring beetles, depending on species, can cause damage that may include tip and twig dieback, individual tree mortality, or large outbreaks leading to landscape level mortality events. Throughout the forest types of the Southwest, numerous pulses of landscape-scale mortality events caused by bark beetles have changed forest cover and structure across large landscapes, with some specific and noteworthy outbreaks in the past three decades (Clifford et al., 2008, Santos and Whitham, 2010, Fettig et al., 2022).

In piñon-juniper forests, extreme drought increases the susceptibility of piñon pine (*Pinus edulis* and *Pinus monophylla*) to its primary mortality agent, the bark beetle species pinyon ips (*Ips confusus*). Pinyon ips populations can expand rapidly causing widespread mortality, which has occurred three times over the past three decades in the Southwest. The result can range from patchy, scattered live overstory trees to complete mortality of the mature and older piñon trees. Similarly, species within the *Dendroctonus* and *Ips* genera are most often associated with noticeable mortality events in ponderosa pine and related species. The structural changes that have occurred with fire-exclusion have created conditions that are especially favorable to bark beetle outbreaks such as in southern California (Fettig et al., 2019), across Arizona (Negrón et al., 2009), and throughout New Mexico, Utah, and Colorado. In some instances, the ingrowth of shade tolerant species with fire-exclusion has altered the species composition of both trees and insects. For example, outbreaks of insects like the Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough, *Lepidoptera*: *Erebidae*: *Lymantriinae*) which prefers true fir (*Abies* spp. Mill.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) first occurred in southern California in 2009–2012 (Coleman et al., 2014). Because many of these beetle species respond positively to drought-stressed trees, more prolonged and intense outbreaks could occur with the additional warming and drying which are projected for the Southwest.

In addition to the direct effects of insects on forests, insect outbreaks that cause extensive tree mortality can also alter forest flammability. Initially, during the ‘red’ phase, when dead leaves remain in the canopy, flammability increases because fuel moisture is low (Jolly et al., 2012). Once beetle-killed trees move from the ‘red’ to ‘gray’ phase (i.e. the needles have fallen), flammability in the canopy decreases. However, the dead trees will fall and increase surface fuel loads substantially over the next 10–20 years, which can provide a significant source of fuel for subsequent fires (Goodwin et al., 2020, 2021, Audley et al., 2021, Hurteau et al., 2024).

Fungi, unlike bark beetles and defoliating insects, serve numerous ecological roles including mutualistic relationships with plants, nutrient cycling, and carbon storage, and in the case of fungal pathogens, as agents of mortality (Korb et al., 2003, Rillig and Mummey, 2006, Hawkins and Henkel, 2011, Xiang et al., 2016). In fire-prone forests, fungi contribute to soil stabilization and nutrient acquisition after fire

events (Claridge et al., 2009). Mycelium extension through soils that have been transformed by heat can aggregate soil particles in an otherwise highly erodible landscape, minimizing soil movement in the absence of plant roots (Claridge et al., 2009). As they grow, mycelium both entangle soil particles and exude organic molecules and polymers that act as cements to adhere soil particles together (Claridge et al., 2009, Lehmann et al., 2020, Fischer et al., 2021, Steindorff et al., 2022). Pyrophilous fungi (e.g. those that grow rapidly after fire) secrete hydrophobin proteins as mycelium grows through the soil and can alter the hydrophilic-hydrophobic character of the soil surface, increasing surfactant capacity and water holding capacity (Bayry et al., 2012, Lehmann et al., 2020, Steindorff et al., 2022).

Fungal pathogens, both native and non-native, are also prominent in southwestern forests and can change species composition and alter forest structure. White pines including sugar pine (*Pinus lambertiana*) in California, southwestern white pine (*Pinus strobiformis*) in Arizona and New Mexico, and limber pine (*Pinus flexilis*) in the southern Rocky Mountains have increasing mortality rates due to white pine blister rust, which is caused by a non-native pathogenic fungus, *Cronartium ribicola* (Schoettle et al., 2014, Goodrich et al., 2018a, Dudney et al., 2020). Live oak (*Quercus agriflora*) has an abundant amount of associated pathogenic fungi that are thought to be non-native species of Botryosphaeriaceae, including *Diplodia corticola*, *Dothiorella iberica* and *Diplodia agrifolia* sp. nov. (Lynch et al., 2013).

Unlike our understanding of tree susceptibility to beetles with increasing drought stress, there is greater uncertainty in how fungal communities will respond to ongoing climate change and how that will impact southwestern forests. Ectomycorrhizal fungal communities associated with piñon (*Pinus edulis*) are essential for host drought tolerance (Gehring et al., 2017). There has been observed decline in the communities of beneficial root-associated fungi hosted by piñon with increasing drought and heat (Gehring et al., 2020). Climate stress has been linked to reduced fungal biomass, abundance, species richness, and community activity in piñon-juniper (*P. edulis*, *Juniperus* spp.) woodlands overall, affecting both piñon and juniper species, potentially leading to an increase in relative abundance of arbuscular mycorrhizal fungi associated with juniper, which may lead to long-term vegetation shifts and decreased piñon seedling survival (Haskins and Gehring, 2004, 2005, Hubert and Gehring, 2008, Warnock et al., 2016). Additionally, piñon can be more susceptible to a pathogenic fungus, *Ophiostoma* spp., introduced by parasitic bark beetles (*Ips confusus*) in drought conditions (Plaut et al., 2012). Our limited understanding of the role of fungi in these ecosystems and the potential for changing climate and disturbance to alter the presence and abundance of both beneficial and pathogenic fungi requires additional investigation to better understand the mechanistic drivers of fungal community composition and change.

4. Wildlife in disturbance structured forests

Wildlife responds to and alters ecosystem structure and processes (Foster et al., 2020) and individual species often serve as response variables for evaluating management actions (Tempel et al., 2014). The same structural changes that are increasing disturbance risk are presenting challenges for wildlife in the southwestern U.S. The region contains some of the most diverse geophysical landscapes in North America and, as such, supports hyper-diverse floral and faunal communities (Coblentz and Riitters, 2004, Albano, 2015). At a regional scale, the natural relegation of forest lands to higher elevation locations create steep vegetation gradients that support high biological diversity (Fleischner et al., 2024). At more local levels within forest landscapes, historical fire regimes have given rise to biological communities that are adapted to and maintained by frequent disturbances and the resulting disturbance structured forests (Hurteau and North, 2008, Goodwin et al., 2018, Odland et al., 2021, Jones et al., 2023). Many wildlife inhabiting southwestern forests are endemic, while others occur across

larger geographic ranges but thrive in southwestern forests (Kier et al., 2009). Some wildlife species are iconic, rare, threatened by human activities, or otherwise of conservation concern, representing deeply held values and are of cultural importance. Other wildlife species are hunted for game or sustenance, while others engineer and regulate the flow of energy and resources through ecosystems themselves. Thus, wildlife help shape forest ecosystems and provide an important connection between humans and forests.

Threatened, endangered, or declining species can engage public sentiment and stir deeply held values, often acting as fulcrums in southwestern forest management decision making (Sagoff, 1996, Plie-ninger et al., 2015, Gutiérrez et al., 2017). The most emblematic of all southwestern wildlife may be the spotted owl (*Strix occidentalis*, including subspecies *occidentalis*, *lucida*, *caurina*), which primarily inhabits ponderosa pine forests with an oak or other hardwood component at lower elevations, and mixed-conifer forests at middle elevations. With few exceptions, spotted owls rely on the presence of late-seral forest conditions wherever they occur, including large, old trees, downed and decaying woody debris, and a complex forest understory (Hunter et al., 1995, Franklin et al., 2000). Recent increases in large, high-severity fires and droughts have driven local population declines and more widespread losses of suitable conditions for nesting and roosting (Jones et al., 2016, 2021). Predictions of future changes to southwestern forests suggest even more widespread losses of spotted owl habitat (Wan et al., 2019). Given a history of large tree logging within spotted owl habitat that led to initial population declines, there is widespread concern that thinning treatments to reduce fuels in spotted owl habitat could exacerbate long-term declines (Ganey et al., 2017). However, recent studies suggest that forest thinning could introduce appropriate ecological heterogeneity that was lost as a result of fire-exclusion, mimicking a type of forest heterogeneity that supports spotted owl prey communities and ultimately individual fitness in owls (Zulla et al., 2023, Kuntze et al., 2023). Thus, there is a growing acknowledgement that ecosystem restoration and spotted owl conservation may be compatible (Jones et al., 2022).

Across the region many species of forest-dependent wildlife provide cultural and provisioning ecosystem services through sport and persistence hunting (Knoche and Lupi, 2007). For millennia, Indigenous peoples in the southwestern US have hunted and continue to hunt forest-dependent wildlife for persistence and cultural reasons (Schollmeyer and Driver, 2013). In broader western American culture, hunting forest-dependent game animals for sport and persistence generates revenue for state wildlife agencies, a significant portion of which is used to facilitate conservation measures for both game and non-game species (Heffelfinger et al., 2013). For example, in New Mexico, over 31,000 hunting licenses for Mule deer (*Odocoileus hemionus*) were purchased each year from 2016 to 2021, generating over 1.1 million USD annually (New Mexico Department of Game and Fish, <https://www.wildlife.state.nm.us>). The distribution and abundance of economically and culturally important species is being influenced by changing disturbance regimes and altered forest structure. For example, both black bears (*Ursus americanus*) and mule deer (*Odocoileus hemionus*) are more abundant in areas that experience heterogeneous fire effects, including small high-severity burn patches (Lewis et al., 2022). These early-seral patches likely provide important pulses of foraging resources while, at least for mule deer, providing nearby cover from predators. Mule deer have been shown to use areas that are burned or thinned via forest restoration but tend to avoid these areas for the first several years following treatment implementation until some forage and vegetation cover has regenerated (Roerick et al., 2019). Thus, as with the spotted owl, there appears to be some compatibility between game species conservation and forest restoration activities, and likely negative effects of expansive land cover transformation from forest to homogenous non-forest vegetation resulting from changing fire regimes.

Some animals in the Southwest alter the functioning of forest ecosystems by providing regulating ecosystem services, such as pollination

and hydrological manipulation. Perhaps one of the more well-understood regulating services that animals provide is the pollination of flowers by bees. Bees are important in driving the exchange of genetic materials in more natural settings, including southwestern forest ecosystems, where most forest plants depend on pollination by bees (Hanula et al., 2016). Fire suppression has generally had negative impacts on pollinators, and conversely, prescribed fire and tree thinning is generally beneficial (Hanula et al., 2016). Moreover, frequent fire regimes that generate high levels of structural heterogeneity in forests produce stronger plant-pollinator interaction networks (Ponisio et al., 2016, Ponisio, 2020, Ulyshen et al., 2022), suggesting benefits for pollinators from the restoration of natural fire regimes. In riparian systems, American beavers (*Castor canadensis*) can transform local forest structure and moisture content, altering hydrological flows and creating highly resistant fire refugia (Fairfax and Whittle, 2020). Within the footprint of large, severe megafires, fire refugia can provide critically important genetic material for tree recolonization (Collins et al., 2017, Tsinnajinnie et al., 2021).

While not exhaustive, these examples demonstrate how ecologically and culturally important southwestern forest wildlife species are affected by land-use, management, and disturbance, as well as the ecosystem services they provide to society. Seed dispersal by birds and mammals (Willson, 1993), soil engineering by invertebrates and small mammals (Lavelle et al., 2006, Davies et al., 2019), and carbon cycling (Schmitz et al., 2018) are several other examples of the ecological roles that wildlife play in generating ecosystem services. As with most systems, increasing heterogeneity provides for increased diversity. In the southwestern US, considerable evidence exists showing that heterogeneity produced by fire (or ‘pyrodiversity’) is associated with more species-rich animal communities (Jones and Tingley, 2022). Thus, restoration of naturally ‘pyrodiverse’ fire regimes in the southwestern US could boost local biodiversity and ecosystem functioning, while simultaneously benefiting species like spotted owls, mule deer, and black bears, as well as pollinator communities.

5. Changing climate and disturbance drive vegetation type change

The direct effects of climate on tree survival, along with increased susceptibility to insects and pathogens, can lead to widespread mortality and transform currently forested landscapes. In the rapidly aridifying Southwest, recurring drought that depletes carbon reserves as trees close their stomata to reduce water loss is increasingly likely (Wahl et al., 2022, Peltier et al., 2023). This effect is exacerbated by ‘hot’ droughts, where atmospheric warming increases the vapor pressure deficit, increasing tree drought stress (Allen et al., 2015, Hammond et al., 2022). Following severe drought events, conifers in the Southwest can experience significant delays in mortality, suggesting insect population dynamics or long-term carbon starvation may be the primary driver (Kane et al., 2014). Drought can also cause tree mortality through hydraulic failure, which occurs when atmospheric water demand exceeds water uptake by roots and high xylem water tension causes cavitation (Hammond et al., 2019). For example, quaking aspens (*Populus tremuloides*), one of the most common broadleaf species at higher elevations in the Southwest and throughout the western US, are impacted by drought primarily through hydraulic failure and are therefore susceptible to single high-intensity drought events (Kane et al., 2014, Anderegg et al., 2015, Anderegg and HilleRisLambers, 2016). The primary driver of a recent mortality event of Utah junipers (*Juniperus osteosperma*) was hydraulic damage, similar in mechanism to that of quaking aspen, but requiring much more severe drought conditions (Kannenberg et al., 2021). Both drought and insect impacts on southwestern forests are compounded by the removal of frequent low-intensity fire in historically frequent fire forests (Stephens et al., 2018). Increased competition because of high tree density (Clark et al., 2016), as well as reduced tree function can increase susceptibility to insects (Kolb et al., 2016, Young

et al., 2017). Trees growing at lower density are less water stressed than those growing at high density, making density reduction a possible strategy for reducing drought-induced mortality (Hurteau et al., 2007, Steel et al., 2021, McCauley et al., 2022, Bernal et al., 2023). Yet, untangling the primary cause for geographically or temporally isolated die-off events in southwestern forests is often challenging, due to multiple, potentially related, disturbances acting concurrently (Stevens et al., 2021).

Changes in both the ranges and regenerative ability of forests throughout the Southwest are inevitable, yet predictions still vary on the direction or exact drivers of these changes. Range shifts of tree species may not follow broad climate projections, but rather depend more on local environmental heterogeneity and forest structural variability (Serra-Diaz et al., 2014, McCullough et al., 2016). Additionally, evidence suggests that some conifer species, such as *Pinus albicaulis* Engelm., increase recruitment in response to disturbance, especially at range edges (Slaton et al., 2019). Sensitivity to broader climate may not be consistent across ecosystem types, meaning a regional approach to restoration or ecosystem resilience may benefit some species while harming others. To adequately increase forest resilience, local strategies must be developed which consider the local environmental conditions, including disturbance history.

The challenges facing tree regeneration that are increasingly common across the western US are exacerbated by forest cover loss from high-severity wildfire in the southwestern US (Ouzts et al., 2015, Stevens-Rumann et al., 2018, Rodman et al., 2020, Marsh et al., 2022). In historically frequent fire forests, fire-exclusion has increased forest density and surface fuels and increased atmospheric aridity is drying forests, making them more flammable (Steel et al., 2015, Singleton et al., 2019, Juang et al., 2022, Taylor et al., 2022, Williams et al., 2023, McClure et al., 2024). The increased flammability of these mid-elevation forests can also project fire into upper elevation forests causing substantial changes in these historically infrequent fire forests (O'Connor et al., 2014, Remy et al., 2021, 2024). In Arizona and New Mexico, long-term trends indicate that total area burned increased by 0.1 % yr⁻¹ and the proportion burned at high severity increased by 0.33 % yr⁻¹ between 1984 and 2015, with distinct increases in both these metrics after the year 2000 (Singleton et al., 2019). Similarly, in the Sierra Nevada–Southern Cascades region of California and Nevada, the total area burned and area burned at high-severity has also increased, with the percentage of area burned at high-severity (28 %) exceeding the pre-settlement average (7 % before ca. 1850) (Williams et al., 2023). Most striking is the influence that the top 1 % of fires by size have had on landscape homogenization. The largest fires in California were responsible for 58 % of the cumulative area burned at high-severity over the 1984–2020 period (Cova et al., 2023). While fire is a self-limiting process and high-severity can limit fuel for subsequent fires, the effect is short-lived and large fires will be increasingly likely in both the Southwest and western United States (Collins et al., 2009, Hurteau et al., 2019a, Abatzoglou et al., 2021).

As fire size increases in homogenous forests, so does high-severity patch size and the resulting post-fire vegetation homogeneity (Buonanaduci et al., 2023). Large-scale, high-severity patches act as catalysts for ecological change because of their effect on increasing the distance to live trees, which provide seed for regeneration, and the direct impacts on the abiotic properties of the ecosystem. Dispersal distance of many southwestern conifers is typically short (10 s to 100 s of meters) because of the large seed size, although factors such as topographic position and prevailing wind direction can increase dispersal distance when favorable (Korb et al., 2019, Vander Wall, 2023, Willson and Hurteau, 2024). Yet, even when seeds are capable of reaching the burn area, forest canopy loss reduces retention of winter snow cover, decreases soil moisture, and increases near-ground temperatures, all of which change the thermal landscape of previously forested areas (Winstral and Marks, 2002, Stielstra et al., 2015, Wolf et al., 2021). For tree seedlings, whose climate niche space is fundamentally narrower

than mature individuals of the same species, these conditions are often challenging for their successful establishment and are leading to substantial declines in natural regeneration because of high rates of seedling mortality in locations where adults of the species occur (Bell et al., 2014, Davis et al., 2016, Stevens-Rumann et al., 2018, Rodman et al., 2020, Pirtel et al., 2021, Marsh et al., 2023). While artificial regeneration can overcome the dispersal limitations of many southwestern conifer species, shifts in locations where species are capable of establishing may not be consistent with predicted northward or upslope migration to track climate, as was observed for *Pinus longaeva*, *P. flexilis*, and *Quercus kelloggii* (Serra-Diaz et al., 2016, Smithers et al., 2021).

Limitations on tree seedling establishment contribute to vegetation-type changes from forest to non-forest conditions as other plant species establish in place of the previously dominant tree species (Coop et al., 2020, Stevens et al., 2021). Resprouting shrubs can act both as a facilitator of post-fire conifer establishment and growth and as an impediment to establishment as they can quickly capture a site, excluding the establishment of conifer species (Guiterman et al., 2018, Marsh et al., 2023, Goodwin and Hurteau, 2024). The increased probability of high-severity fire following high-severity fire in these shrub dominated landscapes can inhibit future conifer forest regeneration and reinforce ecological state change (Collins and Roller, 2013, Coppoletta et al., 2016, Keyser et al., 2020). However, certain conifer species, such as *P. leiophylla* may persist because their ability to resprout after being top-killed allows them to outcompete resprouting oaks (Barton et al., 2023). This trait may make this species suitable for reforestation in areas that are likely to re-burn. Ecological state changes such as these are often reinforced by subsequent drought, potentially catalyzing range contractions of tree species by limiting reproduction (Parks et al., 2019, Rodman et al., 2022, Crockett and Hurteau, 2024). In Arizona and New Mexico, the resulting predicted reduction in forest area by 2050 is as much as 40 % for the Colorado Plateau due to these impacts (Parks et al., 2019).

6. Forests, water, and a changing climate

Forests are an important source of surface water for society. Warming temperatures are having, and will continue to have, a profound impact on snowmelt-dominated watersheds (Mote et al., 2018). The Southwest has been in drought since the 1990s with temperatures increasing by about two degrees Celsius over the historical average (Bennett et al., 2020). While climate naturally fluctuates between wet and dry, Barnett et al. (2008) statistically demonstrated that the majority of changes in hydrology over the western US are from anthropogenically induced climate change. An additional snowpack decline of 40–75 % is projected across the western US by 2100 due to additional warming (Koshkin et al., 2022). While declining snowpack is problematic for both forests and society in the Southwest, the rate and form (rain vs. snow) of precipitation events is as, if not more, important than total quantity (Bennett et al., 2020).

The influence of decreasing snowpack stretches far beyond winter, increasing fire risk and forest mortality (Gottlieb and Mankin, 2022, Hatchett et al., 2023, McGrath et al., 2023). From 1984–2017 there was a 9 % increase per year in area burned in the seasonal snow zone (Hatchett et al., 2023). Burned area in the headwater regions of the Rio Grande and Colorado river basins are projected to increase an additional 300–700 % with one degree Celsius of warming, which has important implications for snowpack development and persistence (Moeser et al., 2020). The timing of snow accumulation and melt depends on the energy balance of the snowpack which is strongly influenced by forest canopy and wildfire (Giovando and Niemann, 2022). Wildfire's effect on forest canopy contributes to several competing processes that influence snow accumulation. Reduced canopy can simultaneously increase snow accumulation by reducing interception and longwave radiation, while also decreasing peak snow water equivalent due to an increase in shortwave radiation (Moeser et al., 2020). When black carbon produced

by wildfire is deposited on snow, it can decrease albedo and substantially increase snowmelt rates (Koshkin et al., 2022). While the impacts of burn scars on snow vary regionally, lower latitude areas experience greater impacts due to higher levels of shortwave radiation (Maxwell et al., 2019, Giovando and Niemann, 2022, Kampf et al., 2022). Following high-severity wildfire, albedo changes dominate in the short term, but canopy loss eventually drives post-fire snowpack energy balance and melt rates (Hatchett et al., 2022). The effects of burns on snow phenology can persist for decades (Giovando and Niemann, 2022, Kampf et al., 2022).

Wildfires can have positive and negative effects on water supply. At the larger watershed (i.e. HUC 12) and western United States scales, fires can significantly increase streamflow, as high as 20 % (Wine and Cadol, 2016, Wine et al., 2018, Williams et al., 2022). However, large high-severity fires can be detrimental to an already decreasing snowpack. Following a high-severity fire in northern New Mexico, single snowfall events resulted in 25–45 % more snow in the burned area, yet peak snowpack depths were significantly larger in unburned areas (Harbold et al., 2014); a result that is similar to other studies in the Southwest (Kampf et al., 2022, McGrath et al., 2023, Kan et al., 2023). Shorter snow seasons lead to reduced vegetation recovery after a fire, delaying or limiting the establishment of trees which can shade the snowpack (Kampf et al., 2022). While these are extreme numbers, changes in peak snow water equivalent is highly variable and site specific, depending largely on aspect and gap size and structure (Maxwell et al., 2019, Moeser et al., 2020, Koshkin et al., 2022).

7. Forest carbon and a changing climate

Forests help regulate the climate by sequestering carbon from the atmosphere. In the southwestern US, many locations currently store more aboveground carbon than would have been present with historical fire regimes, with a few exceptions where modern carbon density is lower as a result of disturbance, including logging (North et al., 2009, North and Hurteau, 2011, Hurteau et al., 2011, Wiechmann et al., 2015, Harris et al., 2019). In many areas increased tree density and surface fuel build-up in forests that historically burned at high frequency have exceeded the total stock of carbon that these systems are capable of supporting under prevailing climate and natural disturbance conditions, especially given increased temperature, drought, and disturbance (Hurteau et al., 2019b, Anderegg et al., 2020). Widespread tree mortality can shift a substantial fraction of aboveground carbon from the live tree to the dead tree pool, increasing its susceptibility to combustion (Goodwin et al., 2020, 2021, Hurteau et al., 2024). Thus, changing climate and increasing disturbance are decreasing the carbon carrying capacity of many southwestern forests.

Fire severity influences the distribution of carbon between different pools and total emissions from combustion (Yocom Kent et al., 2015, Maestrini et al., 2017, Xu et al., 2022). High-severity fire, by killing the overstory, causes the forest to transition from carbon sink to carbon source because of the loss in carbon uptake and decomposition of the dead trees (Dore et al., 2012, Liang et al., 2017b, Krofcheck et al., 2019). Overstory canopy loss and the change in energy balance reduce natural regeneration and, increasingly, decrease survival rates of planted seedlings which are used to overcome dispersal limitations (Stevens-Rumann et al., 2018, Marsh et al., 2022, Davis et al., 2023). The change from forest to non-forest vegetation causes lower carbon sequestration rates and lower overall aboveground carbon storage (Dore et al., 2012, Keyser et al., 2020, Jung et al., 2023). Insect and drought-induced mortality can have a similar effect on carbon dynamics, increasing its availability to burn (Goodwin et al., 2020).

Restoring frequent low to moderate severity fire to dry conifer forests across the Southwest can restore heterogeneous forest structure and yield stable carbon dynamics, but with a near-term cost from reducing the carbon stock that resulted from fire-exclusion (Wiechmann et al., 2015, Hurteau, 2017, Krofcheck et al., 2019, Stephens et al., 2020).

Keeping forest cover intact by reducing the probability of high-severity wildfire can lead to higher landscape carbon storage over time, but the net carbon benefit of restoring frequent fire to these systems can take several decades to realize (Hurteau, 2017, Krofcheck et al., 2018, 2019, Liang et al., 2018, McDowell et al., 2021). The tree injury associated with surface fire typically has a limited effect on growth and the tree density reductions from restoring frequent fire can help reduce drought impacts on growth, which can lead to higher rates of carbon uptake (Dore et al., 2012, Steel et al., 2021, Fulé et al. 2022, Bernal et al., 2023, Hecht et al., 2024, Willson et al., 2024). Thus, managing for carbon stability in the fire-prone forests of the southwestern US requires evaluating carbon trade-offs over the temporal and spatial scales at which fire is interacting with forests.

As society seeks to leverage nature-based climate solutions to help mitigate fossil carbon emissions to the atmosphere, it is important to understand region specific risks to using this strategy in the Southwest. Given that the current regional stock of aboveground carbon is likely greater than can be sustained given prevailing climate and natural disturbance conditions, let alone projected conditions, (Flatley and Fulé 2016, Liang et al., 2017a, 2017b) managing the carbon that is additional to what a location can support is necessary for improving forest carbon stability (Hurteau et al., 2024). The economics of forest carbon storage are relatively poor because of the low market value for a ton of additional carbon stored in a forest. As a result, forest carbon offset projects have commonly been preferentially developed in locations where current carbon density is above that representative for the area, translating into a substantial upfront tranche of carbon offsets that can be sold to support the development of the project (Badgley et al., 2022b). Yet, conditions in these locations mean that the potential the stored carbon is actually additional to what would happen naturally and that the carbon will remain sequestered for 100 or more years is questionable (Badgley et al., 2022a, 2022b). From the perspective of Earth's energy balance, the surplus carbon stored in southwestern forests is unlikely to be significant, especially when compared to human-caused fossil carbon emissions. However, viewing southwestern forest carbon from an avoided emissions perspective as opposed to attempting to increase carbon density is the more sustainable approach to managing carbon in the region.

8. Managing for forest resilience to changing climate and disturbance

Forests in the southwestern US are functioning as a canary-in-the-coal-mine for western US and Canadian forests. Large extreme fires and widespread tree mortality began in Arizona and New Mexico in the early 2000s (Breshears et al., 2005, Ffolliott et al., 2011). By 2012, widespread mortality was affecting the southern Sierra Nevada, followed by large, severe fires that began occurring throughout mountainous regions of California in 2013 (Harris and Taylor, 2015). As these extreme events continue to occur at higher latitudes, southwestern forests can provide insight into expected trajectories and as a place to experiment with management strategies.

Resilience – the ability of an ecosystem to recover from disturbances and persist over time – is often a stated management objective and is central to the continued provision of ecosystem services (Churchill et al., 2013, Roccaforte et al., 2018, Hessburg et al., 2019). Changing climate and climate-driven increases in disturbance may exceed southwestern forests' resilience; especially given the conditions that have resulted from fire-exclusion. Heterogeneity is a key attribute in the resiliency of an ecosystem (Koontz et al., 2020). Forested ecosystems with variable structure (i.e. individuals, clumps, and openings) are resistant to widespread impacts from certain disturbance agents (e.g. canopy openings serve as a barrier for dwarf mistletoe spread) and are prepared for others such as creating a mosaic of burn severity (Churchill et al., 2013, Francis et al., 2023).

Past land-use and fire suppression have homogenized forests across

the Southwest, increasing their susceptibility to drought, insects, and high-severity wildfire. As disturbance events such as wildfire and drought mortality affect larger areas, we will see increased landscape homogeneity and reduced resilience. Of course, the rate of climate change will drive landscape changes regardless of the amount of forest structural heterogeneity. For example, within the piñon-juniper ecosystem type, *Pinus monophylla*, which grows in more arid regions, is less susceptible to hotter droughts than *Pinus edulis*. The juniper species (*Juniperus monosperma*, *J. osteosperma*, & *J. scopulorum*) which occupy this ecosystem type are even less susceptible to drought stress than *P. monophylla* (Redmond et al., 2018). This species-specific variability in drought tolerance suggests that piñon-juniper woodlands may become juniper dominated as piñon succumb to extreme drought. In some locations, this transition has already occurred when the combined effects of drought and insect outbreak substantially reduced *Pinus edulis* density in parts of Arizona and New Mexico, while *Juniperus* species continue to persist (Breshears et al., 2009, Allen et al., 2015). However, hotter droughts are only one challenge facing piñon-juniper ecosystems, which historically had less frequent fire than ponderosa pine forests. Invasive plant species (e.g. *Bromus tectorum*, *Salsola tragus*, *Acroptilon repens*) are increasing fine fuel density in some locations and increasing fire frequency can reinforce their density and dominance, excluding the establishment of piñon and juniper species (Redmond et al., 2023). Invasive plants establishing following fire and altering fine fuel loads is increasingly common, especially in ecosystems where longer return interval fire was more common historically. Increasing fire frequency in these systems can reinforce dominance by invasive species (Keeley et al., 2011). These additional challenges will need to be addressed as we manage for increased heterogeneity.

Managing changing landscapes where ongoing climate change is interacting with a legacy of past land-use and management requires acknowledging that landscapes are dynamic and restoration to some historical condition may not be desirable or possible. For example, in Sierran mixed-conifer forest, fire-exclusion caused an increase in tree density and surface fuels and a shift in the distribution of basal area by species to more shade-tolerant species (e.g. *Abies concolor*, *Calocedrus decurrens*) (North et al., 2005). Efforts to restore a more heterogeneous overstory structure and reintroduce surface fire have had little effect on increasing regeneration of the fire-tolerant *Pinus* species (*P. lambertiana*, *P. jeffreyi*) that were more dominant prior to fire-exclusion (Zald et al., 2008, 2024, May et al., 2023). Increasing pine density may require planting following fire restoration treatments (May et al., 2023). Alternatively, changing climate may alter species abundance or limit the spatial distribution of species as increasing temperature and drought improve the competitive advantage or exceed the physiological limitations of different species (Hurteau and North, 2008, Crockett and Hurteau, 2024). Acknowledging what is possible and aligning management objectives with the current and projected climate and disturbance reality in a particular location requires a more holistic approach to objective setting than is common.

The resist-accept-direct (RAD) framework considers resistance strategies, future outcomes, and possible consequences to identify locations where maintaining or restoring an ecosystem (resistance), accepting ongoing changes (accept), or steering the ecological trajectory towards a desired new state (direct) are the appropriate response (Crausbay et al., 2022, Schuurman et al., 2022). Managing for resilience is not a one-and-done management strategy and typically requires nuanced management strategies and repeat treatments to maintain an ecosystem or achieve restoration objectives. It will also require increased flexibility in management planning. Management approaches that allow for a dynamic response to changing climate will be necessary to accommodate ecological and societal needs in these novel conditions (Steel et al., 2023). It will also require consideration of socio-ecological trajectories, engaging with stakeholders to develop management pathways, and using a portfolio approach that increases flexibility in management options to deal with uncertainty (Magness et al., 2022).

Across the Southwest, a range of proactive management actions are necessary to restore forest heterogeneity and decrease the extent of severe wildfires (Prichard et al., 2021). While resistance-based management approaches that reduce tree density and increase heterogeneity have been shown to reduce drought stress and susceptibility to disturbance, alignment with historical fire regimes is not always necessary (Kerhoulas et al., 2013, Goodrich et al., 2018b, Stoddard et al., 2021, Zald et al., 2022). As the climate shifts, optimal fire regimes may diverge from historical norms, necessitating an adaptive management approach. For example, fire regimes tend to be fuel limited in southwestern forests and area burned correlates with antecedent precipitation (Swetnam and Betancourt, 1990, Littell et al., 2009). If years with above-average precipitation become less frequent, the fire frequency that is necessary to maintain heterogeneity and ecosystem function could decrease. However, the same climatic conditions that will decrease the fire frequency necessary to manage fine fuels in fire-restored locations will present a challenge in locations requiring a first fire entry. Increasing interannual variability and the increasing flammability of southwestern landscapes with ongoing climate change require preparing the landscape for ecologically appropriate fire with proactive fire use (North et al., 2021).

In many locations across the region, resisting change is not a long-term solution, and accepting change may not always be desirable. Part of the RAD framework involves directing the changing ecosystem when resistance is infeasible, with the objective of maintaining ecosystem function and meeting demand for ecosystem services. This may require further reducing tree density, facilitating the transition to a non-forest condition, or introducing the more drought tolerant tree species that are likely to colonize the site in the future. These approaches are probably the best option for the lower elevation range of a particular species or forest type. These so-called trailing edge portions of species ranges are where we expect to see increased mortality and limited regeneration (Parks et al., 2019, Crockett and Hurteau, 2024). Preparing to direct change using active management requires testing management approaches now that may be useful in the future. For example, prolonged drought from 2012 to 2015 in the Sierra Nevada increased tree susceptibility to insects and widespread tree mortality occurred following insect outbreak, which transitioned a substantial portion of live tree biomass to the dead biomass pool, making it a source of fuel (Swain, 2015, Fettig et al., 2019, Goodwin et al., 2020, Robbins et al., 2022). These types of mortality events increase the risk of mortality for the remaining live trees because of the substantial increase in fuel, which will require that we consider shorter-term options for dealing with the accumulation of dead biomass that is resulting from ongoing mortality events (Goodwin et al., 2021, Hurteau et al., 2024).

Forests that experience uncharacteristic disturbance will be another opportunity to direct change. In severely burned locations or areas of widespread insect-induced mortality, accurate assessment of post-disturbance cover combined with anticipation of future fire and climate are important for guiding postfire management strategies (Stevens et al., 2021). At the core of any informed management response is an understanding of how ecosystems are changing. Long-term datasets and monitoring designed to detect system shifts and increases in variability are central to predicting the rate and direction of change. However, monitoring is costly, and land management agencies typically do not devote the resources necessary to implement a monitoring plan that will facilitate pre-emptive or quick-response reactive changes to management (Lynch et al., 2021). Additionally, in some instances (e.g. US Forest Service National Forest Management Plans) the planning horizon for management plans may be too long to allow for truly adaptive management given the unprecedented rate of change that is currently underway. Understanding change is critical because these post-disturbance landscapes may also be locations where we choose to accept change because the cost of directing change or the uncertainty about the proper direction is too high to warrant intervention. We must prioritize monitoring to have sufficient information to make informed decisions and we must build flexibility into management plans to allow

for truly adaptive management to occur.

9. Conclusion

Climate-driven changes are occurring rapidly in southwestern forests and the primary tool that we have available to increase resilience is the restoration of heterogeneity. In some cases, this will require land management activities immediately following natural disturbances such as intentionally burning from recently burned areas or planting species up in elevation following disturbance. This type of proactive management requires social license and policy flexibility. Earning and maintaining social license will require transparent decision-making and engagement with stakeholders while objective setting, two things that land management agencies are doing increasingly well. However, agency policies and inertia are currently and likely to remain an impediment to flexible management decision-making. Managing for resilient southwestern forests will require agency policies and management plans that support managing for change. Choosing locations to resist, accept, or direct change is a proactive approach to managing landscapes to maintain functional forest ecosystems that meet societal need. Similarly, inaction or implementing a management strategy at a pace that is insufficient given the rate of change are also choices, but these choices are limiting.

To manage the change that is occurring in a manner that supports resilient forest ecosystems, we recommend an active monitoring program where response variables are selected based on ecosystem management objectives and the sensitivity of the response variable to changing climate. Part of this process will require land managers to engage with stakeholders to identify management objectives. However, management objectives must be evaluated for feasibility given local conditions. This will require active engagement with the scientific community, with scientists helping to determine what is feasible given current and projected climate and which response variables to monitor for identifying change. Given the stakeholder engagement and practitioner-researcher collaboration required to manage for resilient systems, it is critical that we do not become paralyzed by uncertainty in our understanding of what will occur in the future. We know that restoring heterogeneity reduces susceptibility to disturbance-induced loss and can serve as a management starting point while additional specific plans are developed.

CRedit authorship contribution statement

Lorraina S. Rojas: Writing – original draft. **Lindsey Rotche:** Writing – original draft. **Josh Lopez-Binder:** Writing – original draft. **M. Dylan Taylor:** Writing – original draft. **Gavin Jones:** Writing – original draft. **Christopher Marsh:** Writing – review & editing, Writing – original draft, Visualization. **Matthew D. Hurteau:** Writing – review & editing, Writing – original draft, Conceptualization. **Andy Graves:** Writing – original draft. **Marissa J. Goodwin:** Writing – original draft. **Reese Baker:** Writing – original draft. **Kyle Gonterman:** Writing – original draft. **Abigail Granath:** Writing – original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data Availability

No data was used for the research described in the article.

References

- Abatzoglou, J.T., Battisti, D.S., Williams, A.P., Hansen, W.D., Harvey, B.J., Kolden, C.A., 2021. Projected increases in western US forest fire despite growing fuel constraints. *Commun. Earth Environ.* 2, 1–8.
- Albano, C.M., 2015. Identification of geophysically diverse locations that may facilitate species' persistence and adaptation to climate change in the southwestern United States. *Landsc. Ecol.* 30, 1023–1037.
- 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.
- Anderegg, L.D.L., HilleRisLambers, J., 2016. Drought stress limits the geographic ranges of two tree species via different physiological mechanisms. *Glob. Change Biol.* 22, 1029–1045.
- Anderegg, W.R.L., Hicke, J.A., Fisher, R.A., Allen, C.D., Aukema, J., Bentz, B., Hood, S., Lichstein, J.W., Macalady, A.K., McDowell, N., Pan, Y., Raffa, K., Sala, A., Shaw, J. D., Stephenson, N.L., Tague, C., Zeppel, M., 2015. Tree mortality from drought, insects, and their interactions in a changing climate. *N. Phytol.* 208, 674–683.
- Anderegg, W.R.L., Trugman, A.T., Badgley, G., Anderson, C.M., Bartuska, A., Ciais, P., Cullenward, D., Field, C.B., Freeman, J., Goetz, S.J., Hicke, J.A., Huntzinger, D., Jackson, R.B., Nickerson, J., Pacala, S., Randerson, J.T., 2020. Climate-driven risks to the climate mitigation potential of forests. *Science* 368, eaaz7005.
- Audley, J.P., Fettig, C.J., Steven Munson, A., Runyon, J.B., Mortenson, L.A., Steed, B.E., Gibson, K.E., Jørgensen, C.L., McKelvey, S.R., McMillin, J.D., Negrón, J.F., 2021. Dynamics of beetle-killed snags following mountain pine beetle outbreaks in lodgepole pine forests. *For. Ecol. Manag.* 482, 118870.
- Badgley, G., Chay, F., Chegwidan, O.S., Hamman, J.J., Freeman, J., Cullenward, D., 2022a. California's forest carbon offsets buffer pool is severely undercapitalized. *Front. For. Glob. Change* 5.
- Badgley, G., Freeman, J., Hamman, J.J., Haya, B., Trugman, A.T., Anderegg, W.R.L., Cullenward, D., 2022b. Systematic over-crediting in California's forest carbon offsets program. *Glob. Change Biol.* 28, 1433–1445.
- Baker, W.L., Shinneman, D.J., 2004. Fire and restoration of piñon-juniper woodlands in the western United States: a review. *For. Ecol. Manag.* 189, 1–21.
- Barnett, T.P., Pierce, D.W., Hidalgo, H.G., Bonfils, C., Santer, B.D., Das, T., Bala, G., Wood, A.W., Nozawa, T., Mirin, A.A., Cayan, D.R., Dettinger, M.D., 2008. Human-induced changes in the hydrology of the western United States. *Science* 319, 1080–1083.
- Barton, A.M., Poulos, H.M., Koch, G.W., Kolb, T.E., Thode, A.E., 2023. Detecting patterns of post-fire pine regeneration in a Madiran Sky Island with field surveys and remote sensing. *Sci. Total Environ.* 867, 161517.
- Bauer, J.M., Weisberg, P.J., 2009. Fire history of a central Nevada pinyon-juniper woodland. *Can. J. For. Res.* 39, 1589–1599.
- Bayry, J., Aïmanian, V., Guijarro, J.I., Sunde, M., Latgé, J.-P., 2012. Hydrophobins—unique fungal proteins. *PLOS Pathog.* 8, e1002700.
- Beaty, R.M., Taylor, A.H., 2008. Fire history and the structure and dynamics of a mixed conifer forest landscape in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. *For. Ecol. Manag.* 255, 707–719.
- Bell, D.M., Bradford, J.B., Lauenroth, W.K., 2014. Early indicators of change: divergent climate envelopes between tree life stages imply range shifts in the western United States. *Glob. Ecol. Biogeogr.* 23, 168–180.
- Bennett, K.E., Miller, G., Talsma, C., Jonko, A., Bruggeman, A., Atchley, A., Lavadie-Bulnes, A., Kwicklis, E., Middleton, R., 2020. Future water resource shifts in the high desert Southwest of Northern New Mexico, USA. *J. Hydrol.: Reg. Stud.* 28, 100678.
- Bernal, A.A., Kane, J.M., Knapp, E.E., Zald, H.S.J., 2023. Tree resistance to drought and bark beetle-associated mortality following thinning and prescribed fire treatments. *For. Ecol. Manag.* 530, 120758.
- Biondi, F., Jamieson, L.P., Strachan, S., Sibold, J., 2011. Dendroecological testing of the pyroclimatic hypothesis in the central Great Basin, Nevada, USA. *Ecosphere* 2, art5.
- Boerigter, C.E., Parks, S.A., Long, J.W., Coop, J.D., Armstrong, M., Hankins, D.L., 2024. Untrammeling the wilderness: restoring natural conditions through the return of human-ignited fire. *Fire Ecol.* 20, 76.
- Bradford, John B., Shriver, R.K., Robles, M.D., McCauley, L.A., Woolley, T.J., Andrews, C.A., Crimmins, M., Bell, D.M., 2022. Tree mortality response to drought-dynamics interactions suggests opportunities to enhance drought resistance. *J. Appl. Ecol.* 59, 549–559.
- Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W. H., Kastens, J.H., Floyd, M.L., Belnap, J., Anderson, J.J., Myers, O.B., Meyer, C.W., 2005. Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad. Sci.* 102, 15144–15148.
- Breshears, D.D., Myers, O.B., Meyer, C.W., Barnes, F.J., Zou, C.B., Allen, C.D., McDowell, N.G., Pockman, W.T., 2009. Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Front. Ecol. Environ.* 7, 185–189.
- Broxton, P.D., van Leeuwen, W.J.D., Biederman, J.A., 2020. Forest cover and topography regulate the thin, ephemeral snowpacks of the semiarid Southwest United States. *Ecohydrology* 13, e2202.
- Buonanduci, M.S., Donato, D.C., Halofsky, J.S., Kennedy, M.C., Harvey, B.J., 2023. Consistent spatial scaling of high-severity wildfire can inform expected future patterns of burn severity. *Ecol. Lett.* 26, 1687–1699.
- 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. Manag.* 291, 442–457.
- Claridge, A.W., Trappe, J.M., Hansen, K., 2009. Do fungi have a role as soil stabilizers and remediators after forest fire? *For. Ecol. Manag.* 257, 1063–1069.
- Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C., D'Amato, A. W., Davis, F.W., Hersh, M.H., Ibanez, I., Jackson, S.T., Matthews, S., Pederson, N., Peters, M., Schwartz, M.W., Waring, K.M., Zimmermann, N.E., 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Glob. Change Biol.* 22, 2329–2352.
- Clifford, M.J., M.E. Rocca, R. Delph, P.L. Ford, and N.S. Cobb. 2008. Drought induced tree mortality and ensuing bark beetle outbreaks in southwestern pinyon-juniper woodlands. Pages 39–51 Ecology, management, and restoration of piñon-juniper and ponderosa pine ecosystems: combined proceedings of the 2005 St. George, Utah and 2006 Albuquerque, New Mexico workshops. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Coblentz, D.D., Riitters, K.H., 2004. Topographic controls on the regional-scale biodiversity of the South-western USA. *J. Biogeogr.* 31, 1125–1138.
- Coleman, T.W., Jones, M.I., Courtial, B., Graves, A.D., Woods, M., Roques, A., Seybold, S. J., 2014. Impact of the first recorded outbreak of the Douglas-fir tussock moth, *Orgyia pseudotsugata*, in southern California and the extent of its distribution in the Pacific Southwest region. *For. Ecol. Manag.* 329, 295–305.
- Collins, B.M., Roller, G.B., 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. *Landsc. Ecol.* 28, 1801–1813.
- Collins, B.M., Miller, J.D., Thode, A.E., Kelly, M., van Wagtenonk, 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., Stevens, J.T., Miller, J.D., Stephens, S.L., Brown, P.M., North, M.P., 2017. Alternative characterization of forest fire regimes: incorporating spatial patterns. *Landsc. Ecol.* 32, 1543–1552.
- Coop, J.D., Parks, S.A., Stevens-Rumann, C.S., Crausbay, S.D., Higuera, P.E., Hurteau, M. D., Tepley, A., Whitman, E., Assal, T., Collins, B.M., Davis, K.T., Dobrowski, S., Falk, D.A., Fornwalt, P.J., Fulé, P.Z., Harvey, B.J., Kane, V.R., Littlefield, C.E., Margolis, E.Q., North, M., Parisien, M.-A., Prichard, S., Rodman, K.C., 2020. Wildfire-driven forest conversion in Western North American landscapes. *BioScience* 70, 659–673.
- 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.
- Cova, G., Kane, V.R., Prichard, S., North, M., Cansler, C.A., 2023. The outsized role of California's largest wildfires in changing forest burn patterns and coarsening ecosystem scale. *For. Ecol. Manag.* 528, 120620.
- Covington, W.W., Fule, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.E., Sackett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. *J. For.* 95, 23–29.
- Crausbay, S.D., Sofaer, H.R., Cravens, A.E., Chaffin, B.C., Clifford, K.R., Gross, J.E., Knapp, C.N., Lawrence, D.J., Magness, D.R., Miller-Rushing, A.J., Schuurman, G.W., Stevens-Rumann, C.S., 2022. A science agenda to inform natural resource management decisions in an era of ecological transformation. *BioScience* 72, 71–90.
- Crockett, J.L., Hurteau, M.D., 2024. Ability of seedlings to survive heat and drought portends future demographic challenges for five southwestern US conifers. *Tree Physiol.* 44, tpad136.
- Davies, G.T.O., Kirkpatrick, J.B., Cameron, E.Z., Carver, S., Johnson, C.N., 2019. Ecosystem engineering by digging mammals: effects on soil fertility and condition in Tasmanian temperate woodland. *R. Soc. Open Sci.* 6, 180621.
- Davis, F.W., Sweet, L.C., Serra-Diaz, J.M., Franklin, J., McCullough, I., Flint, A., Flint, L., Dingman, J.R., Regan, H.M., Syphard, A.D., Hannah, L., Redmond, K., Moritz, M.A., 2016. Shrinking windows of opportunity for oak seedling establishment in southern California mountains. *Ecosphere* 7, e01573.
- Davis, K.T., Robles, M.D., Kemp, K.B., Higuera, P.E., Chapman, T., Metlen, K.L., Peeler, J. L., Rodman, K.C., Woolley, T., Addington, R.N., Buma, B.J., Cansler, C.A., Case, M.J., Collins, B.M., Coop, J.D., Dobrowski, S.Z., Gill, N.S., Haffey, C., Harris, L.B., Harvey, B.J., Haugo, R.D., Hurteau, M.D., Kulakowski, D., Littlefield, C.E., McCauley, L.A., Povak, N., Shive, K.L., Smith, E., Stevens, J.T., Stevens-Rumann, C. S., Taylor, A.H., Tepley, A.J., Young, D.J.N., Andrus, R.A., Battaglia, M.A., Berkeley, J. K., Busby, S.U., Carlson, A.R., Chambers, M.E., Dodson, E.K., Donato, D.C., Downing, W.M., Fornwalt, P.J., Halofsky, J.S., Hoffman, A., Holz, A., Iniguez, J.M., Krawchuk, M.A., Kreider, M.R., Larson, A.J., Meigs, G.W., Roccaforte, J.P., Rother, M.T., Safford, H., Schaedel, M., Sibold, J.S., Singleton, M.P., Turner, M.G., Urza, A.K., Clark-Wolf, K.D., Yocom, L., Fontaine, J.B., Campbell, J.L., 2023. Reduced fire severity offers near-term buffer to climate-driven declines in conifer resilience across the western United States. *Proc. Natl. Acad. Sci.* 120, e2208120120.
- Dore, S., Montes-Helu, M., Hart, S.C., Hungate, B.A., Koch, G.W., Moon, J.B., Finkral, A. J., Kolb, T.E., 2012. Recovery of ponderosa pine ecosystem carbon and water fluxes from thinning and stand-replacing fire. *Glob. Change Biol.* 18, 3171–3185.
- Dudney, J.C., Nesmith, J.C.B., Cahill, M.C., Cribbs, J.E., Duriscoe, D.M., Das, A.J., Stephenson, N.L., Battles, J.J., 2020. Compounding effects of white pine blister rust, mountain pine beetle, and fire threaten four white pine species. *Ecosphere* 11, e03263.
- Fairfax, E., Whittle, A., 2020. Smokey the Beaver: beaver-dammed riparian corridors stay green during wildfire throughout the western United States. *Ecol. Appl.* 30, e02225.
- Farris, C.A., Baisan, C.H., Falk, D.A., Yool, S.R., Swetnam, T.W., 2010. Spatial and temporal corroboration of a fire-scar-based fire history in a frequently burned ponderosa pine forest. *Ecol. Appl.* 20, 1598–1614.
- Fettig, C.J., Mortenson, L.A., Bulaon, B.M., Foulk, P.B., 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, U.S. *For. Ecol. Manag.* 432, 164–178.

- Fettig, C.J., Runyon, J.B., Homicz, C.S., James, P.M.A., Ulyshen, M.D., 2022. Fire and insect interactions in North American forests. *Curr. For. Rep.* 8, 301–316.
- Ffolliott, P.F., C.L. Stropki, H. Chen, and D.G. Neary. 2011. The 2002 Rodeo-Chediski Wildfire's impacts on southwestern ponderosa pine ecosystems, hydrology, and fuels. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Fischer, M.S., Stark, F.G., Berry, T.D., Zeba, N., Whitman, T., Traxler, M.F., 2021. Pyrolyzed substrates induce aromatic compound metabolism in the post-fire fungus, *pyrenoma domesticum*. *Front. Microbiol.* 12, 729289.
- Flake, S.W., Weisberg, P.J., 2019. Fine-scale stand structure mediates drought-induced tree mortality in pinyon-juniper woodlands. *Ecol. Appl.* 29, e01831.
- Flatley, W.T., Fulé, P.Z., 2016. Are historical fire regimes compatible with future climate? Implications for forest restoration. *Ecosphere* 7, e01471.
- Fleischner, T.L., Floyd, M.L., Rack, J., Hanna, D., Blevins, K., Christman, B., Holycross, A. T., 2024. The mogollon highlands ecoregion of the American Southwest: a neglected center of ecological diversity. *Nat. Areas J.* 44.
- Foster, C.N., Banks, S.C., Cary, G.J., Johnson, C.N., Lindenmayer, D.B., Valentine, L.E., 2020. Animals as agents in fire regimes. *Trends Ecol. Evol.* 35, 346–356.
- Francis, E.J., Pourmohammadi, P., Steel, Z.L., Collins, B.M., Hurteau, M.D., 2023. Proportion of forest area burned at high-severity increases with increasing forest cover and connectivity in western US watersheds. *Landsc. Ecol.* 38, 2501–2518.
- Franklin, A.B., Anderson, D.R., Gutiérrez, R.J., Burnham, K.P., 2000. Climate, habitat quality, and fitness in northern spotted owl populations in Northwestern California. *Ecol. Monogr.* 70, 539–590.
- Fulé, P.Z., Covington, W.W., Moore, M.M., 1997. Determining reference conditions for ecosystem management of Southwestern Ponderosa pine forests. *Ecol. Appl.* 7, 895–908.
- Fulé, P.Z., Heinlein, T.A., Covington, W.W., Moore, M.M., 2003. Assessing fire regimes on Grand Canyon landscapes with fire-scar and fire-record data. *Int. J. Wildland Fire* 12, 129–145.
- Fulé, P.Z., Sánchez Meador, A.J., Moore, M.M., Covington, W.W., Kolb, T.E., Huffman, D. W., Normandin, D.P., Roccaforte, J.P., 2022. Forest restoration treatments increased growth and did not change survival of ponderosa pines in severe drought, Arizona. *Ecol. Appl.* 32, e2717.
- Ganey, J.L., Wan, H.Y., Cushman, S.A., Vojta, C.D., 2017. Conflicting perspectives on spotted owls, wildfire, and forest restoration. *Fire Ecol.* 13, 146–165.
- Gehring, C., Sevanto, S., Patterson, A., Ulrich, D.E.M., Kuske, C.R., 2020. Ectomycorrhizal and dark septate fungal associations of pinyon pine are differentially affected by experimental drought and warming. *Front. Plant Sci.* 11, 582574.
- Gehring, C.A., Shultz, C.M., Flores-Rentería, L., Whipple, A.V., Whitham, T.G., 2017. Tree genetics defines fungal partner communities that may confer drought tolerance. *Proc. Natl. Acad. Sci.* 114, 11169–11174.
- Giovando, J., Niemann, J.D., 2022. Wildfire impacts on snowpack phenology in a changing climate within the Western U.S. *Water Resour. Res.* 58.
- Goodrich, B.A., Waring, K.M., Auty, D., Sánchez Meador, A.J., 2018b. Interactions of management and white pine blister rust on *Pinus strobus* regeneration abundance in southwestern USA. *For. Int. J. For. Res.* 91, 492–505.
- Goodrich, B.A., Waring, K.M., Auty, D., Sánchez Meador, A.J., 2018a. Interactions of management and white pine blister rust on *Pinus strobus* regeneration abundance in southwestern USA. *For. Int. J. For. Res.* 91, 492–505.
- Goodwin, M.J., Hurteau, M.D., 2024. The effect of shrub cover on conifer water-use patterns, growth and response to precipitation variability in the southern Sierra Nevada. *Tree Physiol.* 44:tpae004.
- Goodwin, M.J., North, M.P., Zald, H.S.J., Hurteau, M.D., 2018. The 15-year post-treatment response of a mixed-conifer understory plant community to thinning and burning treatments. *For. Ecol. Manag.* 429, 617–624.
- Goodwin, M.J., North, M.P., Zald, H.S.J., Hurteau, M.D., 2020. Changing climate reallocates the carbon debt of frequent-fire forests. *Glob. Change Biol.* 26, 6180–6189.
- Goodwin, M.J., Zald, H.S.J., North, M.P., Hurteau, M.D., 2021. Climate-driven tree mortality and fuel aridity increase wildfire's potential heat flux. *Geophys. Res. Lett.* 48, e2021GL094954.
- Gottlieb, A.R., Mankin, J.S., 2022. Observing, measuring, and assessing the consequences of snow drought. *Bull. Am. Meteorol. Soc.* 103, E1041–E1060.
- Goulden, M.L., Bales, R.C., 2019. California forest die-off linked to multi-year deep soil drying in 2012–2015 drought. *Nat. Geosci.* 12, 632–637.
- Guiterman, C.H., Margolis, E.Q., Allen, C.D., Falk, D.A., Swetnam, T.W., 2018. Long-term persistence and fire resilience of oak shrubfields in dry conifer forests of Northern New Mexico. *Ecosystems* 21, 943–959.
- Guiterman, C.H., Margolis, E.Q., Baisan, C.H., Falk, D.A., Allen, C.D., Swetnam, T.W., 2019. Spatiotemporal variability of human–fire interactions on the Navajo Nation. *Ecosphere* 10, e02932.
- Gutiérrez, R.J., P.N. Manley, and P.A. Stine. 2017. The California spotted owl: current state of knowledge. Page PSW-GTR-254. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA.
- Hagmann, R.K., Hessburg, P.F., Prichard, S.J., Povak, N.A., Brown, P.M., Fulé, P.Z., Keane, R.E., Knapp, E.E., Lydersen, J.M., Metlen, K.L., Reilly, M.J., Sánchez Meador, A.J., Stephens, S.L., Stevens, J.T., Taylor, A.H., Yocom, L.L., Battaglia, M.A., Churchill, D.J., Daniels, L.D., Falk, D.A., Henson, P., Johnston, J.D., Krawchuk, M.A., Levine, C.R., Meigs, G.W., Merschel, A.G., North, M.P., Safford, H.D., Swetnam, T. W., Waltz, A.E.M., 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecol. Appl.* 31, e02431.
- Hammond, W.M., Yu, K., Wilson, L.A., Will, R.E., Anderegg, W.R.L., Adams, H.D., 2019. Dead or dying? Quantifying the point of no return from hydraulic failure in drought-induced tree mortality. *N. Phytol.* 223, 1834–1843.
- Hammond, W.M., Williams, A.P., Abatzoglou, J.T., Adams, H.D., Klein, T., López, R., Sáenz-Romero, C., Hartmann, H., Breshears, D.D., Allen, C.D., 2022. Global field observations of tree die-off reveal hotter-drought fingerprint for Earth's forests. *Nat. Commun.* 13, 1761.
- Hanberry, B.B., 2014. Compositional changes in selected forest ecosystems of the western United States. *Appl. Geogr.* 52, 90–98.
- Hankins, D.L., 2024. Climate resilience through ecocultural stewardship. *Proc. Natl. Acad. Sci.* 121, e2310072121.
- Hanula, J.L., Ulyshen, M.D., Horn, S., 2016. Conserving pollinators in North American forests: a review. *Nat. Areas J.* 36, 427–439.
- Harpold, A.A., Biederman, J.A., Condon, K., Merino, M., Korgaonkar, Y., Nan, T., Sloat, L.L., Ross, M., Brooks, P.D., 2014. Changes in snow accumulation and ablation following the Las Conchas Forest Fire, New Mexico, USA: changes in snow following fire. *Ecophysiology* 7, 440–452.
- Harris, L., Taylor, A.H., 2015. Topography, fuels, and fire exclusion drive fire severity of the rim fire in an old-growth mixed-conifer forest, Yosemite National Park, USA. *Ecosystems* 18, 1192–1208.
- Harris, L.B., Scholl, A.E., Young, A.B., Estes, B.L., Taylor, A.H., 2019. Spatial and temporal dynamics of 20th century carbon storage and emissions after wildfire in an old-growth forest landscape. *For. Ecol. Manag.* 449, 117461.
- Haskins, K.E., Gehring, C.A., 2004. Interactions with juniper alter pinyon pine ectomycorrhizal fungal communities. *Ecology* 85, 2687–2692.
- Haskins, K.E., Gehring, C.A., 2005. Evidence for mutualist limitation: the impacts of conspecific density on the mycorrhizal inoculum potential of woodland soils. *Oecologia* 145, 123–131.
- Hatchett, B.J., Rhoades, A.M., McEvoy, D.J., 2022. Decline in seasonal snow during a projected 20-year dry spell. *Hydrology* 9, 155.
- Hatchett, B.J., Koshkin, A.L., Guirguis, K., Rittger, K., Nolin, A.W., Heggli, A., Rhoades, A.M., East, A.E., Siirila-Woodburn, E.R., Brandt, W.T., Gershunov, A., Haleakala, K., 2023. Midwinter dry spells amplify post-fire snowpack decline. *Geophys. Res. Lett.* 50, e2022GL101235.
- Hawkins, A.E., Henkel, T.W., 2011. Native forest pathogens facilitate persistence of Douglas-fir in old-growth forests of northwestern California. *Can. J. For. Res.* 41, 1256–1266.
- Hecht, H., Krofcheck, D.J., Carril, D., Hurteau, M.D., 2024. Estimating the influence of field inventory sampling intensity on forest landscape model performance for determining high-severity wildfire risk. *Sci. Rep.* 14, 3073.
- Heffelfinger, J.R., Geist, V., Wishart, W., 2013. The role of hunting in North American wildlife conservation. *Int. J. Environ. Stud.* 70, 399–413.
- Hessburg, P.F., Miller, C.L., Parks, S.A., Povak, N.A., Taylor, A.H., Higuera, P.E., Prichard, S.J., North, M.P., Collins, B.M., Hurteau, M.D., Larson, A.J., Allen, C.D., Stephens, S.L., Rivera-Huerta, H., Stevens-Rumann, C.S., Daniels, L.D., Gedalof, Z., Gray, R.W., Kane, V.R., Churchill, D.J., Haggmann, R.K., Spies, T.A., Cansler, C.A., Belote, R.T., Veblen, T.T., Battaglia, M.A., Hoffman, C., Skinner, C.N., Safford, H.D., Salter, R.B., 2019. Climate, environment, and disturbance history govern resilience of Western North American forests. *Front. Ecol. Evol.* 7, 239.
- Hubert, N.A., Gehring, C.A., 2008. Neighboring trees affect ectomycorrhizal fungal community composition in a woodland-forest ecotone. *Mycorrhiza* 18, 363–374.
- Huffman, D.W., Fulé, P.Z., Pearson, K.M., Crouse, J.E., 2008. Fire history of pinyon-juniper woodlands at upper ecotones with ponderosa pine forests in Arizona and New Mexico. *Can. J. For. Res.* 38, 2097–2108.
- Huffman, D.W., Roccaforte, J.P., Springer, J.D., Crouse, J.E., 2020. Restoration applications of resource objective wildfires in western US forests: a status of knowledge review. *Fire Ecol.* 16, 18.
- Hunter, J.E., Gutiérrez, R.J., Franklin, A.B., 1995. Habitat configuration around spotted owl sites in Northwestern California. *Condor* 97, 684–693.
- Hurteau, M., North, M., 2008. Mixed-conifer understory response to climate change, nitrogen, and fire. *Glob. Change Biol.* 14, 1543–1552.
- Hurteau, M., Zald, H., North, M., 2007. Species-specific response to climate reconstruction in upper-elevation mixed-conifer forests of the western Sierra Nevada, California. *Can. J. For. Res.* 37, 1681–1691.
- Hurteau, M.D., 2017. Quantifying the carbon balance of forest restoration and wildfire under projected climate in the fire-prone Southwestern US. *PLOS ONE* 12, e0169275.
- Hurteau, M.D., Stoddard, M.T., Fulé, P.Z., 2011. The carbon costs of mitigating high-severity wildfire in southwestern ponderosa pine: carbon costs of mitigating wildfire. *Glob. Change Biol.* 17, 1516–1521.
- Hurteau, M.D., Liang, S., Westerling, A.L., Wiedinmyer, C., 2019a. Vegetation-fire feedback reduces projected area burned under climate change. *Sci. Rep.* 9, 2838.
- Hurteau, M.D., North, M.P., Koch, G.W., Hungate, B.A., 2019b. Managing for disturbance stabilizes forest carbon. *Proc. Natl. Acad. Sci.* 116, 10193–10195.
- Hurteau, M.D., Goodwin, M.J., Marsh, C., Zald, H.S., Collins, B., Meyer, M., North, M.P., 2024. Managing fire-prone forests in a time of decreasing carbon carrying capacity. *Front. Ecol. Environ.*, e2801.
- Jolly, W.M., Parsons, R.A., Hadlow, A.M., Cohn, G.M., McAllister, S.S., Popp, J.B., Hubbard, R.M., Negron, J.F., 2012. Relationships between moisture, chemistry, and ignition of *Pinus contorta* needles during the early stages of mountain pine beetle attack. *For. Ecol. Manag.* 269, 52–59.
- Jones, G.M., Tingley, M.W., 2022. Pyrodiversity and biodiversity: a history, synthesis, and outlook. *Divers. Distrib.* 28, 386–403.
- Jones, G.M., Gutiérrez, R., Tempel, D.J., Whitmore, S.A., Berigan, W.J., Peery, M.Z., 2016. Megafires: an emerging threat to old-forest species. *Front. Ecol. Environ.* 14, 300–306.

- Jones, G.M., Kramer, H.A., Berigan, W.J., Whitmore, S.A., Gutiérrez, R.J., Peery, M.Z., 2021. Megafire causes persistent loss of an old-forest species. *Anim. Conserv.* 24, 925–936.
- Jones, G.M., Keyser, A.R., Westerling, A.L., Baldwin, W.J., Keane, J.J., Sawyer, S.C., Clare, J.D., Gutiérrez, R., Peery, M.Z., 2022. Forest restoration limits megafires and supports species conservation under climate change. *Front. Ecol. Environ.* 20, 210–216.
- Jones, G.M., Goldberg, J.F., Wilcox, T.M., Buckley, L.B., Parr, C.L., Linck, E.B., Fountain, E.D., Schwartz, M.K., 2023. Fire-driven animal evolution in the Pliocene. *Trends Ecol. Evol.* 38, 1072–1084.
- Juang, C.S., Williams, A.P., Abatzoglou, J.T., Balch, J.K., Hurteau, M.D., Moritz, M.A., 2022. Rapid growth of large forest fires drives the exponential response of annual forest-fire area to aridity in the western United States. *Geophys. Res. Lett.* 49, e2021GL097131.
- Jung, C.G., Keyser, A.R., Remy, C.C., Krofcheck, D., Allen, C.D., Hurteau, M.D., 2023. Topographic information improves simulated patterns of post-fire conifer regeneration in the southwest United States. *Glob. Change Biol.* 29, 4342–4353.
- Kampf, S.K., McGrath, D., Sears, M.G., Fassnacht, S.R., Kiewiet, L., Hammond, J.C., 2022. Increasing wildfire impacts on snowpack in the western U.S. *Proc. Natl. Acad. Sci.* 119, e2200333119.
- Kan, J.-Y., Li, T.-F., Xu, M., Zhang, R.-Y., Wang, Z.-X., Feng, Y.-X., 2023. A song of ice and fire: Spatiotemporal visual variations in the snow water equivalent (SWE) for identification of wildfire risk areas in a snow mountainous region. *Ecol. Indic.* 154, 110497.
- Kane, J.M., Kolb, T.E., McMillin, J.D., 2014. Stand-scale tree mortality factors differ by site and species following drought in southwestern mixed conifer forests. *For. Ecol. Manag.* 330, 171–182.
- Kannenberg, S.A., Driscoll, A.W., Malesky, D., Anderegg, W.R.L., 2021. Rapid and surprising dieback of Utah juniper in the southwestern USA due to acute drought stress. *For. Ecol. Manag.* 480, 118639.
- Keeley, J.E., Franklin, J., D'Antonio, C., 2011. Fire and Invasive Plants on California Landscapes. In: McKenzie, D., Miller, C., Falk, D.A. (Eds.), *The Landscape Ecology of Fire*. Springer Netherlands, Dordrecht, pp. 193–221.
- Kerhoulas, L.P., Kolb, T.E., Hurteau, M.D., Koch, G.W., 2013. Managing climate change adaptation in forests: a case study from the U.S. Southwest. *J. Appl. Ecol.* 50, 1311–1320.
- Keyser, A.R., Krofcheck, D.J., Remy, C.C., Allen, C.D., Hurteau, M.D., 2020. Simulated increases in fire activity reinforce shrub conversion in a southwestern US forest. *Ecosystems* 23, 1702–1713.
- Kier, G., Kref, H., Lee, T.M., Jetz, W., Ibsch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. *Proc. Natl. Acad. Sci.* 106, 9322–9327.
- Kitchen, S.G., 2012. Historical fire regime and forest variability on two eastern Great Basin fire-sheds (USA). *For. Ecol. Manag.* 285, 53–66.
- Knight, C.A., Anderson, L., Bunting, M.J., Champagne, M., Clayburn, R.M., Crawford, J.N., Klimaszewski-Patterson, A., Knapp, E.E., Lake, F.K., Mensing, S.A., Wahl, D., Wanket, J., Watts-Tobin, A., Potts, M.D., Battles, J.J., 2022. Land management explains major trends in forest structure and composition over the last millennium in California's Klamath Mountains. *Proc. Natl. Acad. Sci.* 119, e2116264119.
- Knoche, S., Lupi, F., 2007. Valuing deer hunting ecosystem services from farm landscapes. *Spec. Sect. - Ecosyst. Serv. Agric.* 64, 313–320.
- Kolb, T.E., Fettig, C.J., Ayres, M.P., Bentz, B.J., Hicke, J.A., Mathiasen, R., Stewart, J.E., Weed, A.S., 2016. Observed and anticipated impacts of drought on forest insects and diseases in the United States. *Spec. Sect.: Drought US For.: Impacts Potential Manag. Responses* 380, 321–334.
- Koontz, M.J., North, M.P., Werner, C.M., Fick, S.E., Latimer, A.M., 2020. Local forest structure variability increases resilience to wildfire in dry western U.S. coniferous forests. *Ecol. Lett.* 23, 483–494.
- Korb, J.E., Johnson, N.C., Covington, W.W., 2003. Arbuscular mycorrhizal propagule densities respond rapidly to ponderosa pine restoration treatments. *J. Appl. Ecol.* 40, 101–110.
- Korb, J.E., Fornwalt, P.J., Stevens-Rumann, C.S., 2019. What drives ponderosa pine regeneration following wildfire in the western United States? *For. Ecol. Manag.* 454, 117663.
- Koshkin, A.L., Hatchett, B.J., Nolin, A.W., 2022. Wildfire impacts on western United States snowpacks. *Front. Water* 4, 971271.
- Krofcheck, D.J., Hurteau, M.D., Scheller, R.M., Loudermilk, E.L., 2018. Prioritizing forest fuels treatments based on the probability of high-severity fire restores adaptive capacity in Sierran forests. *Glob. Change Biol.* 24, 729–737.
- Krofcheck, D.J., Remy, C.C., Keyser, A.R., Hurteau, M.D., 2019. Optimizing forest management stabilizes carbon under projected climate and wildfires. *J. Geophys. Res.: Biogeosci.* 124, 3075–3087.
- Kuntze, C.C., Pauli, J.N., Zulla, C.J., Keane, J.J., Roberts, K.N., Dotters, B.P., Sawyer, S.C., Peery, M.Z., 2023. Landscape heterogeneity provides co-benefits to predator and prey. *Ecol. Appl.* 33, e2908.
- Lavelle, P., Decaens, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi, J.-P., 2006. Soil invertebrates and ecosystem services. *ICSZ* 42, S3–S15.
- Lehmann, A., Zheng, W., Ryo, M., Soutschek, K., Roy, J., Rongstock, R., Maaß, S., Rillig, M.C., 2020. Fungal traits important for soil aggregation. *Front. Microbiol.* 10, 1075.
- Lewis, J.S., LeSueur, L., Oakleaf, J., Rubin, E.S., 2022. Mixed-severity wildfire shapes habitat use of large herbivores and carnivores. *For. Ecol. Manag.* 506, 119933.
- Liang, S., Hurteau, M.D., Westerling, A.L., 2017b. Potential decline in carbon carrying capacity under projected climate-wildfire interactions in the Sierra Nevada. *Sci. Rep.* 7, 2420.
- Liang, S., Hurteau, M.D., Westerling, A.L., 2017a. Response of Sierra Nevada forests to projected climate-wildfire interactions. *Glob. Change Biol.* 23, 2016–2030.
- Liang, S., Hurteau, M.D., Westerling, A.L., 2018. Large-scale restoration increases carbon stability under projected climate and wildfire regimes. *Front. Ecol. Environ.* 16, 207–212.
- Liebmman, M.J., Farella, J., Roos, C.I., Stack, A., Martini, S., Swetnam, T.W., 2016. Native American depopulation, reforestation, and fire regimes in the Southwest United States, 1492–1900 CE. *Proc. Natl. Acad. Sci.* 113, E696–E704.
- Littell, J.S., McKenzie, D., Peterson, D.L., Westerling, A.L., 2009. Climate and wildfire area burned in western U.S. ecoprovinces, 1916–2003. *Ecol. Appl.* 19, 1003–1021.
- 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. Manag.* 304, 370–382.
- Lynch, A.J., Thompson, L.M., Beever, E.A., Cole, D.N., Engman, A.C., Hawkins Hoffman, C., Jackson, S.T., Krabbenhoft, T.J., Lawrence, D.J., Limpinsel, D., Magill, R.T., Melvin, T.A., Morton, J.M., Newman, R.A., Peterson, J.O., Porath, M.T., Rahel, F.J., Schuurman, G.W., Sethi, S.A., Wilkening, J.L., 2021. Managing for RADical ecosystem change: applying the resist-accept-direct (RAD) framework. *Front. Ecol. Environ.* 19, 461–469.
- Lynch, S.C., Eskalen, A., Zambino, P.J., Mayorquin, J.S., Wang, D.H., 2013. Identification and pathogenicity of Botryosphaeriaceae species associated with coast live oak (*Quercus agrifolia*) decline in southern California. *Mycologia* 105, 125–140.
- Maestrini, B., Alvey, E.C., Hurteau, M.D., Safford, H., Miesel, J.R., 2017. Fire severity alters the distribution of pyrogenic carbon stocks across ecosystem pools in a Californian mixed-conifer forest. *J. Geophys. Res.: Biogeosci.* 122, 2338–2355.
- Magness, D.R., Hoang, L., Belote, R.T., Brennan, J., Carr, W., Stuart Chapin, F., Clifford, K., Morrison, W., Morton, J.M., Sofaer, H.R., 2022. Management foundations for navigating ecological transformation by resisting, accepting, or directing social-ecological change. *BioScience* 72, 30–44.
- Margolis, E.Q., Balmat, J., 2009. Fire history and fire-climate relationships along a fire regime gradient in the Santa Fe Municipal Watershed, NM, USA. *For. Ecol. Manag.* 258, 2416–2430.
- Marsh, C., Crockett, J.L., Krofcheck, D., Keyser, A., Allen, C.D., Litvak, M., Hurteau, M.D., 2022. Planted seedling survival in a post-wildfire landscape: from experimental planting to predictive probabilistic surfaces. *For. Ecol. Manag.* 525, 120524.
- Marsh, C., Blankinship, J.C., Hurteau, M.D., 2023. Effects of nurse shrubs and biochar on planted conifer seedling survival and growth in a high-severity burn patch in New Mexico, USA. *For. Ecol. Manag.* 537, 120971.
- Maxwell, J.D., Call, A., St. Clair, S.B., 2019. Wildfire and topography impacts on snow accumulation and retention in montane forests. *For. Ecol. Manag.* 432, 256–263.
- May, C.J., Zald, H.S.J., North, M.P., Gray, A.N., Hurteau, M.D., 2023. Repeated burns fail to restore pine regeneration to the natural range of variability in a Sierra Nevada mixed-conifer forest, U.S.A. *Restor. Ecol.* 31, e13863.
- McCauley, L.A., Bradford, John B., Robles, M.D., Shriver, R.K., Woolley, T.J., Andrews, C.A., 2022. Landscape-scale forest restoration decreases vulnerability to drought mortality under climate change in southwest USA ponderosa forest. *For. Ecol. Manag.* 509, 120088.
- McClure, E.J., Coop, J.D., Guiterman, C.H., Margolis, E.Q., Parks, S.A., 2024. Contemporary fires are less frequent but more severe in dry conifer forests of the southwestern United States. *Commun. Earth Environ.* 5, 581.
- McCullough, I.M., Davis, F.W., Dingman, J.R., Flint, L.E., Flint, A.L., Serra-Diaz, J.M., Syphard, A.D., Moritz, M.A., Hannah, L., Franklin, J., 2016. High and dry: high elevations disproportionately exposed to regional climate change in Mediterranean-climate landscapes. *Landsc. Ecol.* 31, 1063–1075.
- McDowell, N.G., Tan, Z., Hurteau, M.D., Prasad, R., 2021. Trade-offs of forest management scenarios on forest carbon exchange and threatened and endangered species habitat. *Ecosphere* 12, e03779.
- McGrath, D., Zeller, L., Bonnell, R., Reis, W., Kampf, S., Williams, K., Okal, M., Olsen-Mikitowicz, A., Bump, E., Sears, M., Rittger, K., 2023. Declines in Peak Snow Water Equivalent and Elevated Snowmelt Rates Following the 2020 Cameron Peak Wildfire in Northern Colorado. *Geophys. Res. Lett.* 50, e2022GL101294.
- Miller, R.F., Heyerdahl, E.K., 2008. Fine-scale variation of historical fire regimes in sagebrush-steppe and juniper woodland: an example from California, USA. *Int. J. Wildland Fire* 17, 245–254.
- Moeser, C.D., Broxton, P.D., Harpold, A., Robertson, A., 2020. Estimating the effects of forest structure changes from wildfire on snow water resources under varying meteorological conditions. *Water Resour. Res.* 56, e2020WR027071.
- Moore, M.M., Huffman, D.W., Fulé, P.Z., Covington, W.W., Crouse, J.E., 2004. Comparison of historical and contemporary forest structure and composition on permanent plots in Southwestern Ponderosa Pine forests. *For. Sci.* 50, 162–176.
- Mote, P.W., Li, S., Lettenmaier, D.P., Xiao, M., Engel, R., 2018. Dramatic declines in snowpack in the western US. *npj Clim. Atmos. Sci.* 1, 2.
- Negrón, J.F., McMillin, J.D., Anhold, J.A., Coulson, D., 2009. Bark beetle-caused mortality in a drought-affected ponderosa pine landscape in Arizona, USA. *For. Ecol. Manag.* 257, 1353–1362.
- North, M., Hurteau, M., Fiegner, R., Barbour, M., 2005. Influence of fire and El Niño on tree recruitment varies by species in sierran mixed conifer. *For. Sci.* 51, 187–197.
- North, M., Hurteau, M., Innes, J., 2009. Fire suppression and fuels treatment effects on mixed-conifer carbon stocks and emissions. *Ecol. Appl.* 19, 1385–1396.
- North, M.P., Hurteau, M.D., 2011. High-severity wildfire effects on carbon stocks and emissions in fuels treated and untreated forest. *For. Ecol. Manag.* 261, 1115–1120.
- North, M.P., York, R.A., Collins, B.M., Hurteau, M.D., Jones, G.M., Knapp, E.E., Kobziar, L., McCann, H., Meyer, M.D., Stephens, S.L., Tompkins, R.E., Tubbesing, C.L., 2021. Pyrosilviculture needed for landscape resilience of dry Western United States forests. *J. For.* 119, 520–544.

- O'Connor, C.D., Falk, D.A., Lynch, A.M., Swetnam, T.W., 2014. Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleno Mountains, Arizona, USA. *For. Ecol. Manag.* 329, 264–278.
- Odland, M.C., Goodwin, M.C., Smithers, B.V., Hurteau, M.D., North, M.P., 2021. Plant community response to thinning and repeated fire in Sierra Nevada mixed-conifer forest understories. *For. Ecol. Manag.* 495, 119361.
- Ouzts, J., Kolb, T., Huffman, D., Sánchez Meador, A., 2015. Post-fire ponderosa pine regeneration with and without planting in Arizona and New Mexico. *For. Ecol. Manag.* 354, 281–290.
- Parks, S.A., Dobrowski, S.Z., Shaw, J.D., Miller, C., 2019. Living on the edge: trailing edge forests at risk of fire-facilitated conversion to non-forest. *Ecosphere* 10, e02651.
- Peltier, D.M.P., Carbone, M.S., McIntire, C.D., Robertson, N., Thompson, R.A., Malone, S., LeMoine, J., Richardson, A.D., McDowell, N.G., Adams, H.D., Pockman, W.T., Trowbridge, A.M., 2023. Carbon starvation following a decade of experimental drought consumes old reserves in *Pinus edulis*. *N. Phytol.* 240, 92–104.
- Pirtel, N.L., Hubbard, R.M., Bradford, J.B., Kolb, T.E., Litvak, M.E., Abella, S.R., Porter, S. L., Petrie, M.D., 2021. The aboveground and belowground growth characteristics of juvenile conifers in the southwestern United States. *Ecosphere* 12, e03839.
- Plaut, J.A., Yezpe, E.A., Hill, J., Pangle, R., Sperry, J.S., Pockman, W.T., McDowell, N.G., 2012. Hydraulic limits preceding mortality in a piñon-juniper woodland under experimental drought: hydraulic limits in a piñon-juniper woodland. *Plant, Cell Environ.* 35, 1601–1617.
- Plieninger, T., Bieling, C., Fagerholm, N., Byg, A., Hartel, T., Hurley, P., López-Santiago, C.A., Nagabhatla, N., Oteros-Rozas, E., Raymond, C.M., van der Horst, D., Huntsinger, L., 2015. The role of cultural ecosystem services in landscape management and planning. *Open Issue* 14, 28–33.
- Ponisio, L.C., 2020. Pyrodiversity promotes interaction complementarity and population resistance. *Ecol. Evol.* 10, 4431–4447.
- Ponisio, L.C., Wilkin, K., McGonigle, L.K., Kulhanek, K., Cook, L., Thorp, R., Griswold, T., Kremen, C., 2016. Pyrodiversity begets plant–pollinator community diversity. *Glob. Change Biol.* 22, 1794–1808.
- Prichard, S.J., Hessburg, P.F., Hagmann, R.K., Povak, N.A., Dobrowski, S.Z., Hurteau, M. D., Kane, V.R., Keane, R.E., Kobziar, L.N., Kolden, C.A., North, M., Parks, S.A., Safford, H.D., Stevens, J.T., Yocom, L.L., Churchill, D.J., Gray, R.W., Huffman, D.W., Lake, F.K., Khatri-Chhetri, P., 2021. Adapting western North American forests to climate change and wildfires: 10 common questions. *Ecol. Appl.* 31, e02433.
- Redmond, M.D., Weisberg, P.J., Cobb, N.S., Clifford, M.J., 2018. Woodland resilience to regional drought: Dominant controls on tree regeneration following overstorey mortality. *J. Ecol.* 106, 625–639.
- Redmond, M.D., Urza, A.K., Weisberg, P.J., 2023. Managing for ecological resilience of piñon–juniper ecosystems during an era of woodland contraction. *Ecosphere* 14, e4505.
- Remy, C.C., Keyser, A.R., Krofcheck, D.J., Litvak, M.E., Hurteau, M.D., 2021. Future fire-driven landscape changes along a southwestern US elevation gradient. *Clim. Change* 166, 46.
- Remy, C.C., Krofcheck, D.J., Keyser, A.R., Hurteau, M.D., 2024. Restoring frequent fire to dry conifer forests delays the decline of subalpine forests in the southwest United States under projected climate. *J. Appl. Ecol.* 1365–2664, 14689.
- Rillig, M.C., Mummey, D.L., 2006. Mycorrhizas and soil structure. *N. Phytol.* 171, 41–53.
- Robbins, Z.J., Xu, C., Aukema, B.H., Buotte, P.C., Chitra-Tarak, R., Fetting, C.J., Goulden, M.L., Goodsman, D.W., Hall, A.D., Koven, C.D., Kueppers, L.M., Madakumbura, G.D., Mortenson, L.A., Powell, J.A., Scheller, R.M., 2022. Warming increased bark beetle-induced tree mortality by 30% during an extreme drought in California. *Glob. Change Biol.* 28, 509–523.
- Roccaforte, J.P., Sánchez Meador, A., Waltz, A.E.M., Gaylord, M.L., Stoddard, M.T., Huffman, D.W., 2018. Delayed tree mortality, bark beetle activity, and regeneration dynamics five years following the Wallow Fire, Arizona, USA: assessing trajectories towards resiliency. *For. Ecol. Manag.* 428, 20–26.
- Rodman, K.C., Veblen, T.T., Battaglia, M.A., Chambers, M.E., Fornwalt, P.J., Holden, Z. A., Kolb, T.E., Ouzts, J.R., Rother, M.T., 2020. A changing climate is snuffing out post-fire recovery in montane forests. *Glob. Ecol. Biogeogr.* 29, 2039–2051.
- Rodman, K.C., Crouse, J.E., Donager, J.J., Huffman, D.W., Sánchez Meador, A.J., 2022. Patterns and drivers of recent land cover change on two trailing-edge forest landscapes. *For. Ecol. Manag.* 521, 120449.
- Roerick, T.M., Cain, J.W., Gedir, J.V., 2019. Forest restoration, wildfire, and habitat selection by female mule deer. *For. Ecol. Manag.* 447, 169–179.
- Roos, C.I., Swetnam, T.W., Ferguson, T.J., Liebmann, M.J., Loehman, R.A., Welch, J.R., Margolis, E.Q., Guiterman, C.H., Hockaday, W.C., Aiuvalasit, M.J., Battillo, J., Farella, J., Kiahtipes, C.A., 2021. Native American fire management at an ancient wildland–urban interface in the Southwest United States. *Proc. Natl. Acad. Sci.* 118, e2018733118.
- Sagoff, M., 1996. On the value of endangered and other species. *Environ. Manag.* 20, 897–911.
- Sánchez, J.J., Marcos-Martínez, R., Srivastava, L., Soonsawad, N., 2021. Valuing the impacts of forest disturbances on ecosystem services: An examination of recreation and climate regulation services in U.S. national forests. *Trees, For. People* 5, 100123.
- Santos, M.J., Whitham, T.G., 2010. Predictors of *Ips confusus* outbreaks during a record drought in southwestern USA: implications for monitoring and management. *Environ. Manag.* 45, 239–249.
- Savage, M., Swetnam, T.W., 1990. Early 19th-century fire decline following sheep pasturing in a Navajo Ponderosa Pine forest. *Ecology* 71, 2374–2378.
- Schmitz, O.J., Wilmers, C.C., Leroux, S.J., Doughty, C.E., Atwood, T.B., Galetti, M., Davies, A.B., Goetz, S.J., 2018. Animals and the zoogeography of the carbon cycle. *Science* 362, eaar3213.
- Schoettle, A.W., Sniezko, R.A., Kegley, A., Burns, K.S., 2014. White pine blister rust resistance in limber pine: evidence for a major gene. *Phytopathology*® 104, 163–173.
- Schollmeyer, K.G., Driver, J.C., 2013. Settlement patterns, source–sink dynamics, and artiodactyl hunting in the prehistoric U.S. Southwest. *J. Archaeol. Method Theory* 20, 448–478.
- Schuurman, G.W., Cole, D.N., Cravens, A.E., Covington, S., Crausbay, S.D., Hoffman, C. H., Lawrence, D.J., Magness, D.R., Morton, J.M., Nelson, E.A., O'Malley, R., 2022. Navigating ecological transformation: resist–accept–direct as a path to a new resource management paradigm. *BioScience* 72, 16–29.
- Serra-Díaz, J.M., Franklin, J., Ninyerola, M., Davis, F.W., Syphard, A.D., Regan, H.M., Ikegami, M., 2014. Bioclimatic velocity: the pace of species exposure to climate change. *Divers. Distrib.* 20, 169–180.
- Serra-Díaz, J.M., Franklin, J., Dillon, W.W., Syphard, A.D., Davis, F.W., Meentemeyer, R. K., 2016. California forests show early indications of both range shifts and local persistence under climate change: early indications of tree range shifts. *Glob. Ecol. Biogeogr.* 25, 164–175.
- Singleton, M.P., Thode, A.E., Sánchez Meador, A.J., Iniguez, J.M., 2019. Increasing trends in high-severity fire in the southwestern USA from 1984 to 2015. *For. Ecol. Manag.* 433, 709–719.
- Slaton, M.R., MacKenzie, M., Kohler, T., Ramirez, C.M., 2019. Whitebark pine recruitment in Sierra Nevada driven by range position and disturbance history. *Forests* 10, 455.
- Smithers, B.V., Alongi, F., North, M.P., 2021. Live fast, die young: climate shifts may favor Great Basin bristlecone pine or limber pine in sub-alpine forest establishment. *For. Ecol. Manag.* 494, 119339.
- 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., Goodwin, M.J., Meyer, M.D., Fricker, G.A., Zald, H.S.J., Hurteau, M.D., North, M.P., 2021. Do forest fuel reduction treatments confer resistance to beetle infestation and drought mortality? *Ecosphere* 12, e03344.
- Steel, Z.L., Jones, G.M., Collins, B.M., Green, R., Koltunov, A., Purcell, K.L., Sawyer, S.C., Slaton, M.R., Stephens, S.L., Stine, P., Thompson, C., 2023. Mega-disturbances cause rapid decline of mature conifer forest habitat in California. *Ecol. Appl.* 33, e2763.
- Steindorff, A.S., Seong, K., Carver, A., Calhoun, S., Fischer, M.S., Stillman, K., Liu, H., Drula, E., Henrissat, B., Simpson, H.J., Schilling, J.S., Lipzen, A., He, G., Yan, M., Andreopoulos, B., Pangilinan, J., LaButti, K., Ng, V., Traxler, M., Bruns, T.D., Grigoriev, I.V., 2022. Diversity of genomic adaptations to the post-fire environment in *Pezizales* fungi points to crosstalk between charcoal tolerance and sexual development. *N. Phytol.* 236, 1154–1167.
- 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 art79.
- Stephens, S.L., Collins, B.M., Fetting, 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., Westerling, A.L., Hurteau, M.D., Peery, M.Z., Schultz, C.A., Thompson, S., 2020. Fire and climate change: conserving seasonally dry forests is still possible. *Front. Ecol. Environ.* 18, 354–360.
- Stevens, J.T., Haffey, C.M., Coop, J.D., Fornwalt, P.J., Yocom, L., Allen, C.D., Bradley, A., Burney, O.T., Carril, D., Chambers, M.E., Chapman, T.B., Haire, S.L., Hurteau, M.D., Iniguez, J.M., Margolis, E.Q., Marks, C., Marshall, L.A.E., Rodman, K.C., Stevens-Rumann, C.S., Thode, A.E., Walker, J.J., 2021. Tamm Review: Postfire landscape management in frequent-fire conifer forests of the southwestern United States. *For. Ecol. Manag.* 502, 119678.
- 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.
- Stielstra, C.M., Lohse, K.A., Chorover, J., McIntosh, J.C., Barron-Gafford, G.A., Perdrial, J.N., Litvak, M., Barnard, H.R., Brooks, P.D., 2015. Climatic and landscape influences on soil moisture are primary determinants of soil carbon fluxes in seasonally snow-covered forest ecosystems. *Biogeochemistry* 123, 447–465.
- Stoddard, M.T., Roccaforte, J.P., Meador, A.J.S., Huffman, D.W., Fulé, P.Z., Waltz, A.E. M., Covington, W.W., 2021. Ecological restoration guided by historical reference conditions can increase resilience to climate change of southwestern U.S. Ponderosa pine forests. *For. Ecol. Manag.* 493, 119256.
- Swain, D.L., 2015. A tale of two California droughts: Lessons amidst record warmth and dryness in a region of complex physical and human geography. *Geophys. Res. Lett.* 42, 9999.
- Swetnam, T.W., Betancourt, J.L., 1990. Fire-Southern Oscillation Relations in the Southwestern United States. *Science* 249, 1017–1020.
- Swetnam, T.W., Baisan, C.H., Caprio, A.C., Brown, P.M., Touchan, R., Anderson, R.S., Hallett, D.J., 2009. Multi-millennial fire history of the giant forest, Sequoia National Park, California, USA. *Fire Ecol.* 5, 120–150.
- Swetnam, T.W., Farella, J., Roos, C.I., Liebmann, M.J., Falk, D.A., Allen, C.D., 2016. Multiscale perspectives of fire, climate and humans in western North America and the Jemez Mountains, USA. *Philos. Trans. R. Soc. B: Biol. Sci.* 371, 20150168.
- Syphard, A.D., Keeley, J.E., 2020. Mapping fire regime ecoregions in California. *Int. J. Wildland Fire* 29, 595–601.
- Taylor, A.H., 1993. Fire history and structure of red fir (*Abies magnifica*) forests, swain mountain experimental forest, Cascade Range, northeastern California. *Can. J. For. Res.* 23, 1672–1678.
- Taylor, A.H., Trouet, V., Skinner, C.N., Stephens, S., 2016. Socioecological transitions trigger fire regime shifts and modulate fire–climate interactions in the Sierra Nevada, USA, 1600–2015 CE. *Proc. Natl. Acad. Sci.* 113, 13684–13689.

- Taylor, A.H., Harris, L.B., Skinner, C.N., 2022. Severity patterns of the 2021 dixie fire exemplify the need to increase low-severity fire treatments in California's forests. *Environ. Res. Lett.* 17, 071002.
- Tempel, D.J., Gutiérrez, R.J., Whitmore, S.A., Reetz, M.J., Stoelting, R.E., Berigan, W.J., Seamans, M.E., Peery, M.Z., 2014. Effects of forest management on California Spotted Owls: implications for reducing wildfire risk in fire-prone forests. *Ecol. Appl.* 24, 2089–2106.
- Tsinajinnie, L.M., Frisbee, M.D., Wilson, J.L., 2021. Groundwater from perennial springs provide refuge from wildfire impacts in mountainous semiarid watershed. *J. Hydrol.* 596, 125701.
- Ulyshen, M.D., Hiers, J.K., Pokswinski, S.M., Fair, C., 2022. Pyrodiversity promotes pollinator diversity in a fire-adapted landscape. *Front. Ecol. Environ.* 20, 78–83.
- Vaillant, N.M., Stephens, S.L., 2009. Fire History of a lower elevation jeffrey pine-mixed conifer forest in the Eastern Sierra Nevada, California, USA. *Fire Ecol.* 5, 4–19.
- Van de Water, K.M., Safford, H.D., 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. *Fire Ecol.* 7, 26–58.
- Vander Wall, S.B., 2023. Seed dispersal in pines (pinus). *Bot. Rev.* 89, 275–307.
- Wahl, E.R., Zorita, E., Diaz, H.F., Hoell, A., 2022. Southwestern United States drought of the 21st century presages drier conditions into the future. *Commun. Earth Environ.* 3, 202.
- Wan, H.Y., Cushman, S.A., Ganey, J.L., 2019. Recent and projected future wildfire trends across the ranges of three spotted owl subspecies under climate change. *Front. Ecol. Evol.* 7.
- Warnock, D.D., Litvak, M.E., Morillas, L., Sinsabaugh, R.L., 2016. Drought-induced piñon mortality alters the seasonal dynamics of microbial activity in piñon-juniper woodland. *Soil Biol. Biochem.* 92, 91–101.
- Wiechmann, M.L., Hurteau, M.D., North, M.P., Koch, G.W., Jerabkova, L., 2015. The carbon balance of reducing wildfire risk and restoring process: an analysis of 10-year post-treatment carbon dynamics in a mixed-conifer forest. *Clim. Change* 132, 709–719.
- 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., Gangadagamage, 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.
- Williams, A.P., Livneh, B., McKinnon, K.A., Hansen, W.D., Mankin, J.S., Cook, B.I., Smerdon, J.E., Varuolo-Clarke, A.M., Bjarke, N.R., Juang, C.S., Lettenmaier, D.P., 2022. Growing impact of wildfire on western US water supply. *Proc. Natl. Acad. Sci.* 119, e2114069119.
- Williams, J.N., Safford, H.D., Enstice, N., Steel, Z.L., Paulson, A.K., 2023. High-severity burned area and proportion exceed historic conditions in Sierra Nevada, California, and adjacent ranges. *Ecosphere* 14, e4397.
- Willson, K.G., Hurteau, M.D., 2024. Abiotic factors modify ponderosa pine regeneration outcomes after high-severity fire. *Ecosystems* 27, 606–620.
- Willson, K.G., Margolis, E.Q., Hurteau, M.D., 2024. Trees have similar growth responses to first-entry fires and reburns following long-term fire exclusion. *For. Ecol. Manag.* 571, 122226.
- Willson, M.F., 1993. Mammals as seed-dispersal mutualists in North America. *Oikos* 67, 159–176.
- Wine, M.L., Cadol, D., 2016. Hydrologic effects of large southwestern USA wildfires significantly increase regional water supply: fact or fiction? *Environ. Res. Lett.* 11, 085006.
- Wine, M.L., Makhnin, O., Cadol, D., 2018. Nonlinear long-term large watershed hydrologic response to wildfire and climatic dynamics locally increases water yields. *Earth's Future* 6, 997–1006.
- Winstral, A., Marks, D., 2002. Simulating wind fields and snow redistribution using terrain-based parameters to model snow accumulation and melt over a semi-arid mountain catchment. *Hydrol. Process.* 16, 3585–3603.
- Wolf, K.D., Higuera, P.E., Davis, K.T., Dobrowski, S.Z., 2021. Wildfire impacts on forest microclimate vary with biophysical context. *Ecosphere* 12, e03467.
- Xiang, L., Gong, S., Yang, L., Hao, J., Xue, M., Zeng, F., Zhang, X., Shi, W., Wang, H., Yu, D., 2016. Biocontrol potential of endophytic fungi in medicinal plants from Wuhan Botanical Garden in China. *Biol. Control* 94, 47–55.
- Xu, Q., Westerling, A.L., Notohamiprodjo, A., Wiedinmyer, C., Picotte, J.J., Parks, S.A., Hurteau, M.D., Marlier, M.E., Kolden, C.A., Sam, J.A., Baldwin, W.J., Ade, C., 2022. Wildfire burn severity and emissions inventory: an example implementation over California. *Environ. Res. Lett.* 17, 085008.
- Yocom Kent, L.L., Shive, K.L., Strom, B.A., Sieg, C.H., Hunter, M.E., Stevens-Rumann, C. S., Fulé, P.Z., 2015. Interactions of fuel treatments, wildfire severity, and carbon dynamics in dry conifer forests. *For. Ecol. Manag.* 349, 66–72.
- 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., Gray, A.N., North, M., Kern, R.A., 2008. Initial tree regeneration responses to fire and thinning treatments in a Sierra Nevada mixed-conifer forest, USA. *For. Ecol. Manag.* 256, 168–179.
- Zald, H.S.J., Callahan, C.C., Hurteau, M.D., Goodwin, M.J., North, M.P., 2022. Tree growth responses to extreme drought after mechanical thinning and prescribed fire in a Sierra Nevada mixed-conifer forest, USA. *For. Ecol. Manag.* 510, 120107.
- Zald, H.S.J., May, C.J., Gray, A.N., North, M.P., Hurteau, M.D., 2024. Thinning and prescribed burning increase shade-tolerant conifer regeneration in a fire excluded mixed-conifer forest. *For. Ecol. Manag.* 551, 121531.
- Zulla, C.J., Jones, G.M., Kramer, H.A., Keane, J.J., Roberts, K.N., Dotters, B.P., Sawyer, S. C., Whitmore, S.A., Berigan, W.J., Kelly, K.G., Gutiérrez, R.J., Peery, M.Z., 2023. Forest heterogeneity outweighs movement costs by enhancing hunting success and reproductive output in California spotted owls. *Landsc. Ecol.* 38, 2655–2673.