

INVITED FEATURE: CLIMATE CHANGE AND WESTERN WILDFIRES

Ecological Applications, 31(8), 2021, e02431

© 2021 The Authors. *Ecological Applications* published by Wiley Periodicals LLC on behalf of Ecological Society of America. This article has been contributed to by US Government employees and their work is in the public domain in the USA. This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests

R. K. HAGMANN¹, P. F. HESSBURG^{1,3}, S. J. PRICHARD¹, N. A. POVAK^{3,4}, P. M. BROWN⁵, P. Z. FULÉ⁶, R. E. KEANE⁷, E. E. KNAPP⁸, J. M. LYDERSEN⁹, K. L. METLEN¹⁰, M. J. REILLY¹¹, A. J. SÁNCHEZ MEADOR¹², S. L. STEPHENS¹³, J. T. STEVENS¹⁴, A. H. TAYLOR¹⁵, L. L. YOCOM¹⁶, M. A. BATTAGLIA¹⁷, D. J. CHURCHILL¹⁸, L. D. DANIELS¹⁹, D. A. FALK^{20,26}, P. HENSON²¹, J. D. JOHNSTON²², M. A. KRAWCHUK²², C. R. LEVINE²³, G. W. MEIGS¹⁸, A. G. MERSCHER²², M. P. NORTH²⁴, H. D. SAFFORD²⁵, T. W. SWETNAM²⁶, AND A. E. M. WALTZ¹²

¹College of the Environment-SEFS, University of Washington, Seattle, Washington 98195 USA

²Applegate Forestry LLC, Corvallis, Oregon 97330 USA

³USDA-FS, Forestry Sciences Laboratory, Pacific Northwest Research Station, Wenatchee, Washington 98801 USA

⁴USDA-FS, Pacific Southwest Research Station, Placerville, California 95667 USA

⁵Rocky Mountain Tree-Ring Research, Fort Collins, Colorado 80526 USA

⁶School of Forestry, Northern Arizona University, Flagstaff, Arizona 86011 USA

⁷Missoula Fire Sciences Laboratory, USDA-FS, Rocky Mountain Research Station, Missoula, Montana 59808 USA

⁸USDA-FS, Pacific Southwest Research Station, Redding, California 96002 USA

⁹Fire and Resource Assessment Program, California Department of Forestry and Fire Protection, Sacramento, California 94244 USA

¹⁰The Nature Conservancy, Ashland, Oregon 97520 USA

¹¹USDA-FS, Pacific Northwest Research Station, Corvallis, Oregon 97333 USA

¹²Ecological Restoration Institute, Northern Arizona University, Flagstaff, Arizona 86011 USA

¹³Department of Environmental Science, Policy, and Management, University of California–Berkeley, Berkeley, California 94720 USA

¹⁴U.S. Geological Survey, Fort Collins Science Center, New Mexico Landscapes Field Station, Santa Fe, New Mexico 87508 USA

¹⁵Department of Geography, Earth and Environmental Systems Institute, The Pennsylvania State University, University Park, Pennsylvania 16802 USA

¹⁶Department of Wildland Resources and the Ecology Center, Utah State University, Logan, Utah 84322 USA

¹⁷USDA-FS, Rocky Mountain Research Station, Fort Collins, Colorado 80526 USA

¹⁸Washington State Department of Natural Resources, Olympia, Washington 98504 USA

¹⁹Department of Forest and Conservation Sciences, University of British Columbia, Vancouver, British Columbia V6T 1Z4 Canada

²⁰School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona 85721 USA

²¹Oregon Fish and Wildlife Office, USDI Fish & Wildlife Service, Portland, Oregon 97232 USA

²²College of Forestry, Oregon State University, Corvallis, Oregon 97333 USA

²³Spatial Informatics Group, Pleasanton, California 94566 USA

²⁴USDA-FS, Pacific Southwest Research Station, Mammoth Lakes, California 93546 USA

²⁵USDA-FS, Pacific Southwest Region, Vallejo, California 94592 USA

²⁶Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona 85721 USA

Citation: Hagmann, R. K., P. F. Hessburg, S. J. Prichard, N. A. Povak, P. M. Brown, P. Z. Fulé, R. E. Keane, E. E. Knapp, J. M. Lydersen, K. L. Metlen, M. J. Reilly, A. J. Sánchez Meador, S. L. Stephens, J. T. Stevens, A. H. Taylor, L. L. Yocom, M. A. Battaglia, D. J. Churchill, L. D. Daniels, D. A. Falk, P. Henson, J. D. Johnston, M. A. Krawchuk, C. R. Levine, G. W. Meigs, A. G. Merschel, M. P. North, H. D. Safford, T. W. Swetnam, and A. E. M. Waltz. 2021. Evidence for widespread changes in the structure, composition, and fire regimes of western North American forests. *Ecological Applications* 31(8):e02431. 10.1002/eap.2431

Abstract. Implementation of wildfire- and climate-adaptation strategies in seasonally dry forests of western North America is impeded by numerous constraints and uncertainties. After more than a century of resource and land use change, some question the need for proactive management, particularly given novel social, ecological, and climatic conditions. To address this question, we first provide a framework for assessing changes in landscape conditions and fire regimes. Using this framework, we then evaluate evidence of change in contemporary conditions relative to those maintained by active fire regimes, i.e., those uninterrupted by a century or more of human-induced fire exclusion. The cumulative results of more than a century of research document a persistent and substantial fire deficit and widespread alterations to

Manuscript received 17 November 2020; revised 4 March 2021; accepted 22 March 2021; final version received 8 July 2021. Corresponding Editor: David S. Schimel.

²⁷ E-mail: hokulea@uw.edu

ecological structures and functions. These changes are not necessarily apparent at all spatial scales or in all dimensions of fire regimes and forest and nonforest conditions. Nonetheless, loss of the once abundant influence of low- and moderate-severity fires suggests that even the least fire-prone ecosystems may be affected by alteration of the surrounding landscape and, consequently, ecosystem functions. Vegetation spatial patterns in fire-excluded forested landscapes no longer reflect the heterogeneity maintained by interacting fires of active fire regimes. Live and dead vegetation (surface and canopy fuels) is generally more abundant and continuous than before European colonization. As a result, current conditions are more vulnerable to the direct and indirect effects of seasonal and episodic increases in drought and fire, especially under a rapidly warming climate. Long-term fire exclusion and contemporaneous social-ecological influences continue to extensively modify seasonally dry forested landscapes. Management that realigns or adapts fire-excluded conditions to seasonal and episodic increases in drought and fire can moderate ecosystem transitions as forests and human communities adapt to changing climatic and disturbance regimes. As adaptation strategies are developed, evaluated, and implemented, objective scientific evaluation of ongoing research and monitoring can aid differentiation of warranted and unwarranted uncertainties.

Key words: climate adaptation; Climate Change and Western Wildfires; ecosystem management; fire exclusion; forested landscapes; frequent fire; high-severity fire; landscape restoration; multi-dimensional fire regimes; multi-scale spatial patterns; reference conditions; wildfire adaptation.

INTRODUCTION

Social and ecological impacts of large and intense wildfires present enormous challenges to land and resource managers of western North America (Franklin and Agee 2003, North et al. 2015, Moreira et al. 2020, Hessburg et al. 2021). In the near term, wildfire frequency, area burned, and area burned at high severity will likely continue to increase as the climate warms; however, despite recent climatically driven increases in area burned, fire deficits in seasonally dry forests remain high (reviewed by Hessburg et al. 2021). After more than a century of fire exclusion (Fig. 1), increased density, abundance, and continuity of live and dead vegetation interact with increased seasonal warming and drying to drive wildfire severity (Miller et al. 2009b, Steel et al. 2015, Parks et al. 2018, Parks and Abatzoglou 2020). While modern wildfire management suppresses most fire starts, those that exceed suppression capacity account for the majority of burned area, often during the most extreme fire weather (North et al. 2015, Moreira et al. 2020). A paradigm shift that recognizes wildfire and extreme fire weather as inevitable and characteristic of seasonally dry forested ecosystems may better foster fire- and climate-adapted forests and human communities (Moreira et al. 2020).

Some restoration of low- and moderate-severity fire is occurring (Parks et al. 2014, Stevens-Rumann et al. 2016, Walker et al. 2018a, Brown et al. 2019, Kane et al. 2019, Mueller et al. 2020). However, as described above, current live and dead fuel loads and management emphases diminish the likelihood of recapturing the once extensive influence of low- and moderate-severity fires. Departures from the successional patterns that resulted from and supported active fire regimes (*i.e.*, those uninterrupted by more than a century of human-induced fire exclusion) have left many forests vulnerable to the direct and indirect effects of seasonal and episodic increases in drought and fire, especially under a warming

climate (Allen et al. 2002, Noss et al. 2006, Daniels et al. 2011, Chavardès et al. 2018, Keane et al. 2018, Stephens et al. 2018a, Bryant et al. 2019).

Fire regime changes also influence other pattern-process interactions and ecosystem functions, including primary productivity relations, carbon and nutrient cycling, evapotranspiration and distributed hydrology, and the movement and persistence of organisms (Turner 1989, Bowman et al. 2009). Thus, implementation of scientifically credible adaptation strategies can benefit numerous social values, including quantity and quality of water supply, stability of carbon stores, and air quality (Stephens et al. 2020) as well as Indigenous fire stewardship and food security (Lake and Long 2014, Norgaard 2014, David et al. 2018, Sowerwine et al. 2019).

Proactive management informed by historical and contemporary forest and fire ecology can strengthen resistance to disturbance and better align forest ecosystems with rapidly changing climatic and disturbance regimes (reviewed by Hessburg et al. 2021, Prichard et al. 2021). Reducing the abundance and connectivity of fuels that accumulated over more than a century of fire exclusion can moderate ecosystem transitions and provide numerous ecological and socioeconomic benefits (reviewed by Prichard et al. 2021). Indigenous fire stewardship practices can inform active management that achieves shared values to benefit tribes, local communities, and the broader society when tribes contribute to leadership and management of collaborative restoration partnerships (Lake et al. 2018, Long and Lake 2018, Long et al. 2020).

Implementing adaptation strategies at scales sufficient to alter contemporary disturbance regimes and recover other ecosystem functions associated with widespread low- and moderate-severity fires involves significantly increasing active management of forested landscapes (Spies et al. 2006, North et al. 2015, Stephens et al. 2016, Barros et al. 2017). Uncertainty, trade-offs, and risks are inevitable components of both action and

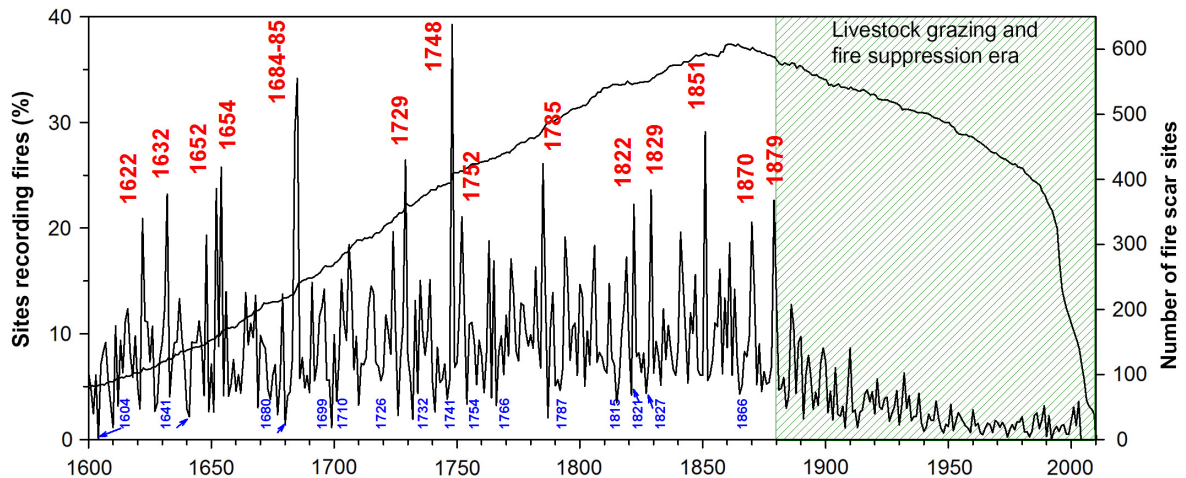


FIG. 1. Across western North America, fire frequency decreased substantially following expansion of colonization by Europeans, intensive livestock grazing, decimation of Indigenous populations and suppression of Indigenous burning in the late 19th century. The combined record of fire occurrence from more than 800 forest and woodland sites, the largest network of tree-ring-based fire-scar chronologies in the world, illustrates this regionwide decrease in fire frequency. Reprinted from Swetnam et al. (2016) with the author's permission.

inaction, whether proactive or reactive; ongoing research, multi-party monitoring, and adaptive management seek to address these components and build trust in proactive management (reviewed by Hessburg et al. 2021, Prichard et al. 2021). While integral to the development of knowledge, dissent in the scientific literature can contribute to conflict, confusion, and lack of consensus in stakeholders, e.g., environmental and conservation organizations and the general public (Maier and Abrams 2018). When fostered by incomplete assessment of the best available science (Esch et al. 2018), this lack of consensus may unnecessarily delay development and implementation of constructive new solutions and policies (reviewed by Hessburg et al. 2021).

To aid those engaged in designing, evaluating, and implementing science-based adaptation options, we evaluate lingering uncertainties about the high-severity component of historical and contemporary fire regimes (e.g., see Moritz et al. 2018). We first provide a framework for objectively assessing change in the structure, composition, and fire regimes of seasonally dry, fire-excluded forested landscapes. We then review key aspects of more than a century of research and observations of changes in forest conditions and fire regimes and the influence of those changes on contemporary processes and functions.

We contrast the evidence of change with evidence suggesting that management that reduces forest density to mitigate high-severity disturbance lacks sound ecological support. Over the past two decades, the ecological and policy implications of these publications (e.g., Baker and Ehle 2001, Williams and Baker 2012, DellaSala and Hanson 2019) have garnered substantial attention and fostered confusion about the best available science. To aid evaluation of the relative merit of this body of evidence and counter-evidence to contemporary

management, we also synthesize independent, peer-reviewed evaluations of methodologies used in the counter-evidence publications.

FRAMEWORK FOR EVALUATING CHANGE

Terms of reference

Forest types.—We focus on temperate forests of interior western North America (Fig. 2). This biogeoclimatically diverse region supports a wide range of forest types composed of broadleaf and coniferous species. Dominant species on the dry end of the gradient include ponderosa and Jeffrey pine (*Pinus ponderosa* and *P. jeffreyi*) and some oak species (*Quercus* spp.). As moisture increases or fire frequency decreases, species with higher shade tolerance and lower drought and fire tolerance increasingly dominate; these include Douglas-fir (*Pseudotsuga menziesii*); western larch (*Larix occidentalis*); sugar, western white, and southwestern white pine (*Pinus lambertiana*, *P. monticola*, and *P. strobiformis*); incense-cedar (*Calocedrus decurrens*); and grand and white fir (*Abies grandis* and *A. concolor*). As mean annual temperatures decrease with elevation or cold air drainage, forests are increasingly dominated by lodgepole pine (*Pinus contorta*); aspen (*Populus tremuloides*); red, silver, and subalpine fir (*Abies magnifica*, *A. amabilis*, and *A. lasiocarpa*); mountain hemlock (*Tsuga mertensiana*); Engelmann spruce (*Picea engelmannii*); or whitebark pine (*Pinus albicaulis*).

Using Landfire (Rollins 2009) Biophysical Settings, we classify these forest types as either cold, moist, or dry (Fig. 2, Appendix S1). We exclude rainforests, coastal forests, and Douglas-fir–western hemlock (*Tsuga heterophylla*) forests of the Coast Ranges and the west slope of the Cascade Mountain Range. These mesic and coastal

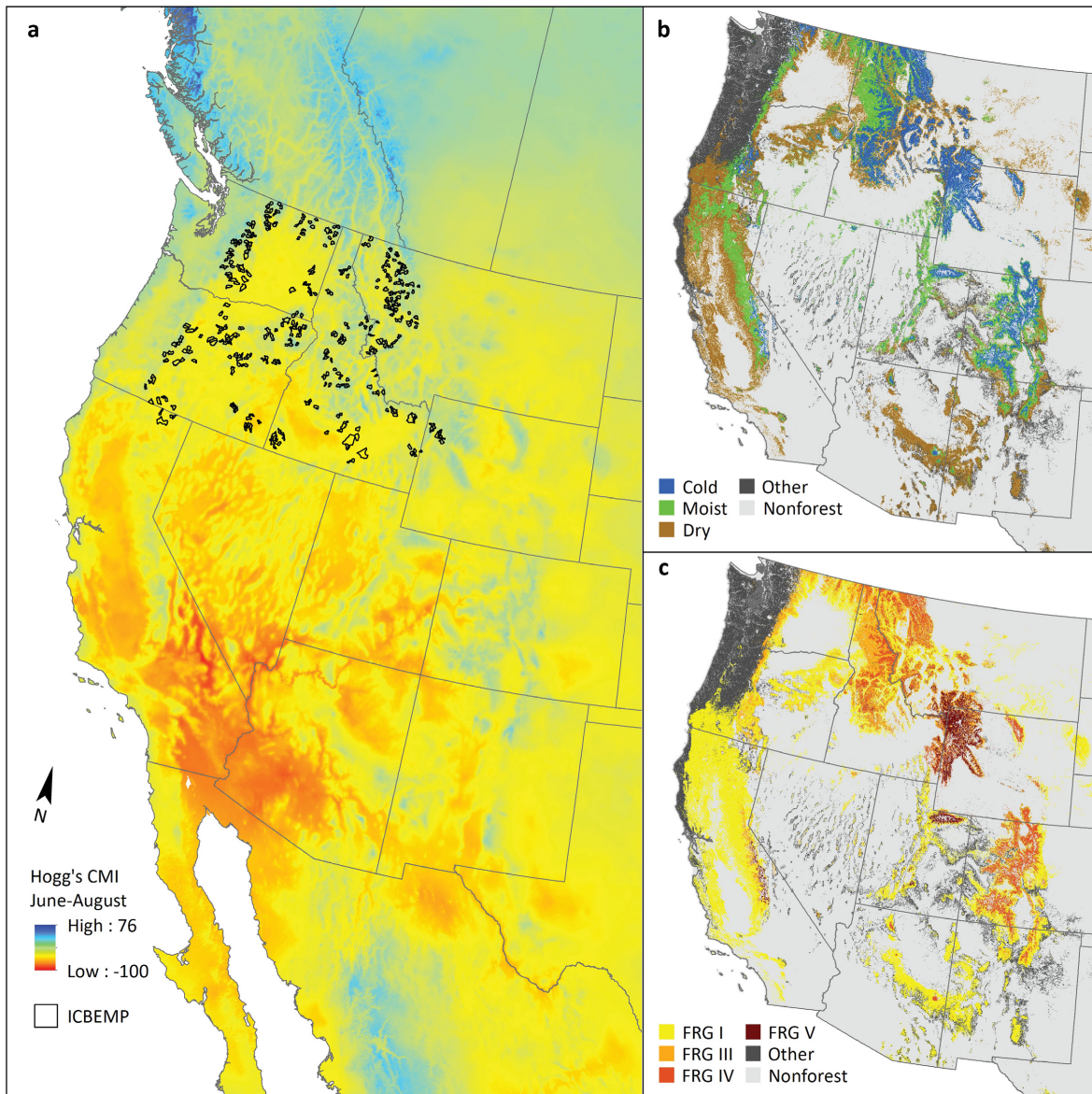


FIG. 2. (a) Summer available moisture and Interior Columbia Basin Ecosystem Management Project (ICBEMP) sampled area, (b) cold, moist, and dry forest types, and (c) fire regime group (FRG) classes. FRG classes reflect strong regional variation in biogeoclimatic conditions between northern and southern North America generally and between the Rocky Mountain ecoregions and those dominated by lower elevations. FRG I, fire return interval ≤ 35 yr, low and mixed severity; FRG III, fire return interval 35–200 yr, low and mixed severity; FRG IV, fire return interval 35–200 yr, replacement or high-severity; FRG V, fire return interval > 200 yr, any severity. Portions of the study area that extend into Mexico and Canada are not shown in b and c because Landfire data are not available for these regions. Data sources are (a) Hogg's Climate Moisture Index (Hogg 1997) from ClimateWNA (Hamann et al. 2013, climatewna.com); (b,c) Landfire (Rollins 2009, landfire.gov).

forests are typically associated with infrequent high-severity fire; however, a growing body of research suggests that low- to moderate-severity fire also likely affected their resistance and resilience (Daniels and Gray 2006), particularly in drier portions of their range (Spies et al. 2018b) and where Indigenous people commonly burned the forest (Pellatt and Gedalof 2014, Hoffman et al. 2017, 2019). Resilience is the capacity of an

ecosystem to recover its essential characteristics (including taxonomic composition, structure, ecosystem function, and process rates) following a disturbance, whereas resistance is the property of an ecosystem to remain essentially unchanged when disturbed (Grimm and Wissel 1997). Additionally, forest types dominated by Douglas-fir, western hemlock, and western redcedar (*Thuja occidentalis*) do occur in the interior east of the

Cascade crest, often mixed with the mesic or cold forest species listed above.

Reference conditions.—The concept of “departure” necessitates knowledge of past conditions and their variability, often referred to as “reference conditions” or the historical or natural “range of variation” (Morgan et al. 1994, Hessburg et al. 1999b, Swetnam et al. 1999, Keane et al. 2009). Comparison of contemporary conditions with reference conditions provides insight into the magnitude, rate, and direction of change (Higgs et al. 2014). Timing of fire exclusion (Fig. 1) varied widely, but commonly accompanied disruption of Indigenous burning and expansion of unregulated grazing of livestock by European settlers, often many decades to more than a century prior to mechanized fire suppression, logging, and land development (Marlon et al. 2012, Swetnam et al. 2016).

Reference baselines are commonly constrained to two to four centuries prior to widespread colonization by Europeans (ca. 1850). Climate and potential vegetation patterns in this period were broadly similar to those of the early 20th century, and data sources with high temporal resolution, e.g., tree-rings and fire scars, can be used to reconstruct environmental conditions for this period (Morgan et al. 1994, Falk et al. 2011). Palaeoecological and archaeological evidence provide insight into the influence of climate variation (Betancourt et al. 1990, Whitlock and Bartlein 1997, Beatty and Taylor 2009, Marlon et al. 2012, Swetnam et al. 2016, Bigio et al. 2017) and Indigenous resource and fire use (Kaye and Swetnam 1999, Klimaszewski-Patterson and Mensing 2016, Roos et al. 2021) as drivers of change over longer time frames. Areas with relatively intact forest conditions or fire regimes (i.e., active fire regimes) provide insight into how historical forests and landscapes might have operated under contemporary climate and disturbance regimes (Stephens and Fulé 2005, Collins et al. 2009). Evaluation of landscape-level forest structure and composition with high spatial resolution, however, relies more heavily on conditions that existed in the early to mid-20th century, the timeframe of the earliest available aerial and oblique photos (Hessburg et al. 2000). Since no single approach addresses all relevant scales of observation, multiple lines of independent corroborating evidence are needed to quantify spatial and temporal variation in reference conditions.

Multi-scale, multi-proxy records increase inference space

While individual methods are particularly well suited for evaluating aspects of forest conditions and disturbance regimes at specific temporal and spatial scales (Wiens et al. 2012, Morgan et al. 2014, Yocom Kent 2014), multi-proxy studies can compensate for limitations in each data source (Swetnam et al. 1999, Daniels et al. 2017). Incorporating several lines of evidence (e.g., multi-scale and multi-proxy studies, meta-analyses, or simulation models) can increase confidence in results,

broaden inference space, clarify the existence and extent of change, and provide insight into change mechanisms (Whitlock et al. 2004, Taylor et al. 2016).

Multi-proxy, multi-scale research also reveals that, when considered in isolation, lack of evidence of change at any single scale of observation or in any single sampled attribute may mislead interpretation of the degree of ecosystem departures. For example, studies conducted at plot or patch-scales may fail to capture variability of vegetation conditions and fire severity across larger landscapes (Marcoux et al. 2015). Thus, while change in one or more aspect of a fire regime, e.g., percentage of land affected by high-severity fire, may have occurred, it may not be evident at all scales of observation. Similarly, while the percentage of the land area affected by high-severity fire may not have changed, spatial patterns of high-severity fire may have (Collins et al. 2017). Reliance on any one methodology or scale of observation is insufficient to understanding the scope of changes given the multi-scale complexities of climate–vegetation–disturbance feedbacks and their influence on patterns and processes (Falk et al. 2019).

Forest conditions exist at multiple spatial scales.—Spatial patterns of vegetation reflect strong linkages between biogeoclimatic conditions, disturbance and succession processes, and plant physiology that vary over space and time. Here, we consider the dominant factors operating at three spatial scales (Fig. 3): broad (>10,000 ha), meso (100 to 10,000 ha), and fine (<100 ha). Each scale of observation is important to understanding vegetation change, subsequent interactions with disturbance processes (i.e., fire, drought, insects, and pathogens), and potential future conditions (Keane et al. 2009, Wiens et al. 2012, Hessburg et al. 2019). To assess whether forest vegetation conditions are trending away from a given baseline, it is essential to consider changes at several spatial scales and in cross-scale linkages (sensu Wu and Loucks 1995).

At broad scales, forests exist within a patchwork of nonforest physiognomic types, including herbland/grassland, shrubland, woodland or savannah, and bare ground. Physiognomic types generally reflect the range of temperature, precipitation, solar radiation, soil, and geomorphic conditions to which they are best adapted. However, overlapping disturbances occurring in rapid succession, e.g., frequent fire, can override site potential, leading to relatively stationary patches of nonforest on forest-capable sites (Coppoletta et al. 2016, Prichard et al. 2017, Coop et al. 2020, McCord et al. 2020).

At meso-scales, heterogeneous patterns of forest and nonforest structures and compositions reflect the history of interacting and overlapping disturbances combined with succession and stand dynamics processes (Perry et al. 2011, Hessburg et al. 2016, 2019) as well as biogeoclimatic conditions, e.g., soil types (Winthers et al. 2005). The result is a mosaic of forest successional patches that reside within the larger physiognomic



FIG. 3. At broad ($>10,000$ ha), meso (100 to 10,000 ha), and fine (<100 ha) scales, spatial patterns of vegetation are influenced by biogeoclimatic conditions, disturbance and succession processes, and plant physiology. Heterogeneity is evident at each spatial scale and can influence the spread of disturbances (e.g., fire) and the movement of resources (e.g., water and sediment) as well as species. Area shown is west of Fort Collins, Colorado, USA.

patchwork. As with physiognomic types, frequent disturbance can override site potential and inhibit succession to closed-canopy forests or dominance by fire-intolerant species (Agee 1996, 1998, Hessburg et al. 2005, North et al. 2009, Stine et al. 2014).

At fine scales, physiological and anatomical traits of tree, shrub, and herb species and interactions with soils influence community structure and composition, canopy and gap dynamics, variation in fuel load, and fire severity (North et al. 2002, Meyer et al. 2007, Reynolds et al. 2013, Strahan et al. 2016, Laughlin et al. 2017, Stevens et al. 2020). These include traits that determine interactions with fire for individual trees (e.g., bark thickness and needle shape) and populations (e.g., reproduction and germination strategies). Overlapping disturbances also modify the imprint of previous events at fine spatial scales (Hansen et al. 1991, Franklin and Van Pelt 2004). Thus, in forests that burned frequently, variation in successional stages typically occurred at very fine spatial scales (<1 ha) resulting in a mosaic of individual trees, clumps of trees, and openings, rather than patches or stands (Franklin and Van Pelt 2004, Kaufmann et al. 2007, Larson and Churchill 2012, Churchill et al. 2013,

2017, Lydersen et al. 2013, Fry et al. 2014, Ng et al. 2020).

Fire regimes are multi-dimensional.—Multiple dimensions of individual fires (Hessburg et al. 2021: Table 1) interacting in a relatively persistent pattern over long periods of time collectively comprise a holistic notion of a fire regime (Agee 1996, Sugihara et al. 2018). Fire frequency and severity are major drivers of ecological and evolutionary response (Keeley 2012). However, limiting definitions of fire regimes to the frequency and severity that dominate a given area (e.g., frequent low-severity or infrequent high-severity) oversimplifies ecological understanding of wildfire regimes, and impedes detection of departures and projection of future conditions (Brown et al. 2008, Collins et al. 2017). Multiple other aspects of fire regimes (e.g., area burned, seasonality, spatial complexity) must also be considered to understand the natural variability of active fire regimes and evaluate departures (Daniels et al. 2017).

Fire severity is often measured as the percentage mortality of tree biomass (e.g., tree basal area or canopy cover) after each fire event. Conventional definitions of

TABLE 1. A sample of the regional syntheses and meta-analyses providing multi-proxy, multi-scale assessments of historical and contemporary forest and fire ecology.

Region and description	Citations
Western North America	
More than 800 fire-scar studies documented abrupt decline in fire frequency in the late 19th century and provide ecological insights into variation in top-down and bottom-up drivers of historical fire regimes.	Falk et al. (2011), Swetnam et al. (2016), Daniels et al. (2017)
Substantial departures in contemporary fire regimes and live and dead vegetation patterns across dry, moist, and cold forested landscapes increase vulnerability of forest ecosystems to drought and fire.	Hessburg et al. (2019)
Canada	
Development and paradigm shift in wildland fire research over past 50 yr.	Coogan et al. (2020)
Climate change impacts on fire regimes and impacts of contemporary fire regimes on social and ecological systems.	Coogan et al. (2019)
Western United States	
Variation in fire activity over the past 3,000 yr.	Marlon et al. (2012)
Fire deficit relative to area expected to burn without fire suppression given contemporary climate 1984–2012; area burned and fire severity increased 1985–2017.	Parks et al. (2015), Parks and Abatzoglou (2020)
Influence of traditional tribal perspectives on ecosystem restoration.	Long et al. (2020), Roos et al. (2021)
Correspondence between conifer species traits conferring fire resistance and independent assessments of historical fire regimes.	Stevens et al. (2020)
Human influence on contemporary fire regimes.	Balch et al. (2017)
Evaluation of conifer regeneration up to 69 yr post fire.	Stevens-Rumann and Morgan (2019)
Colorado and Wyoming Front Ranges	
Historical and contemporary ecology of ponderosa pine and dry mixed-conifer forests.	Addington et al. (2018)
Fire regimes in ponderosa pine forests.	McKinney (2019)
Historical and contemporary ecology of selected national forests.	Dillon et al. (2005), Meyer et al. (2005a, b), Veblen and Donnegan (2005)
Southwestern United States	
Historical and contemporary ecology of ponderosa pine and dry mixed-conifer forests and forest–grassland landscape complexes.	Reynolds et al. (2013), Dewar et al. (2021)
Sierra Nevada bioregion of California	
Historical and contemporary ecology of ponderosa and Jeffrey pine and mixed-conifer forests.	SNEP (1996), North et al. (2009, 2016), Safford and Stevens (2017), van Wagtendonk et al. (2018a)
Historical and contemporary ecology of red fir and subalpine forest types.	Meyer and North (2019), Coppoletta et al. (2021)
Northeastern California plateaus	
Historical and contemporary ecology of dry conifer forests.	Riegel et al. (2018), Dumroese and Moser (2020)
Northern California	
Historical and contemporary ecology of forested landscapes.	Skinner et al. (2018), Stephens et al. (2018b, 2019), Bohlman et al. (2021)
Pacific Northwest	
Departures in contemporary fire regimes.	Reilly et al. (2017), Metlen et al. (2018), Haugo et al. (2019)
Historical and contemporary ecology of ponderosa pine forests in Oregon and Washington; vulnerability of contemporary forests and expanding wildland urban interface to increasing drought and fire severity.	Merschel et al. (2021)
Historical and contemporary ecology of moist mixed conifer forests in seasonally dry landscapes in Oregon, Washington, and Northern California.	Perry et al. (2011), Spies et al. (2018b, 2019), Stine et al. (2014), Hessburg et al. (2016)
Columbia River Basin in northwestern United States	
The Interior Columbia Basin Ecosystem Management Project (ICBEMP) used standard aerial photogrammetric methods, repeat photo-interpretation, and a quantitatively representative sampling scheme to build a data set of wall-to-wall, meso-scale landscape reconstructions for 337 watersheds, mean area 9,500 ha. ICBEMP also incorporated broad-scale succession and disturbance simulation modeling calibrated with the meso-scale results.	Lehmkuhl et al. (1994), Huff et al. (1995), Hann et al. (1997), Hessburg et al. (1999, 2000, 2005), Wisdom (2000), Raphael et al. (2001), Hessburg and Agee (2003)

fire regimes (e.g., Agee 1996) generally reflect the cumulative abundance of low- (<20%), moderate- (20–70%), and high- (>70%) severity fire in individual fire events at broad temporal and spatial scales. However, each of these severity classes (as well as other commonly used terms like mixed or variable severity), encompass a wide range of potential ecological outcomes, i.e., the difference between outcomes at either end of the severity gradient in each of these classes can be substantive. Additionally, these severity classes do not consider spatial patterns of fire severity; without them, however, assessment of the ecological impacts of fire events is incomplete (Miller and Quayle 2015, Collins et al. 2017, Shive et al. 2018, Walker et al. 2019).

EVALUATING EVIDENCE OF CHANGE

The cumulative results of more than a century of research and observation from numerous disciplines document regional and subregional variation in historical and contemporary forest and fire ecology (Table 1). Here, we focus on key elements from this vast body of work to illustrate the magnitude of change in forested landscapes. Comprehensive reviews of departures within and among forest types and regions are available in existing syntheses, meta-analyses, and regionwide studies (Table 1).

We begin with a landscape evaluation of change in vegetation spatial patterns and fire regimes across 61 million ha (Hann et al. 1997, 1998) that encompass the highest concentration of cold and moist forest in the interior western United States (Fig. 2). Landscape assessments that evaluate a broad variety of attributes of fire regimes and forest conditions can reduce the risk of oversimplifying or misrepresenting spatiotemporal variability in fire severity and forest conditions. The substantial departures documented in this assessment underscore those documented in numerous other studies both within this region and in predominantly warmer, drier ecoregions (Table 1). We also consider changes in extent of nonforest, which can reflect significant changes in disturbance processes over space and time (Perry et al. 2011, Hessburg et al. 2016, 2019, Coop et al. 2020).

Next, we review evaluations of departures from active fire regimes. As physical evidence of fire occurrence, fire scar records remain a primary means of exploring historical fire ecology. Networks of fire-scar studies emerging from the cumulative results of a century of tree-ring studies enable insights into landscape and climate controls on fire (Falk et al. 2011). Along with novel research designs for evaluating dendrochronological records of fire history (Farris et al. 2010, Tepley and Veblen 2015, Greene and Daniels 2017, Naficy 2017), landscape-level assessments and simulation models encompassing multiple forest types can address concerns that sampling bias of fire-scar studies favors detection of low-severity fire regimes (e.g., see arguments in Hessburg et al. 2007).

Throughout, we reference results of landscape succession and disturbance models, which provide an important means of extrapolating geographically limited historical data across large areas, over long time periods, under diverse climatic conditions, and over a wide range of fuel characteristics (Bradstock et al. 1998, Keane et al. 2004, Barros et al. 2017). Simulation modeling allows ecologists to integrate what is currently known to evaluate hypotheses that enhance our collective understanding of fire and its distributed effects (Spies et al. 2017, Barros et al. 2018, Keane 2019). Landscape succession and disturbance models combine fire history and biotic information about forest species as parameters (Keane 2019, Loehman et al. 2020) to inform simulations of past, present, and future landscape-wildfire dynamics (Keane et al. 2004, He et al. 2008). Perhaps most importantly, these models can inform and evaluate management scenarios; they can be used to simulate multiple future climate, management, and exotic species scenarios that can then be compared with simulated historical conditions under a consistent framework to evaluate risks, trade-offs, and uncertainties (Keane 2019).

Forest and nonforest conditions are significantly departed

The Interior Columbia Basin Ecosystem Management Project (hereafter, ICBEMP) documented widespread forest expansion and densification between early (primarily 1930s–1950s) and late (primarily 1990s) 20th century (Hann et al. 1997, 1998, Hessburg et al. 2000, 2005). The ICBEMP encompassed the range of interior forest environments distributed across Washington, Idaho, Montana, Oregon, and northern California. Using repeat photo-interpretation, standard aerial photogrammetric methods, and a quantitatively representative sample (337 watersheds, mean area ~10,000 ha), the ICBEMP meso-scale assessment (Hessburg et al. 1999a, 2000, 2005, Hessburg and Agee 2003) evaluated change in forest landscape patterns across the 20th century, and the effects of those changes on fuel and fire regime conditions. The results of this meso-scale assessment were used to calibrate broadscale simulations of changes across the entire ICBEMP area (Keane 1996, Hann et al. 1997).

Both assessments (repeat photo-interpretation and simulation modeling) found that high-severity disturbances at lower frequencies and low- and moderate-severity disturbances at higher frequencies collectively reduced total forested area and perpetuated relatively widespread herbland/grassland, shrubland, woodland, and, often, open-canopy forest, which tended to support high fire spread rates, low flame lengths, and low fireline intensities under most fire weather conditions (Keane 1996, Hann et al. 1997, Hessburg et al. 2016, 2019). By the late 20th century, dry, moist, and cold forest landscapes had become more densely forested, resulting in homogenization of previously diverse forest and nonforest successional conditions, elevated

vulnerability to contagious disturbances, and loss of key habitats (Wisdom 2000, Raphael et al. 2001). These changes were apparent despite extensive logging in the mid to late 20th century and impacts of fire exclusion evident by the 1930s in some areas. By the late 20th century, the area likely to support fire regimes of low-severity had been reduced by 53%, mixed-severity remained roughly the same (although it shifted to sites that supported low-severity fire regimes prior to fire exclusion), and high-severity had nearly doubled (Fig. 4, Keane 1996).

In studies spanning western North America, the extensive influence of frequent low- and moderate-severity fires in maintaining open-canopy dry forests and woodlands has been repeatedly documented (Table 1). Although not as prevalent, departures associated with the loss of low- to moderate-severity fire are also documented in moist and cold forests. Examples include lodgepole pine in the foothills of the Rocky Mountains in Alberta (Amoroso et al. 2011) and in cold-air drainages in the central Oregon Pumice Plateau ecoregion (Heyerdahl et al. 2014, Hagmann et al. 2019); mixed-conifer and subalpine forests in the Canadian Cordillera (Marcoux et al. 2015, Chavardès and Daniels 2016, Rogeau et al. 2016) and southwestern United States (Margolis and Malevich 2016, Johnson and Margolis 2019); red fir forests in California's Sierra Nevada ecoregion (Meyer et al. 2019), and the ICBEMP study area (Fig. 2) described above. As in the ICBEMP area (Fig. 4), increased surface fuel loads and canopy connectivity in mid-elevation forests likely influence the frequency of crown fire spread into more mesic high-elevation forests in the southwest as well (O'Connor et al. 2014a).

Oblique and aerial imagery from the early 20th century document abundant nonforest cover in dry, moist, and cold forest landscapes. The William Osborne survey of Oregon and Washington in the 1930-1940s (Fig. 5) encompasses nearly 1,000 panoramas (120°) taken on ridgetops and at fire lookouts, and the Geological Survey of Canada systematically collected approximately 120,000 high-resolution oblique images from 1880 to 1950 across the mountains of western Canada (Higgs et al. 2009; photos *available online*).²⁸ As in the ICBEMP assessment, repeat photography from other regions shows substantial landscape change through expansion and densification of forest and consequent reduction in open-canopy forest and nonforest. Examples include high-elevation ecosystems in the Pecos Wilderness, New Mexico (deBuys and Allen 2015); pine and mixed-conifer forest over 100,000 ha in northern Sierra Nevada, California (Lydersen and Collins 2018); ponderosa pine in the Black Hills, South Dakota (Grafe and Horsted 2002) and Colorado Front Range (Fig. 6; Veblen and Lorenz 1991); and widespread change across elevations in the Canadian Rocky

Mountains (Rhemtulla et al. 2011, Fortin et al. 2019, Stockdale et al. 2019a, Trant et al. 2020).

From broad- to fine-scales (Fig. 3), the nonforest patchwork influences landscape resilience and fire delivery to adjacent forest types. Flashy fuels, such as graminoids in grasslands, open-canopy forests, and sparse woodlands, may readily spread fire to adjacent cover types (Gartner et al. 2012, Conner et al. 2018, Prichard et al. 2018). Moreover, flashy fuels are typically the first to recover moisture content in the hours after sunset, making them important to restricting the diurnal flow of some wildfires (Simpson et al. 2016). Fine-scale treeless openings, highly variable in shape and abundance (Figs. 5, 6), provided numerous functions, including nutrient cycling and fostering biodiversity, in addition to influencing the delivery of fire to adjacent areas (North et al. 2005b, Larson and Churchill 2012, Churchill et al. 2017, Matonis and Binkley 2018, LeFevre et al. 2020). Changes to spatial patterns of landscape and forest structure (Figs. 5, 6) also influence aspects of the hydrologic cycle (e.g., evapotranspiration, soil water dynamics, snow interception, snow water equivalent, and snow melt timing), which can substantially reduce water available to downstream ecosystems (Boisramé et al. 2017b, 2019, Schneider et al. 2019, Singer et al. 2019, Ma et al. 2020, Rakhmatulina et al. 2021).

Multiple factors, including fire exclusion, have contributed to a reduction of nonforest cover and expansion of dry, moist, and cold closed-canopy forest since the early 19th century (Hessburg and Agee 2003, Chavardès et al. 2018, Eisenberg et al. 2019, Hessburg et al. 2019, Stockdale et al. 2019a). While the departures described above may not be evident in all sampled areas or at all spatial scales, the preponderance of evidence demonstrates that the landscape surrounding apparently unchanged ecosystems has very likely changed even if a particular patch has not. In other words, fuel loads and continuity may be higher than historical levels for a landscape although not necessarily for all patches in that landscape.

Fire regimes are significantly departed

One of the key findings to emerge from nearly every tree-ring reconstruction of fire history is a widespread reduction in fire frequency in the 20th century (Fig. 1) compared to preceding centuries (Falk et al. 2011, Marlon et al. 2012, Swetnam et al. 2016, Coogan et al. 2020). Paired tree-ring and sedimentary charcoal-based fire histories from the same locations show 20th-century decreases in fire occurrence that are unprecedented in recent millennia (Allen et al. 2008, Beaty and Taylor 2009, Swetnam et al. 2009).

Frequent fire reduces the intensities and severities of subsequent fires by maintaining tree densities and live and dead fuel loads at levels below those that local site productivity could readily support (Reynolds et al. 2013, Stine et al. 2014, Safford and Stevens 2017, Addington

²⁸ maps.tnc.org/osbornephotos/ and iamwho.com/cdv2/pages/byname.htm

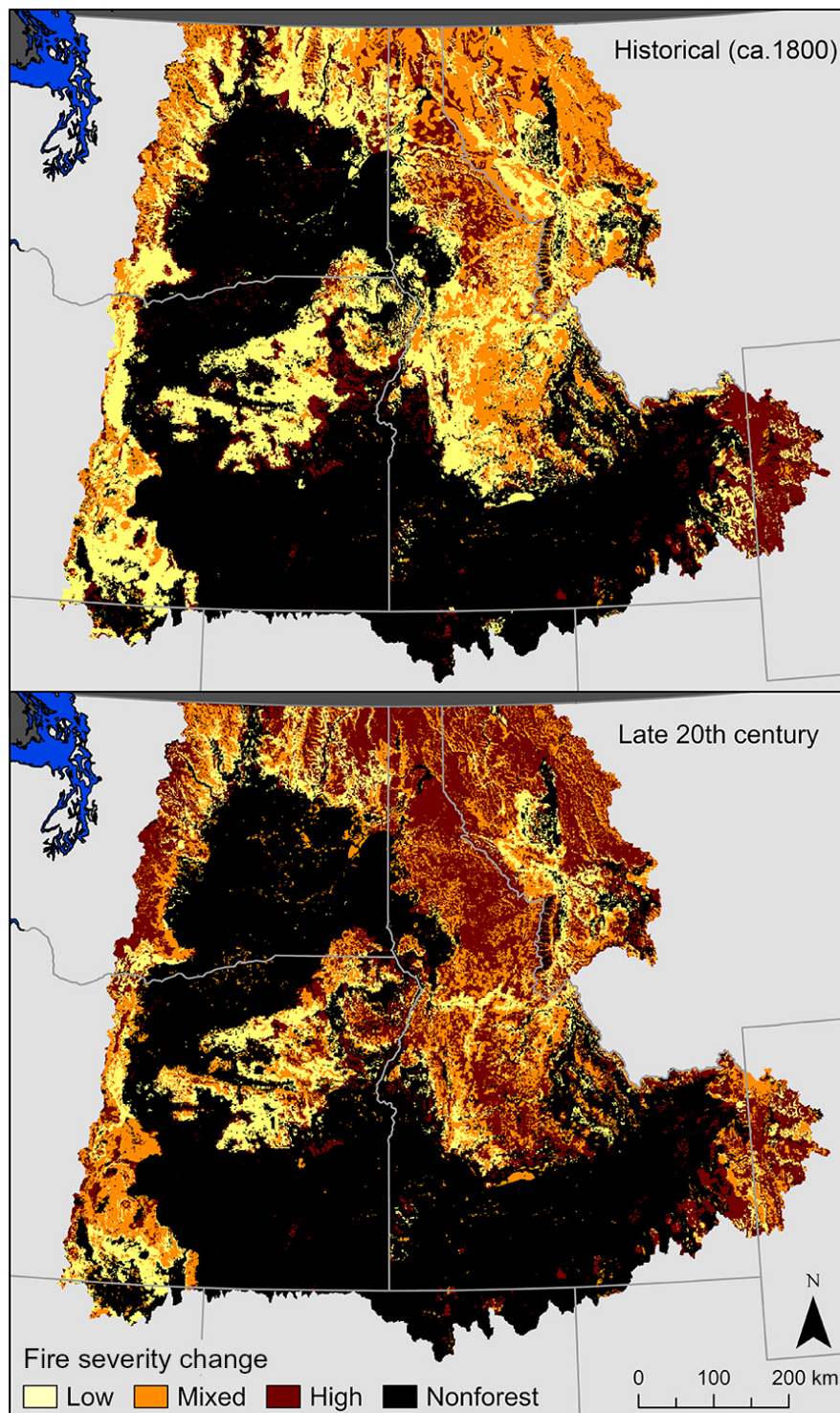


FIG. 4. Broad-scale (1-km² pixel) map of transitions from historical (ca. 1800) to late 20th century fire-severity classes in the Interior Columbia Basin. Adapted from Hessburg et al. (2005).

et al. 2018, Battaglia et al. 2018). Overlapping fires limited the spread of crown fire and other contagious processes (e.g., insect outbreaks and disease epidemics, Hessburg et al. 1994, 1999b) by reinforcing discontinuities

in canopy cover, species composition, tree size and age classes, and surface fuel abundance (Roccaforte et al. 2008, Collins et al. 2009, Fulé et al. 2012a, van Wageningen et al. 2018b). Absence of frequent fire provides

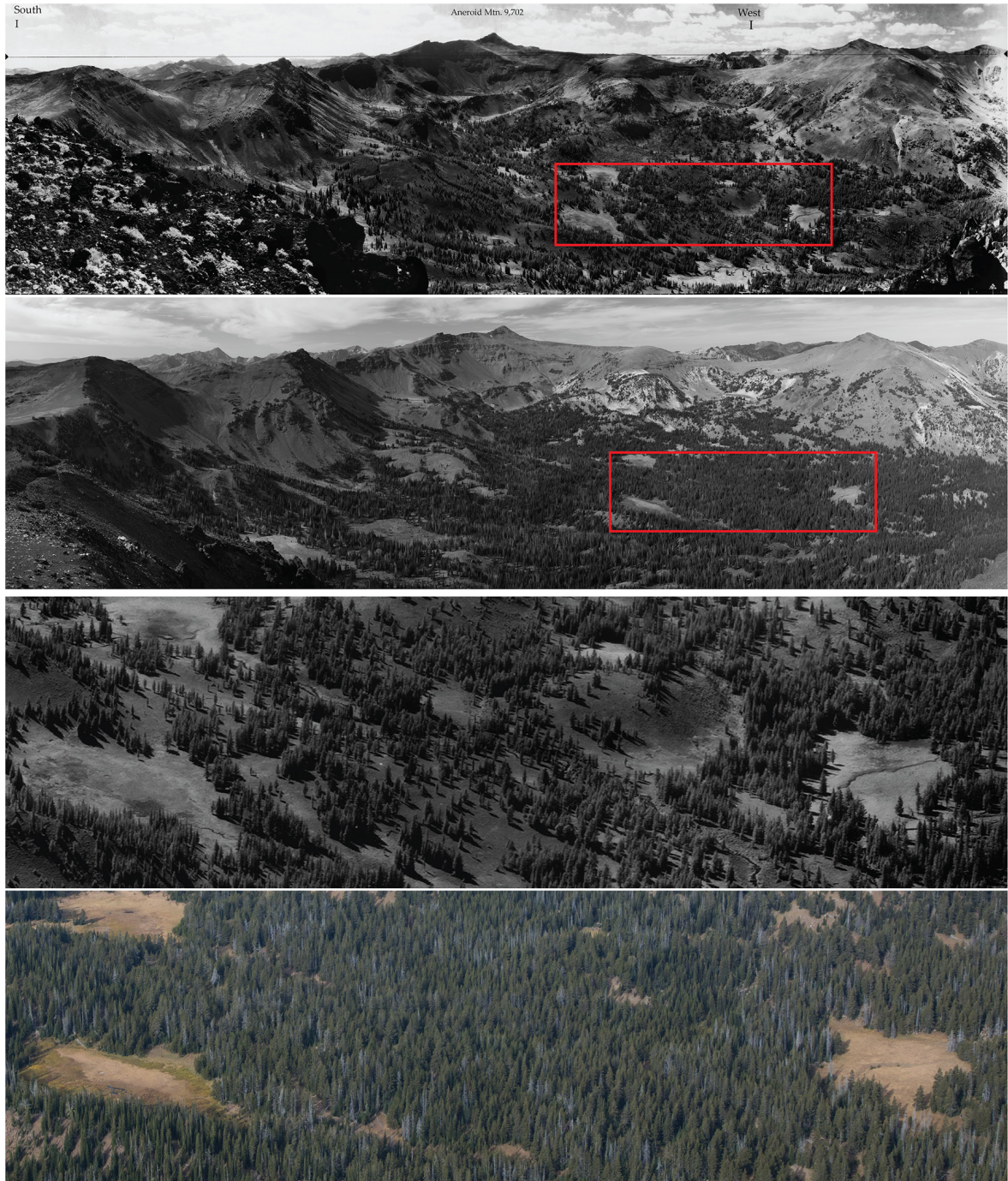


FIG. 5. Repeat photography from 1936 and 2018 demonstrates departure in spatial patterns of wet and dry meadows and cold forest successional conditions resulting from the densification and expansion of forest cover under the influence of fire exclusion, Eagle Cap Wilderness, Wallowa Mountains, Oregon. Bottom pair shows close-up of area outlined in red in the top pair. Top photo in each pair is a U.S. Forest Service 120-degree Osborne panorama dated 7 September 1936, National Archives and Records Administration, Seattle, Washington, USA. Bottom photo in each pair taken from 9,000 feet on 18 September 2018. Copyright 2018 John F. Marshall.

opportunities for abundant tree recruitment, particularly on more productive sites (Merschel et al. 2014, Johnston 2017) and during wet periods (Taylor 2000, Brown and Wu 2005, Brown 2006, Battaglia et al. 2018).

Simulations of wildfire and vegetation dynamics show that when fire is excluded from frequent-fire ecosystems, tree density increases; the proportion of fire-intolerant species increases; surface, ladder, and canopy fuels

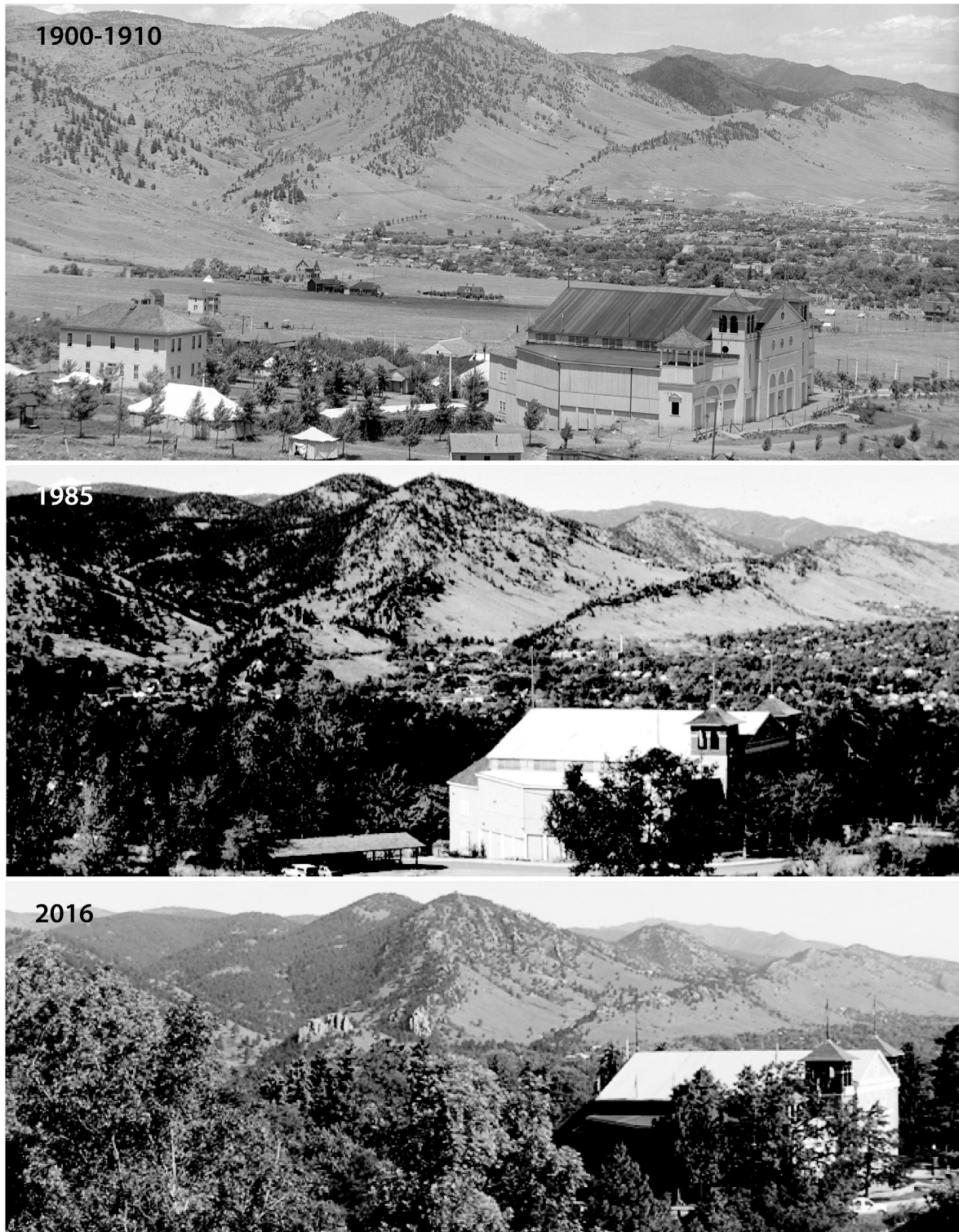


FIG. 6. Repeat photography from 1900 to 1910, 1985, and 2016 illustrates densification and expansion of ponderosa pine cover under fire exclusion in hills west of Boulder, Colorado (Veblen and Lorenz 1991). Photo credits: 1900–1910, Louis C. McClure Courtesy Denver Public Library, Western History Collection, MCC-306; 1985, T. T. Veblen and D. C. Lorenz; 2016, T. T. Veblen.

accumulate; and water available for forest growth declines (Wallin et al. 1996, Wimberly and Kennedy 2008, Diggins et al. 2010). These conditions can foster large and intense fires with effects that are not often observed in simulated historical ranges (Hann et al. 1997, Keane et al. 2009, 2018, Holsinger et al. 2014, Loehman et al. 2017, Haugo et al. 2019, Stockdale et al. 2019b). Correspondingly, forest succession and disturbance modeling projects lighter fuel loads and fewer high-intensity fires when departures from active fire regimes are low (King et al. 2008, Riggs et al. 2015).

Stands and landscapes with relatively intact or restored fire regimes (i.e., active fire regimes) provide insight into how historical forests and landscapes operate under contemporary climate and disturbance regimes (Cortés Montaña et al. 2012, Yocom Kent et al. 2017, Arizpe et al. 2021, Dewar et al. 2021, Murphy et al. 2021; and sources in Prichard et al. 2021: Table 2). Contemporary forests with relatively intact fire regimes experienced the climate variations of the 19th and 20th centuries, but do not exhibit changes in structure and composition comparable to fire-excluded forests (Stephens and Fulé 2005, Lydersen and North 2012, Pawlikowski et al. 2019). Similarly, forests with relatively intact fire regimes have not experienced the increased severity of disturbance events observed on comparable areas affected by fire exclusion (Rivera-Huerta et al. 2016, Murphy et al. 2021).

Broader impacts of fire regime departures

Modern wildfire suppression extinguishes essentially all fire starts except those that overwhelm fire suppression capacity and can only be extinguished when aided by a significant change in the weather (North et al. 2015, Moreira et al. 2020). Despite increasing suppression efforts, both area burned and area severely burned have increased as temperatures and widespread drought accelerated near the end of the 20th century (Westerling et al. 2006, Abatzoglou and Williams 2016, Parks and Abatzoglou 2020). Nonetheless, burned area in most forested ecosystems is still much lower than would be expected based on fire-climate relationships (Stephens et al. 2007, Fulé et al. 2012b, Marlon et al. 2012, Mallek et al. 2013, Parks et al. 2015, Taylor et al. 2016).

Contemporary fires burn in landscapes with greater forest density and connectivity, surface fuel accumulation, and proportion of small trees relative to larger, more fire-resistant trees, all of which contribute to more severe fires (Graham et al. 1999, 2004, Jain and Graham 2007). An eight-fold increase in annual area burned at high-severity occurred between 1985 and 2017 in western U.S. forests (Parks and Abatzoglou 2020), and fuels (i.e., live and dead vegetation) have been implicated as the primary driver of stand-replacing fire in most regions of the western United States (Steel et al. 2015, Parks et al. 2018). Departures from forest structures and compositions maintained by active fire regimes also contributed to

uncharacteristically high levels and patterns of mortality during recent severe droughts (Bentz et al. 2010, Fettig et al. 2013, 2019, Stephens et al. 2018a). During those same droughts, however, stands with lower live basal area or density experienced lower tree mortality rates than stands with higher basal area or density for a given moisture regime, especially on drier sites (Rivera-Huerta et al. 2016, Young et al. 2017, Restaino et al. 2019).

High-severity fire is an essential component of many forested landscapes, not only through the provision of unique snag and complex early seral habitats (Swanson et al. 2011), but also through its influence on numerous other ecosystem functions, including nutrient and hydrological cycles and the rate and abundance of debris flow and sediment deposition (Bisson et al. 2003). However, constraints imposed on the relative abundance and patch sizes of high-severity fire by active fire regimes in dry, moist, and cold forests are also critical to maintaining the diverse and unique ecosystem characteristics of seasonally dry forested landscapes (Fig. 4, Table 1). Given widespread reductions in nonforest in the 20th century, some conversion of forest to nonforest area may aid recovery of ecosystem functions associated with active fire regimes, as seen where wildland fire was restored after nearly a century of fire exclusion (Boisramé et al. 2017a). Additionally, some cover type conversions are inevitable as landscapes adjust to a warming climate, perhaps particularly in southwestern North America (Falk 2013, Loehman et al. 2018, Field et al. 2020).

Studies of contemporary fires demonstrate, however, that high-severity fire is overrepresented in forests historically characterized by frequent low- to moderate-severity fire regimes (Table 2). Increased frequency of high-severity fire in these forest types is a concern for many reasons, including the likelihood that areas burned at high severity often reburn at high severity (Thompson et al. 2007, Lydersen et al. 2017, Prichard et al. 2017, Collins et al. 2018, Coop et al. 2020, Povak et al. 2020) even after a century of fire exclusion and forest succession (Taylor et al. 2020). Spatial patterns of high-severity fire in these forests are also a key departure of contemporary fire regimes (Hessburg et al. 1999a, 2015, 2019, Fulé et al. 2014, Reilly et al. 2017, Stevens et al. 2017). Even in forest types historically dominated by infrequent high-severity fire, fire severity patterns have likely changed given the suppression of most fire starts and absence of fires spreading in from adjacent forest and nonforest (Fig. 4; Perry et al. 2011, O'Connor et al. 2014, Johnson and Margolis 2019).

In landscapes historically dominated by frequent low- and moderate-severity fires, increases in high-severity fire are further reducing the abundance of large and old fire- and drought-tolerant trees (Table 2). These once prevalent trees, are currently rare and “endangered” (Stephens et al. 2016, Miller and Safford 2017, Reilly et al. 2018). Large and old fire- and drought-tolerant trees were heavily logged in the 20th century (Hessburg and Agee 2003, Brown and Cook 2006, Naficy et al.

TABLE 2. High-severity fire effects in recent fires exceed the pre-fire exclusion range of variation in landscapes historically dominated by frequent low- and moderate-severity fires.

Citation	Key findings	Forest type	Methods	Study area
Mallek et al. (2013)	In lower and middle elevation forests, area burned at low- to moderate-severity fire is substantially lower than expected while severity in recent fires is much higher than estimated for conditions prior to fire exclusion. Fires of all severities are at a deficit in upper elevation forests.	Lower (oak woodlands to ponderosa and Jeffrey pine), middle (mixed conifer), and upper (red fir and subalpine forest) elevation forests.	Compared fire severity distributions in modern (1984–2009) fires based on relative delta normalized burn ratio (RdNBR) with pre-fire exclusion fires based on average of LANDFIRE Biophysical Settings (BPS) and Stephens et al. (2007).	Sierra Nevada and southern Cascade Ranges, California
O'Connor et al. (2014)	Conversion of more than 80% of landscape from frequent low- to mixed-severity fire regime to one of infrequent moderate- to high-severity fire. Current high fuel loads shift climate drivers of fire behavior: (1) extreme drought no longer necessary for fire spread to mesic forest types and (2) antecedent moist conditions no longer necessary for spreading fires.	Pine and dry mixed conifer	Compared fire size and severity distributions in modern (1996 and 2004, RdNBR) fires with size and severity of fires prior to 1880 reconstructed from a gridded tree-ring sampling network.	Pinaleno Mountains, southeastern Arizona
Harris and Taylor (2015)	Increases in tree density, basal area, and fuels due to fire exclusion since 1899 shifted fire regime from frequent low severity to mixed severity.	Mixed conifer	Compared fire severity in 2013 (RdNBR) with fire severity prior to 1899 reconstructed from documentary records, radial growth of tree rings, fire-scars, and tree-age structure.	2013 Rim Fire, Yosemite National Park, California
Yocom-Kent et al. (2015)	Largest (>1,000 ha) high-severity patches in modern (2000–2012) fires exceeded those reconstructed for 1,400 ha study area; however, cannot rule out stand-replacing fire prior to mid-1700s	Mixed conifer and aspen	Compared high-severity fire patch size in modern (2000–2012) fires reconstructed from ground-truthing of satellite imagery with historical fires reconstructed from fire-scar and tree-age data.	North Rim, Grand Canyon National Park, Arizona
Fornwalt et al. (2016)	Tree(s) >200 yr old present in 4% area after fire compared to 70% before fire.	Unlogged ponderosa and ponderosa–Douglas-fir	Compared 2013 aerial imagery to pre-fire age structure in randomly selected polygons.	2002 Hayman fire, Colorado
Rivera-Huerta et al. (2016)	Following 30 yr of fire suppression, increasing high-severity patch size; fires remain easy to suppress and predominantly low.	Jeffrey pine and mixed conifer	Quantified area burned at high-severity in fires from the onset of fire suppression (roughly 1984) to 2010. RdNBR threshold of 652 indicates $\geq 90\%$ reduction in basal area.	Baja California, Mexico
Bigio et al. (2010, 2017)	2002 Missionary Ridge fire was the most extensive and severe fire event in at least the past 2,600 yr in this steep, mountainous terrain.	Ponderosa and Gambel oak (<i>Quercus gambelii</i>) to mixed conifer	Compared fire-related deposition from debris flow and sediment-laden floods following the 2002 fire with alluvial-sediment records covering 3,000 yr.	2002 Missionary Ridge fire, San Juan Mountains, Colorado
Reilly et al. (2017)	High-severity fire effects in 23–26% of burned area in 1985–2010 exceeded expectations in most fire history studies.	Ponderosa pine and mixed conifer	Compared fire severity distributions for modern fires (1985–2010, RdNBR) with expected distributions derived from fire history studies; RdNBR burn severity thresholds were derived from pre- and post-fire CVS inventory data.	Oregon and Washington

TABLE 2. Continued

Citation	Key findings	Forest type	Methods	Study area
Safford and Stevens (2017) (Fig. 6 adapted from Miller and Safford 2008)	Area burned at high severity in modern fires exceeded estimates of area burned prior to European colonization.	Ponderosa and Jeffrey pine and mixed conifer	Compared modern fires (1984–2004, RdNBR) with Landfire BPS model estimates of high-severity fire extent prior to European colonization.	Sierra Nevada, California
Walker et al. (2018)	For areas that burned under extreme fire weather, sites lacking recent prior fire overwhelmingly converted to non-forest; more than half the total fire area is >50 m from surviving seed source.	Ponderosa and mixed conifer	Compared burn severity in 2011 (dNBR) on sites that had not burned in >100 yr with sites previously burned in prescribed fire and wildfire events that approximated fire frequency prior to fire exclusion.	2011 Las Conchas fire, northern New Mexico
Hagmann et al. (2019)	Stand-replacing fire effects in 23% of burned area in 1985–2015 compared to 6% in 1918.	Ponderosa pine, lodgepole pine, and mixed conifer	Compared extent of stand-replacing fire (RdNBR threshold of 962) for 1985–2015 fires (61,188 ha) with extent of burned area with no live trees >15 cm dbh following fires that burned >78,900 ha in 1918.	Pumice Plateau ecoregion, Oregon
Haugo et al. (2019)	High-severity fire effects in 36% of burned area in 1984–2015 exceeded 6–9% expected historically.	Frequent low-severity, FRG I	Compared area burned at high severity in modern (1984–2015, RdNBR) fires using previously validated thresholds for low, moderate, and high burn severity classes with simulated historical fire regime using BPS models in LANDFIRE.	Oregon and Washington
Nigro and Molinari (2019)	Average proportion burned at high severity in modern (2000–2016) fires more than 1.5 times greater than historical estimates; largest patch sizes larger than those recorded since 1900.	Ponderosa and Jeffrey pine and mixed conifer	Compared area burned at high severity in modern (2000–2016) fires using RdNBR threshold for ≥90% reduction in basal area with LANDFIRE BPS and relevant literature.	Sky island forests, southern California
Taylor et al. (2020)	In 2008, proportionally more mortality occurred in low and mid-elevation forests and less in high-elevation forests than in the 19th century.	Unlogged low and mid-elevation ponderosa pine, oak, and mixed conifer forests and high-elevation red fir forests.	Compare spatial patterns of fire severity in 2008 fire (RdNBR) burning under moderate weather with those of the late 19th century reconstructed from tree-ring and documentary records.	Cub Creek Research Natural Area, northern California

2010), and populations have continued to decline due to direct and indirect effects of drought stress, bark beetle outbreaks, and wildfire (Bentz et al. 2010, Fettig et al. 2013, 2019, McIntyre et al. 2015, Lydersen et al. 2017, Stephens et al. 2018a, Restaino et al. 2019, van Mantgem et al. 2020). Bark beetle outbreaks, accentuated by high forest density that exacerbates drought stress and facilitates infestation, continue to reduce average tree size and age in ponderosa and Jeffrey pine forests as bark beetles preferentially target larger individuals (Fettig et al. 2019, cf. Hood et al. 2020).

Recent trends in high-severity fire effects may contribute to further departures and present impediments to forest regeneration due to limitations on seed dispersal

capacity and altered site conditions (Stevens-Rumann et al. 2018, Davis et al. 2019, Stevens-Rumann and Morgan 2019), particularly in the case of short interval reburns (Stephens et al. 2018a, Coop et al. 2020). Constraints on tree regeneration may be an inevitable consequence of a warming climate. Note, however, that regeneration in semiarid forest–steppe ecotones exhibited resilience to recent low-severity fires but not high-severity fires (Harris and Taylor 2020). Additionally, recent work shows that the biogeochemical impacts of high-severity fires are much longer-lasting than previously assumed, leading to concern that increased high-severity burning will negatively impact soil organic carbon and nutrient cycling (Dove et al. 2020).

EVALUATING EVIDENCE OF LACK OF CHANGE

In this section, we review publications that suggest the preponderance of evidence misrepresents or overgeneralizes departures from active fire regimes. These publications then suggest that management actions aimed at recapturing the influence of abundant low- and moderate-severity fire lacks a sound ecological foundation. Over the past two decades, independent research groups have evaluated the methods and inferences proposed by these publications and documented multiple weaknesses. Despite demonstrated methodological biases and errors, new papers employing those methods, or results and conclusions derived from them, continue to pass peer review. To aid evaluation of this body of counter-evidence, we apply the same framework used above to evaluate evidence of change in forest conditions and fire regimes. We also synthesize peer-reviewed evaluations of the methods used in counter-evidence publications.

Misrepresented historical forest conditions

Publications based on novel methods for estimating historical forest density (Williams and Baker 2011) from early land surveys conducted by the General Land Office (GLO) have suggested that densities and fire severities of dry forests were higher and more variable than previously thought (Table 3). As described below, limitations of both GLO data and the methods used undermine this conclusion. Additionally, as Fulé et al. (2014) observed, existing research documented even greater heterogeneity in historical forest conditions, including higher densities, than was reconstructed from GLO data. Conflating high-frequency, low-severity fire regimes with homogeneity misrepresents the heterogeneity of those systems and disregards critical ecosystem functions associated with fine-scale spatial patterns in uneven-aged, predominantly open-canopy forests dominated by mature and old trees (Table 1).

Valid methods exist for deriving density estimates from spatial point patterns, such as GLO bearing trees (Cogbill et al. 2018). However, the extremely low sampling density of this national land survey limits reliable estimates to the average forest density for a large area. The typical spacing of 0.8 km between GLO survey points and a maximum of two or four trees per point yields a sample of, at most, eight trees per 260 ha. Levine et al. (2017) documented roughly 50% accuracy given a minimum of 50 GLO survey points (roughly 3,000 ha). Hanberry et al. (2011) documented accuracy of $\pm 10\%$ given GLO survey points in 10–20 townships (90,000–180,000 ha) depending on the number of bearing trees per point.

Thus, even when using independently validated methods, estimates of average density at such coarse spatial scales mask substantial heterogeneity in forest conditions at fine- and meso-scales. These records cover essentially all of the western United States, however, and can provide

valuable insights into landscape change at coarse scales. For example, Knight et al. (2020) reconstructed average tree density for the floristically diverse Klamath Mountains at township (roughly 9,320 ha) resolution and documented substantial departures from historical conditions, including forest densification and loss of oak woodlands.

Williams and Baker (2011) proposed a method for estimating average tree density for three and six pooled GLO survey points (roughly 260 and 520 ha, respectively). However, due to the lack of a correction factor that accounts for the number of trees used to estimate density at individual sampling points, methods developed by Williams and Baker (2011) overestimated tree densities by 24–667% for contemporary stands with known densities (Levine et al. 2017, 2019). Levine et al. (2017, 2019) enabled independent evaluation of their methods and data by archiving all GLO estimator code and data on publicly accessible websites; data and code supporting Williams and Baker (2011) are not similarly accessible (Stephens et al. 2021). Independently validated methods for estimating tree density from point data were shown to yield estimates that were less biased (Levine et al. 2017) as well as more consistent with tree-ring reconstructions and less than half as large (Johnston et al. 2018) as those produced using Williams and Baker (2011) methods.

Density estimates based on Williams and Baker (2011) methods are also inconsistent with tree-ring reconstructions and early 20th-century timber inventory records for areas where the data overlap (Tables 3–5). Counter-evidence publications have suggested that tree-ring reconstructions might overrepresent the historical influence of low- to moderate-severity fire (Table 4) and that early timber inventories (which systematically sampled 10–20% of the area of relatively large landscapes) are biased, inaccurate records of historical tree densities (Table 3). Like all data sets, dendroecological reconstructions and early timber inventories have limitations. However, as described below and in Tables 3–5, independent research groups have tested methodological concerns about underrepresentation of high-severity fire effects and the capacity of early timber inventories to represent early 20th century forest conditions and shown them to be unfounded. Dendrochronological reconstructions and early timber inventories demonstrate consistency with each other and with other independent data sources (Scholl and Taylor 2010, Stephens et al. 2015, Hagmann et al. 2017, 2019).

When comparing study results, accounting for ecologically relevant differences in site conditions or methodologies is essential. However, counter-evidence publications consistently do not account for these differences (Tables 3–6). One of many such comparisons involves a study of ponderosa pine on two 1-ha plots each of which was intentionally selected because it contained >75 trees per hectare >250 yr old (Morrow 1985). Baker and Hanson (2017) compared average tree density in these two selectively sampled hectares (Morrow 1985) with average

TABLE 3. Publications presenting (1) counter-evidence asserting that forests were denser than previously thought and (2) evaluations of methods and inferences in counter-evidence publications.

Counter-evidence		Evaluation of counter-evidence	
Citations	Counter-premise	Citations	Implications of evaluation
Williams and Baker (2011) Baker and Williams (2018)	Novel methods provide estimates of tree density from point data, <i>i.e.</i> , General Land Office (GLO) records of bearing trees.	Levine et al. (2017, 2019) Knight et al. (2020)	Multiple existing plotless density estimators (PDE) provided less biased estimates than the PDE developed by Williams and Baker (2011), which overestimated known tree densities by 24–667% in contemporary stands. Methods supported by PDE sampling theory and multiple accuracy assessments further demonstrate the potential for misrepresentation of historical tree density by biased estimators used at resolutions substantially smaller than the minimum recommended for ~50% accuracy.
Williams and Baker (2012)	Historical forests were denser than previously documented.	Johnston et al. (2018)	Existing methods for estimating tree density from point data (Morisita 1957, Warde and Petranks 1981) yielded densities more consistent with tree-ring reconstructions and less than half as large as estimates using Williams and Baker (2011) methods.
Williams and Baker (2012) Baker (2015a, b, 2012, 2014)	Historical forests were denser than previously documented.	Hagmann et al. (2013, 2014, 2017, 2019), Collins et al. (2015), Stephens et al. (2015, 2018c), Battaglia et al. (2018), Johnston et al. (2018)	Consistent with the finding that Williams and Baker (2011) methods overestimate tree density (Levine et al. 2017, 2019, Johnston et al. 2018, Knight et al. 2020), early timber inventory records and tree-ring reconstructions for the same study areas documented substantially lower tree densities than those estimated using Williams and Baker (2011) methods.
Hanson and Odion (2016)	Managing for dense, old forest and high-severity fire is consistent with historical conditions.	Collins et al. (2016)	Fundamental errors compromise assertions about historical conditions, including: (1) inappropriate use of coarse-scale habitat maps and (2) inaccurate assumption that areas lacking timber volume in early inventories indicate past high-severity fire.
Odion et al. (2014), Baker (2015a, b), Baker and Hanson (2017)	Spatially extensive early timber inventories and bias in their use and interpretation misrepresent historical conditions.	Stephens et al. (2015), Collins et al. (2016), Hagmann et al. (2017, 2018, 2019)	Fundamental errors compromise conclusions, including: (1) use of previously discredited methods (Williams and Baker 2011) to estimate tree density from GLO data as a baseline comparison; (2) incorrect assumptions about the methodological accuracy of early timber inventories; (3) inappropriate comparisons of studies of vastly different spatial scales, forest types, and diameter limits; (4) unsubstantiated assessment of bias in the locations of early timber inventories; and (5) unwarranted assumptions about vegetation patterns as indicators of fire severity.

tree density for >50,000 ha of mixed-conifer forest from a systematic sample of 20% of the area in an early timber inventory (Hagmann et al. 2014). Williams and Baker (2011) and Baker and Williams (2018) also compared average tree density in these two selectively sampled hectares (Morrow 1985) with average density estimated for 520 ha from GLO land survey data. Average tree density in two selectively sampled 1-ha plots cannot credibly be assumed to represent average densities for the substantially larger areas in these comparisons, particularly given abundant documentation of fine- and meso-scale variation in historical forest and landscape structure (Table 1).

The low sampling density and, hence, low spatial resolution of GLO land survey data precludes analysis of the spatial patterns that influence disturbance severity or response to disturbance in forests and forested landscapes. Validated methods for deriving estimates of average tree density from GLO data may support conclusions

about changes in average tree density or composition at broad spatial scales (e.g., Knight et al. 2020). However, objective conclusions about lack of change in forest conditions and fire regimes require additional lines of evidence. Multi-scale analysis of forest conditions and fire regimes (including spatial patterns in tree clumps, canopy gaps, forest successional types, physiognomic types, and stand-replacing fire) is essential to avoid misleading interpretations of the degree of ecosystem departures.

Misrepresented fire regimes

Counter-evidence publications have also posited that the high-severity component of contemporary wildfires is consistent with historical fire regimes based on the suggestions that high-severity fire was common historically (Tables 4 and 5) and modern wildfire severity is overestimated (Table 6). These assertions are

TABLE 4. Publications presenting (1) counter-evidence asserting that tree-ring reconstructions overestimate fire frequency and rotation and (2) evaluations of methods and inferences in counter-evidence publications.

Counter-evidence		Evaluation of counter-evidence	
Citations	Counter-premise	Citations	Implications of evaluation
Baker and Ehle (2001, 2003) Ehle and Baker (2003), Kou and Baker (2006a, b), Baker (2006, 2017), Dugan and Baker (2014)	Tree-ring reconstructions misrepresent historical fire regimes by overestimating fire frequency and extent because (1) unrecorded fires (e.g., fires that did not scar trees) increase uncertainty of mean fire interval (MFI); (2) interval between pith (origin) and first fire scar should be considered a fire-free interval and included in calculations of MFI; (3) targeted sampling of high scar densities biases MFI; (4) mean point fire interval (mean of intervals between fire scars weighted by the number of fire scars) may more accurately represent historical fire rotation than MFI (mean interval between all fire scars).	Collins and Stephens (2007) Brown and Wu (2005), Van Horne and Fulé (2006) Brown et al. (2008) Stephens et al. (2010), Yocom Kent and Fulé (2015) Meunier et al. (2019) Fulé et al. (2003) Van Horne and Fulé (2006) Farris et al. (2010, 2013) O'Connor et al. (2014) Farris et al. (2010) Huffman et al. (2015) Van Horne and Fulé (2006) Farris et al. (2013)	Unrecorded fires (fire did not scar the tree) may contribute to underestimation, not overestimation, of fire frequency and extent in frequent fire systems. Probability of scarring decreased when intervals between successive fires were short in areas burned by up to four late 20th-century fires. Absence of scar does not indicate absence of fire. Including origin-to-first-scar interval erroneously inflates MFI. Not all trees that survive fire are scarred. As an ambiguous indicator of fire-free interval, it should not be included in calculations of MFI. Additionally, tree establishment may not indicate a stand-replacing disturbance in dry forests where regeneration is strongly associated with climate. Complete, systematic (gridded), and random sampling at stand, watershed, and mountain range scales have repeatedly demonstrated fire frequencies similar to those derived from targeted sampling within forest types and scales. In direct comparison studies, no evidence was found that targeted sampling of fire-scarred trees biased MFI estimates. Targeted sampling reconstructed fire parameters comparable to those derived from systematic sampling of both a subset of the trees and all trees in a study area and from independent 20th-century fire atlases. Rather than overestimating fire frequency as suggested in counter-premise papers, MFI may underestimate fire frequency, especially where small fires were abundant. Composite mean fire intervals (CMFI, e.g., fires recorded on 25% of samples) are relatively stable across changes in sample area or size. See the section on “Underestimated historical fire frequency” for a more detailed summary of CMFI and the highly problematic and inherently biased alternatives proposed in counter-evidence publications.

compromised by methodological errors leading to underestimation of historical fire frequency, overestimation of historical fire severity, and underestimation of contemporary fire severity, as described in this section. Additionally, without consideration of all dimensions of a fire regime, one cannot objectively conclude that ecologically relevant departures have not occurred. For example, while fire regimes may not differ in one dimension (e.g., abundance of high-severity fire), they may differ in other dimensions (e.g., size or complexity of patches of high-severity fire). Similarly, while the dominant fire severity class (e.g., moderate) may not have changed for a given area, median percent mortality may have (e.g., a shift from 30% to 70%).

Underestimated historical fire frequency.—Dendroecological methods for reconstructing spatial point patterns of fire history have well-documented strengths and limitations (Stokes and Dieterich 1980, Baisan and Swetnam 1990, Falk et al. 2011, Daniels et al. 2017). Fire scars record low-severity (non-lethal) fire at a specific place

and time; however, absence of a scar on nearby trees may indicate either that the area did not burn or that it burned without scarring (i.e., absence of evidence is not evidence of absence; Fig. 7c). A common approach to overcoming this uncertainty is to composite fire scar dates from multiple trees. As more trees are sampled, the probability of detecting additional fires increases and eventually plateaus (Falk and Swetnam 2003). As trees are sampled across larger landscapes, the composite mean fire interval (CMFI) may be reduced as more fire-scar dates are found, especially in forests that historically experienced numerous relatively small fires (Collins and Stephens 2007). To avoid overestimating fire return intervals based on point sampling, researchers recommend (1) limiting compositing of fire dates to relatively small areas where fuel and topographic conditions would likely have resulted in generally uniform burning conditions; (2) collecting numerous samples to saturate the list of fire dates, reporting the point fire interval, and demonstrating a sampling plateau (Falk and Swetnam 2003, Van Horne and Fulé 2006); (3) using minimum

TABLE 5. Publications presenting (1) counter-evidence asserting that modern wildfires are not unlike historical fires because severity of historical fires is underestimated and (2) evaluations of methods and inferences in counter-evidence publications.

Counter-evidence		Evaluation of counter-evidence	
Citations	Counter-premise	Citations	Implications of evaluation
Shinneman and Baker (1997)	Based on early forest inventory age data sets, “nonequilibrium” areas of extensive, high-severity fires in the Black Hills led to landscapes dominated by dense, closed-canopy forests.	Brown (2006)	Tree-ring reconstructions of ponderosa pine forest age structures and fire regimes across the Black Hills found synchronous regional tree recruitment largely in response to pluvials and longer intervals between surface fires, especially during the late 1700s/early 1800s, which is when early inventory data report similar patterns of recruitment. No evidence of crown fires was found in relation to past fire dates.
Baker et al. (2007)	Most ponderosa pine forests in the Rocky Mountains were capable of supporting high-severity crown fires as well as low-severity surface fires.	Brown et al. (2008)	Tree-ring reconstruction of ponderosa pine forests in the Black Hills of South Dakota (included in Baker et al. 2007) demonstrated that roughly 3.3% of the study area burned as crown fire between 1529 and 1893; however, tree density in most stands in 1870 could not have supported crown fire.
Williams and Baker (2012), Baker (2012, 2014)	Fire severity inferred from tree density by size class estimated from GLO bearing trees (Williams and Baker 2011) and surveyors’ descriptions suggests low-severity fire dominated only a minority of ponderosa and mixed-conifer forests.	Levine et al. (2017, 2019)	Plotless density estimator used by Williams and Baker (2011) overestimated known tree densities due to a scaling factor that does not correct for the number of trees sampled and therefore systematically underestimates the area per tree relationship.
		Fulé et al. (2014), Merschel et al. (2014), O’Connor et al. (2017)	Substantial errors of method and interpretation invalidate inferences about historical fire severity. These include (1) tree size is an ambiguous indicator of tree age; (2) tree regeneration is an ambiguous indicator of disturbance severity, particularly in dry forests where climate conditions strongly influence regeneration; and (3) lack of direct documentary evidence (e.g., primary observation) of extensive crown fire in historical ponderosa pine forests has been widely noted for nearly 90 yr.
		Stephens et al. (2015), Huffman et al. (2015), Miller and Safford (2017), Hagmann et al. (2019)	Multi-proxy records documented substantially lower levels of high-severity fire in ponderosa and Jeffrey pine and mixed-conifer forests in overlapping study areas.
Baker (2012), Baker and Hanson (2017)	Estimates of area burned at high severity in Hessburg et al. (2007) validate estimates derived using Williams and Baker (2011) methods.	Hagmann et al. (2018), Spies et al. (2018a)	Inappropriate comparisons are not validation. Baker (2012) limited assessment of high-severity fire to tree mortality in dry forests whereas Hessburg et al. (2007) estimated high-severity fire in the dominant cover type whether that be grass or tree for “moist and cold forest” type, with lesser amounts of dry forests
Odion et al. (2014)	Modern, high-severity crown-fires are within historical range of variation. Inferred fire severity from current tree-age data for unmanaged forests in the U.S. Forest Service Inventory and Analysis (FIA) program. Compared inferences about modern fire severity to estimates of historical forest conditions and fire severity inferred using Williams and Baker (2011) methods.	Fulé et al. (2014), Levine et al. (2017, 2019), Knight et al. (2020)	Overestimation of historical tree density and unsupported inferences of fire severity from GLO records weaken conclusions based on Williams and Baker (2011) methods.
		Stevens et al. (2016)	Substantial errors of method and interpretation invalidate inferences about historical fire severity. These include (1) FIA stand age variable does not reflect the large range of individual tree ages in the FIA plots and (2) recruitment events are not necessarily related to high-severity fire occurrence.
		Spies et al. (2018a, b)	In contradiction of the counter-premise, Odion et al. documented only three patches of high-severity fire larger than >1,000 ha in Oregon and Washington in the early 1900s, which account for 1% of the area of historical low-severity fire regime managed under the Northwest Forest Plan.

TABLE 5. Continued

Counter-evidence		Evaluation of counter-evidence	
Citations	Counter-premise	Citations	Implications of evaluation
Baker and Hanson (2017)	Stephens et al. (2015) underrepresented the historical extent of high-severity fire in their interpretation of surveyor notes in early timber inventory.	Hagmann et al. (2018)	Substantial errors of method and interpretation invalidate inferences about the historical extent of high-severity fire. Inferences were based on (1) inappropriate assumptions about the size and abundance of small trees given the ambiguity of data describing small trees in the 1911 inventory, (2) averaging of values derived from different areas and vegetation classifications, and (3) inappropriate assumption that the presence of chaparral (common on sites with thin soils and high solar radiation) indicates high-severity fire.

sample depths to account for periods when fire records may be missing; and (4) proportional filtering of fire dates to distinguish smaller from larger fires (Swetnam and Baisan 1996).

The efficacy of these methods has been repeatedly demonstrated, often through direct testing of criticisms raised in counter-evidence publications (Table 4). For example, to evaluate Baker and Ehle (2001) assertions that targeted sampling of high fire scar densities biases MFI, Van Horne and Fulé (2006) compared targeted, random, and grid-based sampling of fire-scarred trees to a census of all fire-scarred trees ($n = 1,479$) in a 1-km² area. Given a minimum sample size of 50 trees (3%), all methods accurately reproduced the mean fire interval of the census of all fire-scarred trees. Farris et al. (2013) also found a high degree of accuracy across multiple sampling regimes. Similarly, Farris et al. (2010) tested Baker and Ehle (2001) assertions that fire-scar histories overestimated fire frequency by giving undue importance to small fires. First, Farris et al. (2010) demonstrated that spatially distributed fire-scar samples accurately reconstructed the existing spatial and temporal record of mapped fire events >100 ha that occurred from 1937 to 2000. Contrary to Baker and Ehle (2001) assertions, Farris et al. (2010) found that fires <100 ha were more common in the record of mapped fire events than suggested by dendrochronological reconstruction. Fire-scar records for hundreds of studies across western North America are archived on publicly accessible databases (Falk et al. 2011), which enables independent evaluation of methods and inferences. Fire-scar data supporting counter-evidence publications (Tables 4 and 5) are not similarly accessible.

Compositing of fire-scar records has proven to be a reliable, repeatable, and robust method (Heyerdahl et al. 2001, Fulé et al. 2003, Taylor and Skinner 2003, Van Horne and Fulé 2006, Hessler et al. 2007, Farris et al. 2010, 2013, O'Connor et al. 2014a). However, counter-evidence publications present and support the use of alternative methods that are problematic to calculate and biased (Table 4). For example, Kou and Baker (2006a) proposed an “all-tree fire interval” (ATFI) metric that includes a “scarring fraction” (SF, estimated fraction of unscarred trees) to derive a “population mean fire

interval” (PMFI). Few studies have tried to estimate SF (Kou and Baker 2006a); thus, few estimates of ATFI are available (Baker 2017). Additionally, as acknowledged by Kou and Baker (2006a: Accessory Publication), ATFI will always be much longer than any MFI, even for non-composited MFIs based on individual trees.

ATFI and SF are inaccurate indicators of historical fire occurrence. ATFI and SF depend on the false assumption that absence of scarring indicates absence of fire (Table 4). Reconstructing SF for each fire in a historical record is not feasible given that scarring can vary considerably with variations in weather and live and dead fuels between and within individual fires (Fig. 7a). Studies that have estimated SF (cited in Baker 2017) used data from recent fires that burned after a century or more of fire exclusion (Fig. 1) and are, therefore, not representative of historical fuel or fire behavior conditions. Additionally, ATFI inflates mean fire intervals by equating tree age with the period of fire regime analysis, thereby including origin-to-first-scar and time-since-last-fire intervals (Table 4, Fig. 7b). Abundant evidence indicates that origin-to-first-scar intervals are not reliable indicators of fire-free intervals and should be omitted from calculations of MFI (Table 4). Similarly, time-since-last-fire intervals that overlap more than a century of fire exclusion (Fig. 1) are not credible representations of fire frequency in active fire regimes (Figs. 1, 7).

Overestimated historical fire severity.—The indicators of high-severity fire events used in counter-evidence publications (e.g., average stand age, abundance of small trees, and presence of shrub fields) are ambiguous given ample viable alternative explanations for those conditions, as described below and in Table 5. High tree regeneration densities do not necessarily indicate prior fire events, a concept well-documented by the densification that has occurred in the absence of fire during the long 19th- to 21st-century period of fire exclusion (Hessburg and Agee 2003, Fulé et al. 2014, Merschel et al. 2014, O'Connor et al. 2017). Nonetheless, publications from Shinneman and Baker (1997) to those based on Williams and Baker (2011) use this metric to infer high-severity fire extent (Table 5). Climatic drivers of regeneration are often disassociated with disturbance events (Brown and Wu

TABLE 6. Publications presenting (1) counter-evidence asserting that modern wildfires are comparable to historical fires because severity of modern fires is overestimated and (2) evaluations of methods and inferences in counter-evidence publications.

Counter-evidence		Evaluation of counter-evidence	
Citations	Counter-premise	Citations	Implications of evaluation
Odion and Hanson (2006)	High-severity fire was rare in recent fires in the Sierra Nevada based on analysis of Burned Area Emergency Response (BAER) soil burn severity maps.	Safford et al. (2008)	BAER maps greatly underestimate stand-replacing fire area and heterogeneity in burn severity for vegetation. BAER maps are soil burn-severity maps, not vegetation burn-severity maps.
Hanson et al. (2009)	Changes in conservation strategies for Northern Spotted Owl (NSO) were unwarranted due to overestimation of high-severity fire in the NSO recovery plan.	Spies et al. (2010)	Use of a higher relative delta normalized burn ratio (RdNBR) threshold substantially increased misclassification errors and reduced estimates of high-severity fire extent. Hanson et al. (2009) used an RdNBR threshold of 798 rather than 574 as recommended in the literature (Miller et al. 2009) they cited as the source of the threshold used.
Williams and Baker (2012)	Severity distributions in recent fires do not depart from historical.	Steel et al. (2015), Guiterman et al. (2015), Reilly et al. (2017), Steel et al. (2018)	Extent and spatial patterns of fire severity in some recent fires have departed from pre-fire exclusion range of variation for some forest types.
Hanson and Odion (2014)	Previous assessments overestimate extent of high-severity fire in modern fires.	Safford et al. (2015)	Use of coarse-scale, highly inaccurate, and geographically misregistered vegetation map and averaging across unrelated vegetation types and diverse ownerships undermine confidence in Hanson and Odion (2014).

2005, North et al. 2005a, Brown 2006, Brown et al. 2008, Swetnam and Brown 2010, Heyerdahl et al. 2014). Moreover, widespread livestock grazing promoted abundant regeneration by exposing mineral soil, reducing competition from grasses and herbs for resources (Rummell 1951, McKelvey and Johnston 1992, Hessburg and Agee 2003), and reducing fire spread by disrupting fuel continuity (Savage and Swetnam 1990, Belsky 1992, Belsky and Blumenthal 1997, Swetnam et al. 2016). Similarly, while shrub fields may be a legacy of type conversion after high-severity forest fires, other factors also maintained shrubs and constrained forest development, including frequent fire (Knapp et al. 2013, Guiterman et al. 2018), Indigenous resource management (Marks-Block et al. 2021), and biophysical conditions, e.g., thin soils and high solar radiation (Stephens et al. 2015). Thus, multi-proxy evidence and meta-analyses are often needed to reconstruct site history and more credibly evaluate changes to forest conditions.

Other methodological errors also contribute to overestimation of historical fire severity in counter-evidence publications (Table 5). As described above, inferences based on historical tree densities estimated from GLO land survey data using Williams and Baker (2011) methods warrant reconsideration given methodological errors documented by multiple independent research groups (Table 3). Further, estimates of high-severity fire extent in Hessburg et al. (2007) do not validate estimates based on Williams and Baker (2011) methods because they are not comparable (Spies et al. 2018b: 132–137), despite assertions to the contrary (Table 5). Estimates of area

burned at high-severity using Williams and Baker (2011) methods are derived from inferred tree mortality while estimates derived from early aerial imagery (Hessburg et al. 2007) reflect mortality of the dominant cover type whether it be tree, shrub, or grass. Similarly, the use of average stand-age in contemporary Forest Inventory and Analysis (FIA) data by Odion et al. (2014) compromises inferences about the historical extent of high-severity fire due to the failure of this metric to account for the presence of older trees in the plot and the fact that tree age is not a reliable indicator of high-severity fire (Stevens et al. 2016).

Underestimated contemporary fire severity.—Estimates of contemporary fire severity in counter-evidence publications are compromised by non-standard definitions of high-severity fire and the capacity of the data to produce credible estimates of high-severity fire (Table 6). Odion and Hanson (2006) used data sets not designed to measure tree mortality (e.g., Burned Area Emergency Response data sets, BAER), which precludes ecologically meaningful comparisons with studies that classify fire severity as percentage of tree basal area or canopy cover killed (Safford et al. 2008). Hanson et al. (2009) used a higher severity threshold than recommended in the literature cited in support of their methods (Miller et al. 2009a), which yielded lower estimates of area burned by high-severity fire and weakened inferences based on comparisons with studies using the regionally calibrated threshold (Spies et al. 2010). Hanson and Odion (2014) suggested that previous assessments had

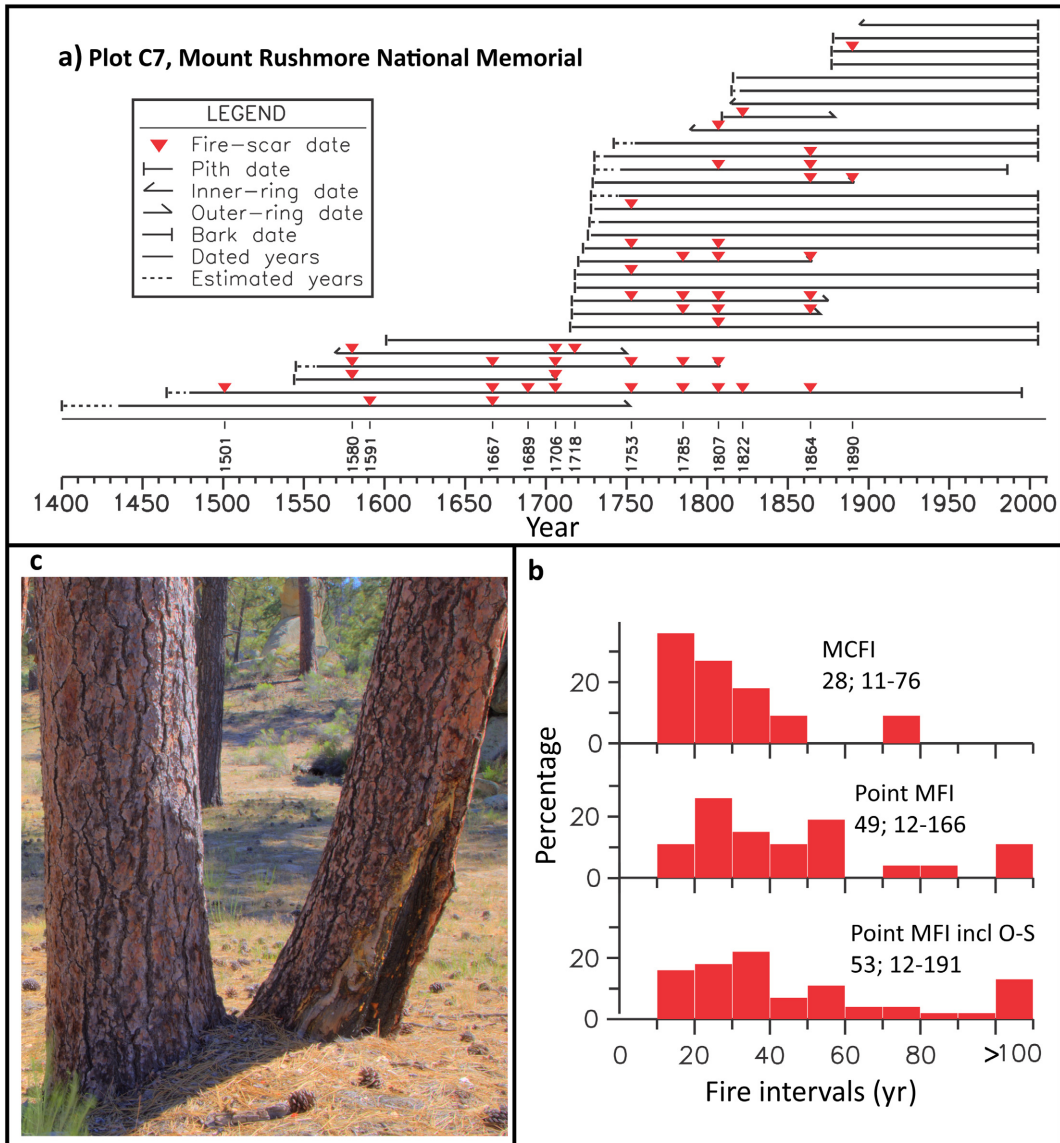


FIG. 7. A comparison of mean fire interval calculations using a fire history plot from Mount Rushmore National Memorial (Brown et al. 2008). (a) Fire-demography diagram of trees collected from n -tree variable radius plot. Data are cross-dated results from the 30 live (≥ 20 cm dbh) and dead trees nearest to a randomly selected grid point. Horizontal lines represent time spans of individual trees. Plot area is 0.11 ha, determined as a circular plot with radius of distance to farthest tree sampled. (b) Mean and range of fire intervals for this plot estimated by different methods. Top panel shows mean composite fire intervals (MCFI) using scar-to-scar intervals composited across all trees in the plot from 1580 to 1890 (11 total intervals). Fire dates used for interval calculation were those with minimum sample depth of five trees because of possible missing fire-scar records with fewer trees (i.e., the period between 1501 and 1580). Middle panel shows point mean fire intervals (point MFI) using scar-to-scar intervals recorded on all trees (27 total intervals). Bottom panel shows point MFI including origin-to-first scar (O-S) intervals on individual trees (45 total intervals). Including time-since-last fire intervals would further increase Point MFI. (c) An example of an unscarred tree of approximately the same age as a close neighbor with 14 fire scars. In a plot area of only 0.11 ha (panel a), all trees must have experienced fire at or very close to their stems for all fire dates listed but did record the event as a fire scar.

overestimated the extent of high-severity fire in modern fires; however, the use of a coarse-scale, highly inaccurate, and geographically misregistered vegetation map and averaging across unrelated vegetation types and diverse ownerships undermine confidence in this suggestion (Safford et al. 2015).

Misrepresented breadth and depth of change

A vast body of research progressively developed over more than a century, conducted at multiple spatial scales, and drawing on numerous intersecting lines of evidence underpins current scientific understanding of

the effects of prolonged fire exclusion on contemporary fire regimes and forest conditions. Given that evidence of change may not be apparent at all spatial scales or in all aspects of forest conditions and fire regimes, the conclusion that pattern-process interactions in fire-excluded forested landscapes have not departed from those characterizing active fire regimes requires strong evidence from multi-scale, multi-dimensional, multi-proxy evaluations. As demonstrated in the multiple independent assessments reviewed here (Tables 3–6), inferences supported by these counter-evidence publications are weakened by multiple methodological errors and warrant critical reevaluation. We conclude that these counter-evidence publications do not meet minimum standards for “best available science” to inform land and resource management on public lands (Esch et al. 2018).

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Based on the strength of evidence, there can be little doubt that the long-term deficit of abundant low- to moderate-severity fire has contributed to modification of seasonally dry forested landscapes across western North America. The magnitude of change in fire regimes and the resultant increases in forest density and fuel connectivity have increased the vulnerability of many contemporary forests to seasonal and episodic increases in drought and fire, exacerbated by rapid climate warming. While some ecosystems within these landscapes have been less directly altered by fire exclusion, they may be indirectly affected by alteration of the surrounding landscape and consequent changes to ecosystem processes, including disturbance and hydrological regimes. These substantial departures as well as on-going wildfire exclusion threaten numerous social and ecological values, including quantity and quality of water supply, stability of carbon stores, and air quality (Stephens et al. 2020), as well as culturally important resources and food security (Norgaard 2014, Sowerwine et al. 2019).

Long-term fire exclusion leads to the loss of informational (species life history traits) and material (biotic and abiotic structures such as seeds and nutrients) legacies (Johnstone et al. 2016) that may compromise fire-dependent diversity and the capacity of forested ecosystems to resist or recover after wildfires, especially under climate change (Franklin et al. 2000, Reilly et al. 2019, Krawchuk et al. 2020). Among these legacies are mature and old trees, in particular, open-canopy forests of mature and old conifers and hardwoods, which provide unique ecosystem functions and which were once substantially more prevalent (Spies et al. 2006, Kolb et al. 2007, Long et al. 2015, Franklin et al. 2018, Long et al. 2018, Hanberry and Dumroese 2020). As climate continues to warm and burned area increases, early seral habitat will likely be created in abundance. However, recapturing the once extensive influence of the low- and moderate-severity fires that shaped and maintained these ecosystems for millennia requires a paradigm shift

from strategies favoring fire suppression to those favoring fire-adapted forests and communities (reviewed by Hessburg et al. 2021, Prichard et al. 2021).

Perpetuating invalidated methods and inferences based on them fosters confusion and controversy, which undermine scientific credibility and impede the development of relevant and timely policy and management options. For example, counter-evidence reviewed here was used to support contentious conclusions in a meta-analysis of the impacts of high-severity fire on California Spotted Owls (*Strix occidentalis occidentalis*; Lee 2018). The authors of many of the studies included in that meta-analysis subsequently demonstrated methodological weaknesses in the meta-analysis that undermine those conclusions (Jones et al. 2020a). Unwarranted uncertainty about the use of high-severity burn areas by California Spotted Owls (Jones et al. 2019, Peery et al. 2019) has detrimentally impacted the management of this sensitive species (Stephens et al. 2019, Jones et al. 2020b). Objective scientific evaluation can aid in differentiating warranted from unwarranted uncertainties and enable timely paradigm shifts to policies and management actions that favor fire- and climate-adapted forests and human communities.

ACKNOWLEDGMENTS

We are grateful for funding from California Department of Forestry and Fire Protection; Ecological Restoration Institute; Washington State Department of Natural Resources; The Wilderness Society; The Nature Conservancy of Oregon; Conservation Northwest; USDA-FS, Pacific Northwest and Pacific Southwest Research Stations; and USDI-FWS Oregon Fish and Wildlife Office. Constructive reviews from K. Norman Johnson, Cameron E. Naficy, James Rosen, Frank K. Lake, Collin Haffey, and two anonymous reviewers substantially improved our manuscript. This paper was written and prepared by U.S. Government employees on official time, and therefore it is in the public domain and not subject to copyright.

DISCLAIMER

The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service or the USDA Forest Service.

LITERATURE CITED

- Abatzoglou, J. T., and A. P. Williams. 2016. Impact of anthropogenic climate change on wildfire across western US forests. *Proceedings of the National Academy of Sciences USA* 113:11770–11775.
- Addington, R. N., et al. 2018. Principles and practices for the restoration of ponderosa pine and dry mixed-conifer forests of the Colorado Front Range. RMRS-GTR-373. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Agee, J. K. 1996. *Fire ecology of Pacific Northwest forests*. Island Press, Washington, D.C., USA.
- Agee, J. K. 1998. The landscape ecology of western forest fire regimes. *Northwest Science* 72:24–34.
- Allen, C. D., R. S. Anderson, R. B. Jass, J. L. Toney, and C. H. Baisan. 2008. Paired charcoal and tree-ring records of

- high-frequency Holocene fire from two New Mexico bog sites. *International Journal of Wildland Fire* 17:115–130.
- Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, P. B. Stacey, P. Morgan, M. Hoffman, and J. T. Klingel. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications* 12:1418–1433.
- Amoroso, M. M., L. D. Daniels, M. Bataineh, and D. W. Anderson. 2011. Evidence of mixed-severity fires in the foothills of the Rocky Mountains of west-central Alberta, Canada. *Forest Ecology and Management* 262:2240–2249.
- Arizpe, A. H., D. A. Falk, C. A. Woodhouse, and T. W. Swetnam. 2021. Widespread fire years in the US–Mexico Sky Islands are contingent on both winter and monsoon precipitation. *International Journal of Wildland Fire* 29:1072–1087.
- Baisan, C. H., and T. W. Swetnam. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, U.S.A. *Canadian Journal of Forest Research* 20:1559–1569.
- Baker, W. L. 2006. Fire history in ponderosa pine landscapes of Grand Canyon National Park: is it reliable enough for management and restoration? *International Journal of Wildland Fire* 15:433–437.
- Baker, W. L. 2012. Implications of spatially extensive historical data from surveys for restoring dry forests of Oregon's eastern Cascades. *Ecosphere* 3:1–39.
- Baker, W. L. 2014. Historical forest structure and fire in Sierran mixed-conifer forests reconstructed from general land office survey data. *Ecosphere* 5:1–70.
- Baker, W. L. 2015a. Historical northern spotted owl habitat and old-growth dry forests maintained by mixed-severity wildfires. *Landscape Ecology* 30:655–666.
- Baker, W. L. 2015b. Are high-severity fires burning at much higher rates recently than historically in dry-forest landscapes of the Western USA? *PLoS ONE* 10:e0136147.
- Baker, W. L. 2017. Restoring and managing low-severity fire in dry-forest landscapes of the western USA. *PLoS ONE* 12:e0172288.
- Baker, W. L., and D. Ehle. 2001. Uncertainty in surface-fire history: the case of ponderosa pine forests in the western United States. *Canadian Journal of Forest Research* 31:1205–1226.
- Baker, W. L., and D. Ehle. 2003. Uncertainty in fire history and restoration of ponderosa pine forests in the western United States. Pages 319–333 *in* P. N. Omi, and L. A. Joyce, editors. Fire, fuel treatments, and ecological restoration: Conference proceedings. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Baker, W. L., and C. T. Hanson. 2017. Improving the use of early timber inventories in reconstructing historical dry forests and fire in the western United States. *Ecosphere* 8:e01935.
- Baker, W. L., T. T. Veblen, and R. L. Sherriff. 2007. Fire, fuels and restoration of ponderosa pine–Douglas fir forests in the Rocky Mountains, USA. *Journal of Biogeography* 34:251–269.
- Baker, W. L., and M. A. Williams. 2018. Land surveys show regional variability of historical fire regimes and dry forest structure of the western United States. *Ecological Applications* 28:284–290.
- Balch, J. K., B. A. Bradley, J. T. Abatzoglou, R. C. Nagy, E. J. Fusco, and A. L. Mahood. 2017. Human-started wildfires expand the fire niche across the United States. *Proceedings of the National Academy of Sciences USA* 114:2946–2951.
- Barros, A. M. G., A. A. Ager, M. A. Day, M. A. Krawchuk, and T. A. Spies. 2018. Wildfires managed for restoration enhance ecological resilience. *Ecosphere* 9:e02161. <https://doi.org/10.5751/ES-08917-220124>.
- Barros, A. M. G., et al. 2017. Spatiotemporal dynamics of simulated wildfire, forest management, and forest succession in central Oregon, USA. *Ecology and Society* 22:24.
- Battaglia, M. A., B. Gannon, P. M. Brown, P. J. Fornwalt, A. S. Cheng, and L. S. Huckaby. 2018. Changes in forest structure since 1860 in ponderosa pine dominated forests in the Colorado and Wyoming Front Range, USA. *Forest Ecology and Management* 422:147–160.
- Beaty, R. M., and A. H. Taylor. 2009. A 14,000 year sedimentary charcoal record of fire from the northern Sierra Nevada, Lake Tahoe Basin, California, USA. *Holocene* 19:347–358.
- Belsky, A. J. 1992. Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science* 3:187–200.
- Belsky, A. J., and D. M. Blumenthal. 1997. Effects of livestock grazing on stand dynamics and soils in upland forests of the interior west. *Conservation Biology* 11:315–327.
- Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. *BioScience* 60:602–613.
- Betancourt, J. L., T. R. V. Devender, and P. S. Martin. 1990. *Packrat middens: the last 40,000 years of biotic change*. University of Arizona Press, Tucson, Arizona, USA.
- Bigio, E., T. W. Swetnam, and C. H. Baisan. 2010. A comparison and integration of tree-ring and alluvial records of fire history at the Missionary Ridge Fire, Durango, Colorado, USA. *Holocene* 20:1047–1061.
- Bigio, E. R., T. W. Swetnam, and P. A. Pearthree. 2017. Late Holocene fire–climate relationships of the western San Juan Mountains, Colorado. *International Journal of Wildland Fire* 26:944–962.
- Bisson, P. A., B. E. Rieman, C. Luce, P. F. Hessburg, D. C. Lee, J. L. Kershner, G. H. Reeves, and R. E. Gresswell. 2003. Fire and aquatic ecosystems of the western USA: current knowledge and key questions. *Forest Ecology and Management* 178:213–229.
- Bohman, G. N., C. N. Skinner, and H. D. Safford. 2021. Natural range of variation (NRV) for yellow pine and mixed conifer forests in northwestern California and southwestern Oregon. General Technical Report PSW-GTR-273. USDA Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- Boisramé, G. F. S., S. E. Thompson, M. Kelly, J. Cavalli, K. M. Wilkin, and S. L. Stephens. 2017a. Vegetation change during 40 years of repeated managed wildfires in the Sierra Nevada, California. *Forest Ecology and Management* 402:241–252.
- Boisramé, G., S. Thompson, B. Collins, and S. Stephens. 2017b. Managed wildfire effects on forest resilience and water in the Sierra Nevada. *Ecosystems* 20:717–732.
- Boisramé, G. F. S., S. E. Thompson, C. Tague, and S. L. Stephens. 2019. Restoring a natural fire regime alters the water balance of a Sierra Nevada catchment. *Water Resources Research* 55:5751–5769.
- Bowman, D. M. J. S., et al. 2009. Fire in the earth system. *Science* 324:481–484.
- Bradstock, R. A., M. Bedward, B. J. Kenny, and J. Scott. 1998. Spatially-explicit simulation of the effect of prescribed burning on fire regimes and plant extinctions in shrublands typical of south-eastern Australia. *Biological Conservation* 86:83–95.
- Brown, P. M. 2006. Climate effects on fire regimes and tree recruitment in Black Hills ponderosa pine forests. *Ecology* 87:2500–2510.
- Brown, P. M., and B. Cook. 2006. Early settlement forest structure in Black Hills ponderosa pine forests. *Forest Ecology and Management* 223:284–290.

- Brown, P. M., C. Gentry, and Q. Yao. 2019. Historical and current fire regimes in ponderosa pine forests at Zion National Park, Utah: restoration of pattern and process after a century of fire exclusion. *Forest Ecology and Management* 445:1–12.
- Brown, P. M., C. L. Wienk, and A. J. Symstad. 2008. Fire and forest history at Mount Rushmore. *Ecological Applications* 18:1984–1999.
- Brown, P. M., and R. Wu. 2005. Climate and disturbance forcing of episodic tree recruitment in a southwestern ponderosa pine landscape. *Ecology* 86:3030–3038.
- Bryant, T., K. Waring, A. Sánchez Meador, and J. B. Bradford. 2019. A framework for quantifying resilience to forest disturbance. *Frontiers in Forests and Global Change* 2:56.
- Chavardès, R. D., and L. D. Daniels. 2016. Altered mixed-severity fire regime has homogenised montane forests of Jasper National Park. *International Journal of Wildland Fire* 25:433–444.
- Chavardès, R. D., L. D. Daniels, Z. Gedalof, and D. W. Anderson. 2018. Human influences superseded climate to disrupt the 20th century fire regime in Jasper National Park, Canada. *Dendrochronologia* 48:10–19.
- Churchill, D. J., G. C. Carnwath, A. J. Larson, and S. A. Jeronimo. 2017. Historical forest structure, composition, and spatial pattern in dry conifer forests of the western Blue Mountains, Oregon. PNW-GTR-956. Page 93. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Churchill, D. J., A. J. Larson, M. C. Dahlgreen, J. F. Franklin, P. F. Hessburg, and J. A. Lutz. 2013. Restoring forest resilience: From reference spatial patterns to silvicultural prescriptions and monitoring. *Forest Ecology and Management* 291:442–457.
- Cogbill, C. V., A. L. Thurman, J. W. Williams, J. Zhu, D. J. Mladenoff, and S. J. Goring. 2018. A retrospective on the accuracy and precision of plotless forest density estimators in ecological studies. *Ecosphere* 9:e02187.
- Collins, B. M., J. M. Lydersen, R. G. Everett, D. L. Fry, and S. L. Stephens. 2015. Novel characterization of landscape-level variability in historical vegetation structure. *Ecological Applications* 25:1167–1174.
- Collins, B. M., J. M. Lydersen, R. G. Everett, and S. L. Stephens. 2018. How does forest recovery following moderate-severity fire influence effects of subsequent wildfire in mixed-conifer forests? *Fire Ecology* 14:3.
- Collins, B. M., J. D. Miller, and S. L. Stephens. 2016. To the editor: a response to Hanson and Odion. *Natural Areas Journal* 36:234–242.
- Collins, B. M., J. D. Miller, A. E. Thode, M. Kelly, J. W. van Wagtendonk, and S. L. Stephens. 2009. Interactions among wildland fires in a long-established Sierra Nevada natural fire area. *Ecosystems* 12:114–128.
- Collins, B. M., and S. L. Stephens. 2007. Fire scarring patterns in Sierra Nevada wilderness areas burned by multiple wildland fire use fires. *Fire Ecology* 3:53–67.
- Collins, B. M., J. T. Stevens, J. D. Miller, S. L. Stephens, P. M. Brown, and M. P. North. 2017. Alternative characterization of forest fire regimes: incorporating spatial patterns. *Landscape Ecology* 32:1543–1552.
- Conver, J. L., D. A. Falk, S. R. Yool, and R. Parmenter. 2018. Stochastic fire modeling of a montane grassland and ponderosa pine fire regime in the Valles Caldera National Preserve, New Mexico, USA. *Fire Ecology* 14:17–31.
- Coogan, S. C. P., L. D. Daniels, D. Boychuk, P. J. Burton, M. D. Flannigan, S. Gauthier, V. Kafka, J. S. Park, and B. M. Wotton. 2020. Fifty years of wildland fire science in Canada. *Canadian Journal of Forest Research* 51:283–302.
- Coogan, S. C. P., F. Robinne, J. Piyush, and M. D. Flannigan. 2019. Scientists' warning on wildfire—a Canadian perspective. *Canadian Journal of Forest Research* 49:1015–1023.
- Coop, J. D., et al. 2020. Wildfire-driven forest conversion in western North American landscapes. *BioScience* 70:659–673.
- Coppoletta, M., K. E. Merriam, and B. M. Collins. 2016. Post-fire vegetation and fuel development influences fire severity patterns in reburns. *Ecological Applications* 26:686–699.
- Coppoletta, M., M. D. Meyer, and M. P. North. 2021. Natural range of variation for red fir and subalpine forests in northwestern California and southwestern Oregon. General Technical Report PSW-GTR-269. US Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- Cortés Montaña, C., P. Z. Fulé, D. A. Falk, J. Villanueva-Díaz, and L. L. Yocom. 2012. Linking old-growth forest composition, structure, fire history, climate and land-use in the mountains of northern México. *Ecosphere* 3:art106.
- Daniels, L. D., and R. W. Gray. 2006. Disturbance regimes in coastal British Columbia. *Journal of Ecosystems and Management* 7:44–56.
- Daniels, L. D., T. B. Maertens, A. B. Stan, S. P. J. McCloskey, J. D. Cochrane, and R. W. Gray. 2011. Direct and indirect impacts of climate change on forests: three case studies from British Columbia. *Canadian Journal of Plant Pathology* 33:108–116.
- Daniels, L. D., L. L. Yocom Kent, R. L. Sherriff, and E. K. Heyerdahl. 2017. Deciphering the complexity of historical fire regimes: diversity among forests of western North America. Pages 185–210 in M. M. Amoroso, L. D. Daniels, P. J. Baker, and J. J. Camarero, editors. *Dendroecology: tree-ring analyses applied to ecological studies*. Springer International Publishing, Cham, Switzerland.
- David, A. T., J. E. Asarian, and F. K. Lake. 2018. Wildfire smoke cools summer river and stream water temperatures. *Water Resources Research* 54:7273–7290.
- Davis, K. T., S. Z. Dobrowski, P. E. Higuera, Z. A. Holden, T. T. Veblen, M. T. Rother, S. A. Parks, A. Sala, and M. P. Maneta. 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. *Proceedings of the National Academy of Sciences USA* 116:6193–6198.
- deBuys, W., and C. D. Allen. 2015. A historical chronology of events and observations for the Pecos wilderness in the territorial period. *New Mexico Historical Review* 90:415–487.
- DellaSala, D. A., and C. T. Hanson. 2019. Are wildland fires increasing large patches of complex early seral forest habitat? *Diversity* 11:157.
- Dewar, J. J., D. A. Falk, T. W. Swetnam, C. H. Baisan, C. D. Allen, R. R. Parmenter, E. Q. Margolis, and E. J. Taylor. 2021. Valleys of fire: historical fire regimes of forest-grassland ecotones across the montane landscape of the Valles Caldera National Preserve, New Mexico, USA. *Landscape Ecology* 36:331–352.
- Diggins, C., P. Z. Fulé, J. P. Kaye, and W. W. Covington. 2010. Future climate affects management strategies for maintaining forest restoration treatments. *International Journal of Wildland Fire* 19:903–913.
- Dillon, G. K., D. H. Knight, and C. B. Meyer. 2005. Historic range of variability for upland vegetation in the Medicine Bow National Forest, Wyoming. General Technical Report RMRS-GTR-139. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Dove, N. C., H. D. Safford, G. N. Bohlman, B. L. Estes, and S. C. Hart. 2020. High-severity wildfire leads to multi-decadal

- impacts on soil biogeochemistry in mixed-conifer forests. *Ecological Applications* 30:e02072.
- Dugan, A. J., and W. L. Baker. 2014. Modern calibration and historical testing of small-area, fire-interval reconstruction methods. *International Journal of Wildland Fire* 23:58–68.
- Dumroese, R. K., and W. K. Moser. 2020. Northeastern California plateaus bioregion science synthesis. RMRS-GTR-409. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Ehle, D. S., and W. L. Baker. 2003. Disturbance and stand dynamics in ponderosa pine forests in Rocky Mountain National Park, USA. *Ecological Monographs* 73:543–566.
- Eisenberg, C., et al. 2019. Out of the ashes: ecological resilience to extreme wildfire, prescribed burns, and indigenous burning in ecosystems. *Frontiers in Ecology and Evolution* 7:436.
- Esch, B. E., A. E. M. Waltz, T. N. Wasserman, and E. L. Kalies. 2018. Using best available science information: determining best and available. *Journal of Forestry* 116:473–480.
- Falk, D. A. 2013. Are Madrean ecosystems approaching tipping points? Anticipating interactions of landscape disturbance and climate change. Pages 40–47 in G. J. Gottfried, P. F. Ffolliott, B. S. Gebow, L. G. Eskew, and L. C. Collins, comps. 2013. Merging science and management in a rapidly changing world: Biodiversity and management of the Madrean Archipelago III; 2012 May 1–5; Tucson, AZ. Proceedings. RMRS-P-67. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Falk, D. A., E. K. Heyerdahl, P. M. Brown, C. Farris, P. Z. Fulé, D. McKenzie, T. W. Swetnam, A. H. Taylor, and M. L. V. Horne. 2011. Multi-scale controls of historical forest-fire regimes: new insights from fire-scar networks. *Frontiers in Ecology and the Environment* 9:446–454.
- Falk, D. A., and T. W. Swetnam. 2003. Scaling rules and probability models for surface fire regimes in ponderosa pine forests. Pages 301–318 in P. N. Omi and L. A. Joyce, editors. *Fire, Fuel Treatments and Ecological Restoration: Conference Proceedings: April 16–18, 2002*. USDA Forest Service Proceedings RMRS-P-29. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Falk, D. A., A. C. Watts, and A. E. Thode. 2019. Scaling ecological resilience. *Frontiers in Ecology and Evolution* 7:275.
- Farris, C. A., C. H. Baisan, D. A. Falk, M. L. V. Horne, P. Z. Fulé, and T. W. Swetnam. 2013. A comparison of targeted and systematic fire-scar sampling for estimating historical fire frequency in south-western ponderosa pine forests. *International Journal of Wildland Fire* 22:1021–1033.
- Farris, C. A., C. H. Baisan, D. A. Falk, S. R. Yool, and T. W. Swetnam. 2010. Spatial and temporal corroboration of a fire-scar-based fire history in a frequently burned ponderosa pine forest. *Ecological Applications* 20:1598–1614.
- Fettig, C. J., L. A. Mortenson, B. M. Bulaon, and P. B. Foulk. 2019. Tree mortality following drought in the central and southern Sierra Nevada, California, US. *Forest Ecology and Management* 432:164–178.
- Fettig, C. J., M. L. Reid, B. J. Bentz, S. Sevanto, D. L. Spittlehouse, and T. Wang. 2013. Changing climates, changing forests: a western North American perspective. *Journal of Forestry* 111:214–228.
- Field, J., D. Breshears, J. Bradford, D. Law, X. Feng, and C. Allen. 2020. Forest management under megadrought: urgent needs at finer scale and higher intensity. *Frontiers in Forests and Global Change* 3:502669.
- Fornwalt, P. J., L. S. Huckaby, S. K. Alton, M. R. Kaufmann, P. M. Brown, and A. S. Cheng. 2016. Did the 2002 Hayman Fire, Colorado, USA, burn with uncharacteristic severity? *Fire Ecology* 12:117–132.
- Fortin, J. A., J. T. Fisher, J. M. Rhemtulla, and E. S. Higgs. 2019. Estimates of landscape composition from terrestrial oblique photographs suggest homogenization of Rocky Mountain landscapes over the last century. *Remote Sensing in Ecology and Conservation* 5:224–236.
- Franklin, J. F., and J. K. Agee. 2003. Forging a science-based national forest fire policy. *Issues in Science and Technology* 20:59–66.
- Franklin, J. F., K. N. Johnson, and D. L. Johnson. 2018. *Ecological forest management*. Waveland Press, Long Grove, Illinois, USA.
- Franklin, J. F., D. B. Lindenmayer, J. A. MacMahon, A. McKee, J. Magnuson, D. A. Perry, R. Waide, and D. Foster. 2000. Threads of continuity. *Conservation Biology in Practice* 1:8–16.
- Franklin, J. F., and R. Van Pelt. 2004. Spatial aspects of structural complexity in old-growth forests. *Journal of Forestry* 102:22–28.
- Fry, D. L., S. L. Stephens, B. M. Collins, M. P. North, E. Franco-Vizcaino, and S. J. Gill. 2014. Contrasting spatial patterns in active-fire and fire-suppressed Mediterranean climate old-growth mixed conifer forests. *PLoS ONE* 9:e88985.
- Fulé, P. Z., J. E. Crouse, J. P. Roccaforte, and E. L. Kalies. 2012a. Do thinning and/or burning treatments in western USA ponderosa or Jeffrey pine-dominated forests help restore natural fire behavior? *Forest Ecology and Management* 269:68–81.
- Fulé, P. Z., L. L. Yocom, C. C. Montaña, D. A. Falk, J. Cerano, and J. Villanueva-Díaz. 2012b. Testing a pyroclimatic hypothesis on the Mexico-United States border. *Ecology* 93:1830–1840.
- Fulé, P. Z., T. A. Heinlein, W. W. Covington, and M. M. Moore. 2003. Assessing fire regimes on Grand Canyon landscapes with fire-scar and fire-record data. *International Journal of Wildland Fire* 12:129–145.
- Fulé, P. Z., et al. 2014. Unsupported inferences of high-severity fire in historical dry forests of the western United States: response to Williams and Baker. *Global Ecology and Biogeography* 23:825–830.
- Gartner, M. H., T. T. Veblen, R. L. Sherriff, and T. L. Schoenagel. 2012. Proximity to grasslands influences fire frequency and sensitivity to climate variability in ponderosa pine forests of the Colorado Front Range. *International Journal of Wildland Fire* 21:562–571.
- Grafe, E., and P. Horsted. 2002. *Exploring with custer: the 1874 Black Hills expedition*. Golden Valley Press, Custer, South Dakota, USA.
- Graham, R. T., A. E. Harvey, T. B. Jain, and J. R. Tonn. 1999. The effects of thinning and similar stand treatments on fire behavior in Western forests. PNW-GTR-463. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Graham, R. T., S. McCaffrey, and T. B. Jain. 2004. Science basis for changing forest structure to modify wildfire behavior and severity. RMRS-GTR-120. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Greene, G. A., and L. D. Daniels. 2017. Spatial interpolation and mean fire interval analyses quantify historical mixed-severity fire regimes. *International Journal of Wildland Fire* 26:136–147.
- Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109:323–334.
- Guterman, C. H., E. Q. Margolis, C. D. Allen, D. A. Falk, and T. W. Swetnam. 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., E. Q. Margolis, and T. W. Swetnam. 2015. Dendroecological methods for reconstructing high-severity fire in pine-oak forests. *Tree-Ring Research* 71:67–77.
- Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2013. Historical structure and composition of ponderosa pine and mixed-conifer forests in south-central Oregon. *Forest Ecology and Management* 304:492–504.
- Hagmann, R. K., J. F. Franklin, and K. N. Johnson. 2014. Historical conditions in mixed-conifer forests on the eastern slopes of the northern Oregon Cascade Range, USA. *Forest Ecology and Management* 330:158–170.
- Hagmann, R. K., D. L. Johnson, and K. N. Johnson. 2017. Historical and current forest conditions in the range of the Northern Spotted Owl in south central Oregon, USA. *Forest Ecology and Management* 389:374–385.
- Hagmann, R. K., A. G. Merschel, and M. J. Reilly. 2019. Historical patterns of fire severity and forest structure and composition in a landscape structured by frequent large fires: Pumice Plateau ecoregion, Oregon, USA. *Landscape Ecology* 34:551–568.
- Hagmann, R. K., et al. 2018. Improving the use of early timber inventories in reconstructing historical dry forests and fire in the western United States: Comment. *Ecosphere* 9:e02232.
- Hamann, A., T. Wang, D. L. Spittlehouse, and T. Q. Murdock. 2013. A comprehensive, high-resolution database of historical and projected climate surfaces for western North America. *Bulletin of the American Meteorological Society* 94:1307–1309.
- Hanberry, B. B., and R. K. Dumroese. 2020. Biodiversity and representative species in dry pine forests. Pages 85–100 *in* R. K. Dumroese and W. K. Moser, editors. *Northeastern California plateaus bioregion science synthesis*. RMRS-GTR-409. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Hanberry, B. B., S. Fraver, H. S. He, J. Yang, D. C. Dey, and B. J. Palik. 2011. Spatial pattern corrections and sample sizes for forest density estimates of historical tree surveys. *Landscape Ecology* 26:59–68.
- Hann, W. J., et al. 1997. Chapter 3: Landscape dynamics of the basin. *In* T. M. Quigley and S. J. Arbelbide, editors. *An assessment of ecosystem components in the interior Columbia basin and portions of the Klamath and Great Basins: Volume II*. PNW-GTR-405. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Hann, W. J., J. L. Jones, R. E. Keane, P. F. Hessburg, and R. A. Gravenmier. 1998. ICBEMP: landscape dynamics. *Journal of Forestry* 96:10–15.
- Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. *BioScience* 41:382–392.
- Hanson, C. T., and D. C. Odion. 2014. Is fire severity increasing in the Sierra Nevada, California, USA? *International Journal of Wildland Fire* 23:1–8.
- Hanson, C. T., and D. C. Odion. 2016. Historical forest conditions within the range of the Pacific fisher and Spotted Owl in the central and southern Sierra Nevada, California, USA. *Natural Areas Journal* 36:8–19.
- Hanson, C. T., D. C. Odion, D. A. Dellasala, and W. L. Baker. 2009. Overestimation of fire risk in the Northern Spotted Owl recovery plan. *Conservation Biology* 23:1314–1319.
- Harris, L., and A. H. Taylor. 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., and A. H. Taylor. 2020. Rain-shadow forest margins resilient to low-severity fire and climate change but not high-severity fire. *Ecosphere* 11:e03258.
- Haugo, R. D., B. S. Kellogg, C. A. Cansler, C. A. Kolden, K. B. Kemp, J. C. Robertson, K. L. Metlen, N. M. Vaillant, and C. M. Restaino. 2019. The missing fire: quantifying human exclusion of wildfire in Pacific Northwest forests, USA. *Ecosphere* 10:e02702.
- He, H. S., R. E. Keane, and L. R. Iverson. 2008. Forest landscape models, a tool for understanding the effect of the large-scale and long-term landscape processes. *Forest Ecology and Management* 254:371–374, 254.
- Hessburg, P. F., and J. K. Agee. 2003. An environmental narrative of Inland Northwest United States forests, 1800–2000. *Forest Ecology and Management* 178:23–59.
- Hessburg, P. F., J. K. Agee, and J. F. Franklin. 2005. Dry forests and wildland fires of the inland Northwest USA: contrasting the landscape ecology of the pre-settlement and modern eras. *Forest Ecology and Management* 211:117–139.
- Hessburg, P. F., et al. 2015. Restoring fire-prone Inland Pacific landscapes: seven core principles. *Landscape Ecology* 30:1805–1835.
- Hessburg, P. F., et al. 2019. Climate, environment, and disturbance history govern resilience of western North American forests. *Frontiers in Ecology and Evolution* 7:239.
- Hessburg, P. F., R. G. Mitchell, and G. M. Filip. 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forested landscapes. General Technical Report PNW-GTR-327. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Hessburg, P. F., S. J. Prichard, R. K. Hagmann, N. A. Povak, and F. K. Lake. 2021. Wildfire and climate change adaptation of western North American forests: A case for intentional management. *Ecological Applications*, *in press*.
- Hessburg, P. F., R. B. Salter, and K. M. James. 2007. Re-examining fire severity relations in pre-management era mixed conifer forests: inferences from landscape patterns of forest structure. *Landscape Ecology* 22:5–24.
- Hessburg, P. F., B. G. Smith, S. D. Kreiter, C. A. Miller, R. B. Salter, C. H. McNicoll, and W. J. Hann. 1999a. Historical and current forest and range landscapes in the interior Columbia River basin and portions of the Klamath and Great Basins. Part 1: Linking vegetation patterns and landscape vulnerability to potential insect and pathogen disturbances. PNW-GTR-458. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Hessburg, P. F., B. G. Smith, and R. B. Salter. 1999b. Detecting change in forest spatial patterns from reference conditions. *Ecological Applications* 9:1232–1252.
- Hessburg, P. F., B. G. Smith, R. B. Salter, R. D. Ottmar, and E. Alvarado. 2000. Recent changes (1930s–1990s) in spatial patterns of interior northwest forests, USA. *Forest Ecology and Management* 136:53–83.
- Hessburg, P. F., et al. 2016. Tamm Review: Management of mixed-severity fire regime forests in Oregon, Washington, and Northern California. *Forest Ecology and Management* 366:221–250.
- Hessl, A., J. Miller, J. Kernan, D. Keenum, and D. McKenzie. 2007. Mapping paleo-fire boundaries from binary point data: comparing interpolation methods. *Professional Geographer* 59:87–104.
- Heyerdahl, E. K., L. B. Brubaker, and J. K. Agee. 2001. Spatial controls of historical fire regimes: a multiscale example from the interior West, USA. *Ecology* 82:660–678.
- Heyerdahl, E. K., R. A. Loehman, and D. A. Falk. 2014. Mixed-severity fire in lodgepole pine dominated forests: are historical regimes sustainable on Oregon's Pumice Plateau, USA? *Canadian Journal of Forest Research* 44:593–603.
- Higgs, E., G. Bartley, and A. Fisher. 2009. *The Mountain legacy project*. Second edition. University of Victoria Press, Victoria, British Columbia, Canada.

- Higgs, E., D. A. Falk, A. Guerrini, M. Hall, J. Harris, R. J. Hobbs, S. T. Jackson, J. M. Rhemtulla, and W. Throop. 2014. The changing role of history in restoration ecology. *Frontiers in Ecology and the Environment* 12:499–506.
- Hoffman, K. M., K. P. Lertzman, and B. M. Starzomski. 2017. Ecological legacies of anthropogenic burning in a British Columbia coastal temperate rain forest. *Journal of Biogeography* 44:2903–2915.
- Hoffman, K. M., S. B. Wickham, W. S. McInnes, and B. M. Starzomski. 2019. Fire exclusion destroys habitats for at-risk species in a British Columbia protected area. *Fire* 2:48.
- Hogg, E. H. 1997. Temporal scaling of moisture and the forest-grassland boundary in western Canada. *Agricultural and Forest Meteorology* 84:115–122.
- Holsinger, L., R. E. Keane, D. J. Isaak, L. Eby, and M. K. Young. 2014. Relative effects of climate change and wildfires on stream temperatures: a simulation modeling approach in a Rocky Mountain watershed. *Climatic Change* 124:191–206.
- Hood, S. M., C. R. Keyes, K. J. Bowen, D. C. Lutes, and C. Seielstad. 2020. Fuel treatment longevity in ponderosa pine-dominated forest 24 years after cutting and prescribed burning. *Frontiers in Forests and Global Change* 3:78.
- Huff, M. H., R. D. Ottmar, E. Alvarado, R. E. Vihnanek, J. F. Lehmkuhl, P. F. Hessburg, and R. L. Everett. 1995. Historical and current forest landscapes of eastern Oregon and Washington: Part II: linking vegetation characteristics to potential fire behavior and related smoke production. PNW-GTR-355. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Huffman, D. W., T. J. Ziegler, and P. Z. Fulé. 2015. Fire history of a mixed conifer forest on the Mogollon Rim, northern Arizona, USA. *International Journal of Wildland Fire* 24:680–689.
- Jain, T. B., and R. T. Graham. 2007. The relation between tree burn severity and forest structure in the Rocky Mountains. Pages 213–250 in R. F. Powers, technical editor. *Restoring Fire-Adapted Ecosystems: Proceedings of the 2005 National Silviculture Workshop*. General Technical Report PSW-GTR-203. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California, USA.
- Johnson, L. B., and E. Q. Margolis. 2019. Surface fire to crown fire: fire history in the Taos Valley watersheds, New Mexico, USA. *Fire* 2:14.
- Johnston, J. D. 2017. Forest succession along a productivity gradient following fire exclusion. *Forest Ecology and Management* 392:45–57.
- Johnston, J. D., C. J. Dunn, M. J. Vernon, J. D. Bailey, B. A. Morrisette, and K. E. Morici. 2018. Restoring historical forest conditions in a diverse inland Pacific Northwest landscape. *Ecosphere* 9:e02400.
- Johnstone, J. F., et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14:369–378.
- Jones, G. M., et al. 2020a. Spotted owls and forest fire: Comment. *Ecosphere* 11:e03312.
- Jones, G. M., et al. 2020b. Habitat selection by spotted owls after a megafire reflects their adaptation to historical frequent-fire regimes. *Landscape Ecology* 35:1199–1213.
- Jones, G. M. 2019. Megafire effects on spotted owls: elucidation of a growing threat and a response to Hanson et al. (2018). *Nature Conservation* 37:31–51.
- Kane, V. R., B. N. Bartl-Geller, M. P. North, J. T. Kane, J. M. Lydersen, S. M. A. Jeronimo, B. M. Collins, and L. Monika Moskal. 2019. First-entry wildfires can create opening and tree clump patterns characteristic of resilient forests. *Forest Ecology and Management* 454:117659.
- Kaufmann, M. R., D. Binkley, P. Z. Fulé, M. Johnson, S. L. Stephens, and T. W. Swetnam. 2007. Defining old growth for fire-adapted forests of the western United States. *Ecology and Society* 12:15.
- Kaye, M. W., and T. W. Swetnam. 1999. An assessment of fire, climate, and Apache history in the Sacramento mountains, New Mexico. *Physical Geography* 20:305–330.
- Keane, R. E. 1996. Simulating coarse-scale vegetation dynamics using the Columbia River basin succession model—CRBSUM. No. 339-340. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, Utah, USA.
- Keane, R. E. 2019. Applying ecosystem and landscape models in natural resource management. CRC Press, Taylor and Francis Group, Boca Raton, Florida, USA.
- Keane, R. E., P. F. Hessburg, P. B. Landres, and F. J. Swanson. 2009. The use of historical range and variability (HRV) in landscape management. *Forest Ecology and Management* 258:1025–1037.
- Keane, R. E., R. A. Loehman, L. M. Holsinger, D. A. Falk, P. Higuera, S. M. Hood, and P. F. Hessburg. 2018. Use of landscape simulation modeling to quantify resilience for ecological applications. *Ecosphere* 9:e02414.
- Keane, R. E., R. Parsons, and M. G. Rollins. 2004. Predicting fire regimes across multiple scales. Pages 55–69 in A. Perera and L. Buse, editors. *Emulating natural disturbances: concepts and techniques*. Cambridge University Press, Cambridge, UK.
- Keeley, J. E. 2012. Ecology and evolution of pine life histories. *Annals of Forest Science* 69:445–453.
- King, K. J., R. A. Bradstock, G. J. Cary, J. Chapman, and J. B. Marsden-Smedley. 2008. The relative importance of fine-scale fuel mosaics on reducing fire risk in south-west Tasmania, Australia. *International Journal of Wildland Fire* 17:421–430.
- Klimaszewski-Patterson, A., and S. A. Mensing. 2016. Multi-disciplinary approach to identifying Native American impacts on Late Holocene forest dynamics in the southern Sierra Nevada range, California, USA. *Anthropocene* 15:37–48.
- Knapp, E. E., C. N. Skinner, M. P. North, and B. L. Estes. 2013. Long-term overstory and understory change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *Forest Ecology and Management* 310:903–914.
- Knight, C. A., C. V. Cogbill, M. D. Potts, J. A. Wanket, and J. J. Battles. 2020. Settlement-era forest structure and composition in the Klamath Mountains: reconstructing a historical baseline. *Ecosphere* 11:e03250.
- Kolb, T. E., J. K. Agee, P. Z. Fulé, N. G. McDowell, K. Pearson, A. Sala, and R. H. Waring. 2007. Perpetuating old ponderosa pine. *Forest Ecology and Management* 249:141–157.
- Kou, X., and W. L. Baker. 2006a. Accurate estimation of mean fire interval for managing fire. *International Journal of Wildland Fire* 15:489–495.
- Kou, X., and W. L. Baker. 2006b. A landscape model quantifies error in reconstructing fire history from scars. *Landscape Ecology* 21:735–745.
- Krawchuk, M. A., G. W. Meigs, J. M. Cartwright, J. D. Coop, R. Davis, A. Holz, C. Kolden, and A. J. Meddens. 2020. Disturbance refugia within mosaics of forest fire, drought, and insect outbreaks. *Frontiers in Ecology and the Environment* 18:235–244.
- Lake, F. K., and J. W. Long. 2014. Fire and tribal cultural resources, Chapter 4.2. Pages 173–186 in J. W. Long, L. N. Quinn-Davidson, and C. N. Skinner, editors. *Science synthesis to support socioecological resilience in the Sierra Nevada and southern Cascade Range*. General Technical Report

- PSW-GTR-247. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- Lake, F. K., J. Parrotta, C. P. Giardina, I. Davidson-Hunt, and Y. Upreti. 2018. 12: Integration of traditional and western knowledge in forest landscape restoration. Pages 198–226 in S. Mansourian and J. Parrotta, editors. *Forest landscape restoration: integrated approaches to support effective implementation*. Routledge, New York, New York, USA.
- Larson, A. J., and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. *Forest Ecology and Management* 267:74–92.
- Laughlin, D. C., R. T. Strahan, D. W. Huffman, and A. J. S. Meador. 2017. Using trait-based ecology to restore resilient ecosystems: historical conditions and the future of montane forests in western North America. *Restoration Ecology* 25: S135–S146.
- Lee, D. E. 2018. Spotted Owls and forest fire: a systematic review and meta-analysis of the evidence. *Ecosphere* 9: e02354.
- LeFevre, M. E., D. J. Churchill, A. J. Larson, S. M. A. Jeronimo, J. Bass, J. F. Franklin, and V. R. Kane. 2020. Evaluating restoration treatment effectiveness through a comparison of residual composition, structure, and spatial pattern with historical reference sites. *Forest Science* 66:578–588.
- Lehmkuhl, J. F., P. F. Hessburg, R. L. Everett, M. H. Huff, and R. D. Ottmar. 1994. Historical and current forest landscapes of eastern Oregon and Washington: Part I: vegetation pattern and insect and EISEASE hazards. PNW-GTR-328. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Levine, C. R., C. V. Cogbill, B. M. Collins, A. J. Larson, J. A. Lutz, M. P. North, C. M. Restaino, H. D. Safford, S. L. Stephens, and J. J. Battles. 2017. Evaluating a new method for reconstructing forest conditions from General Land Office survey records. *Ecological Applications* 27:1498–1513.
- Levine, C. R., C. V. Cogbill, B. M. Collins, A. J. Larson, J. A. Lutz, M. P. North, C. M. Restaino, H. D. Safford, S. L. Stephens, and J. J. Battles. 2019. Estimating historical forest density from land-survey data: A response to Baker and Williams (2018). *Ecological Applications* 29:e01968.
- Loehman, R., W. Flatley, L. Holsinger, and A. Thode. 2018. Can land management buffer impacts of climate changes and altered fire regimes on ecosystems of the Southwestern United States? *Forests* 9:192.
- Loehman, R. A., R. E. Keane, and L. M. Holsinger. 2020. Simulation modeling of complex climate, wildfire, and vegetation dynamics to address wicked problems in land management. *Frontiers in Forests and Global Change* 3:Article 3.
- Loehman, R. A., R. E. Keane, L. M. Holsinger, and Z. Wu. 2017. Interactions of landscape disturbances and climate change dictate ecological pattern and process: spatial modeling of wildfire, insect, and disease dynamics under future climates. *Landscape Ecology* 32:1447–1459.
- Long, J. W., M. K. Anderson, L. Quinn-Davidson, R. W. Goode, F. K. Lake, and C. N. Skinner. 2015. Restoring California black oak ecosystems to promote tribal values and wildlife. General Technical Report PSW GTR-252. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- Long, J. W., A. Gray, and F. K. Lake. 2018. Recent trends in large hardwoods in the Pacific Northwest, USA. *Forests* 9:651.
- Long, J. W., and F. K. Lake. 2018. Escaping social-ecological traps through tribal stewardship on national forest lands in the Pacific Northwest, United States of America. *Ecology and Society* 23:10.
- Long, J. W., F. K. Lake, R. W. Goode, and B. M. Burnette. 2020. How traditional tribal perspectives influence ecosystem restoration. *Ecopsychology* 12:71–82.
- Lydersen, J. M., and B. M. Collins. 2018. Change in vegetation patterns over a large forested landscape based on historical and contemporary aerial photography. *Ecosystems* 21:1348–1363.
- Lydersen, J. M., B. M. Collins, M. L. Brooks, J. R. Matchett, K. L. Shive, N. A. Povak, V. R. Kane, and D. F. Smith. 2017. Evidence of fuels management and fire weather influencing fire severity in an extreme fire event. *Ecological Applications* 27:2013–2030.
- Lydersen, J., and M. North. 2012. Topographic variation in structure of mixed-conifer forests under an active-fire regime. *Ecosystems* 15:1134–1146.
- Lydersen, J. M., M. P. North, E. E. Knapp, and B. M. Collins. 2013. Quantifying spatial patterns of tree groups and gaps in mixed-conifer forests: reference conditions and long-term changes following fire suppression and logging. *Forest Ecology and Management* 304:370–382.
- Ma, Q., R. C. Bales, J. Rungee, M. H. Conklin, B. M. Collins, and M. L. Goulden. 2020. Wildfire controls on evapotranspiration in California's Sierra Nevada. *Journal of Hydrology* 590:125364.
- Maier, C., and J. B. Abrams. 2018. Navigating social forestry—A street-level perspective on National Forest management in the US Pacific Northwest. *Land Use Policy* 70:432–441.
- Mallek, C., H. Safford, J. Viers, and J. Miller. 2013. Modern departures in fire severity and area vary by forest type, Sierra Nevada and southern Cascades, California, USA. *Ecosphere* 4:1–28.
- Marcoux, H. M., L. D. Daniels, S. E. Gergel, E. Da Silva, Z. Gedalof, and P. F. Hessburg. 2015. Differentiating mixed- and high-severity fire regimes in mixed-conifer forests of the Canadian Cordillera. *Forest Ecology and Management* 341:45–58.
- Margolis, E. Q., and S. B. Malevich. 2016. Historical dominance of low-severity fire in dry and wet mixed-conifer forest habitats of the endangered terrestrial Jemez Mountains salamander (*Plethodon neomexicanus*). *Forest Ecology and Management* 375:12–26.
- Marks-Block, T., F. K. Lake, R. Bliege Bird, and L. M. Curran. 2021. Revitalized Karuk and Yurok cultural burning to enhance California hazelnut for basketweaving in northwestern California, USA. *Fire Ecology* 17:6.
- Marlon, J. R., et al. 2012. Long-term perspective on wildfires in the western USA. *Proceedings of the National Academy of Sciences USA* 109:E535–E543.
- Matonis, M. S., and D. Binkley. 2018. Not just about the trees: Key role of mosaic-meadows in restoration of ponderosa pine ecosystems. *Forest Ecology and Management* 411:120–131.
- McCord, M. G., M. J. Reilly, E. S. Jules, and R. J. Butz. 2020. Early seral pathways of vegetation change following repeated, short interval high-severity wildfire in a low elevation mixed-conifer-hardwood forest landscape of the Klamath Mountains, California. *Canadian Journal of Forest Research* 50:13–23.
- McIntyre, P. J., J. H. Thorne, C. R. Dolanc, A. L. Flint, L. E. Flint, M. Kelly, and D. D. Ackerly. 2015. Twentieth-century shifts in forest structure in California: Denser forests, smaller trees, and increased dominance of oaks. *Proceedings of the National Academy of Sciences USA* 112:1458–1463.
- McKelvey, K. S., and J. D. Johnston. 1992. Historical perspectives on forests of the Sierra Nevada and the transverse ranges of southern California; forest conditions at the turn of

- the century. Page 225–246 in J. Verner, K. S. McKelvey, B. R. Noon, R. J. Gutierrez, Jr., G. I. Gould, and T. W. Beck, Technical Coordinators. The California spotted owl: a technical assessment of its current status. General Technical Report PSW-GTR-133. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California, USA.
- McKinney, S. T. 2019. Systematic review and meta-analysis of fire regime research in ponderosa pine (*Pinus ponderosa*) ecosystems, Colorado, USA. *Fire Ecology* 15:38.
- Merschel, A. G., P. A. Beedlow, D. C. Shaw, D. R. Woodruff, H. E. Lee, S. P. Cline, R. L. Comeleo, R. K. Hagmann, and M. J. Reilly. 2021. An ecological perspective on living with fire in ponderosa pine forests of Oregon and Washington: resistance, gone but not forgotten. *Trees, Forests and People* 4:100074.
- Merschel, A. G., T. A. Spies, and E. K. Heyerdahl. 2014. Mixed-conifer forests of central Oregon: effects of logging and fire exclusion vary with environment. *Ecological Applications* 24:1670–1688.
- Metlen, K. L., C. N. Skinner, D. R. Olson, C. Nichols, and D. Borgias. 2018. Regional and local controls on historical fire regimes of dry forests and woodlands in the Rogue River Basin, Oregon, USA. *Forest Ecology and Management* 430:43–58.
- Meunier, J., N. S. Holoubek, and M. Sebasky. 2019. Fire regime characteristics in relation to physiography at local and landscape scales in Lake States pine forests. *Forest Ecology and Management* 454:117651.
- Meyer, C. B., D. H. Knight, and G. K. Dillon. 2005a. Historic range of variability for upland vegetation in the Bighorn National Forest, Wyoming. General Technical Report RMRS-GTR-140. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Meyer, C. B., D. H. Knight, and G. K. Dillon. 2005b. Historic variability for the upland vegetation of the Shoshone National Forest, Wyoming. Report submitted to the Shoshone National Forest, supervisor's office, Cody, Wyoming and the division of renewable resources, Rocky Mountain region, US Forest Service, Lakewood, Colorado, USA.
- Meyer, M. D., B. L. Estes, A. Wuenschel, B. Bulaon, A. Stucy, D. F. Smith, and A. C. Caprio. 2019. Structure, diversity and health of Sierra Nevada red fir forests with reestablished fire regimes. *International Journal of Wildland Fire* 28:386.
- Meyer, M., and M. North. 2019. Natural range of variation of red fir and subalpine forests in the Sierra Nevada Bioregion. General Technical Report PSW-GTR-263. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- Meyer, M. D., M. P. North, A. N. Gray, and H. S. J. Zald. 2007. Influence of soil thickness on stand characteristics in a Sierra Nevada mixed-conifer forest. *Plant and Soil* 294:113–123.
- Miller, J. D., E. E. Knapp, C. H. Key, C. N. Skinner, C. J. Isbell, R. M. Creasy, and J. W. Sherlock. 2009a. Calibration and validation of the relative differenced Normalized Burn Ratio (RdNBR) to three measures of fire severity in the Sierra Nevada and Klamath Mountains, California, USA. *Remote Sensing of Environment* 113:645–656.
- Miller, J. D., and B. Quayle. 2015. Calibration and validation of immediate post-fire satellite-derived data to three severity metrics. *Fire Ecology* 11:12–30.
- Miller, J. D., and H. D. Safford. 2008. Sierra Nevada fire severity monitoring: 1984–2004. Tech. Report R5-TP-027. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, Vallejo, California, USA, 102 p.
- Miller, J. D., and H. D. Safford. 2017. Corroborating evidence of a pre-Euro-American low- to moderate-severity fire regime in Yellow pine-mixed conifer forests of the Sierra Nevada, California, USA. *Fire Ecology* 13:58–90.
- Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009b. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12:16–32.
- Moreira, F., et al. 2020. Wildfire management in Mediterranean-type regions: paradigm change needed. *Environmental Research Letters* 15:011001.
- Morgan, P., G. H. Aplet, J. B. Haufler, H. C. Humphries, M. M. Moore, and W. D. Wilson. 1994. Historical range of variability. *Journal of Sustainable Forestry* 2:87–111.
- Morgan, P., R. E. Keane, G. K. Dillon, T. B. Jain, A. T. Hudak, E. C. Karau, P. G. Sikkink, Z. A. Holden, and E. K. Strand. 2014. Challenges of assessing fire and burn severity using field measures, remote sensing and modelling. *International Journal of Wildland Fire* 23:1045–1060.
- Morisita, M. 1957. A new method for the estimation of density by the spacing method applicable to nonrandomly distributed populations. *Physiology and Ecology* 7:134–144. English language translation available from <http://math.hws.edu/mitche11/Morisita1957.pdf>
- Moritz, M. A., C. Topik, C. D. Allen, P. F. Hessburg, P. Morgan, D. C. Odion, T. T. Veblen, and I. M. McCullough. 2018. A statement of common ground regarding the role of wildfire in forested landscapes of the western United States. Fire research consensus working group final report. <http://www.nwfirescience.org/biblio/statement-common-ground-regarding-role-wildfire-forested-landscapes-western-united-states>
- Morrow, R. J. 1985. Age structure and spatial pattern of old-growth ponderosa pine in Pringle Falls Experimental Forest, central Oregon. Dissertation. Oregon State University, Corvallis, Oregon, USA.
- Mueller, S. E., A. E. Thode, E. Q. Margolis, L. L. Yocom, J. D. Young, and J. M. Iniguez. 2020. Climate relationships with increasing wildfire in the southwestern US from 1984 to 2015. *Forest Ecology and Management* 460:117861.
- Murphy, J. S., R. York, H. Rivera Huerta, and S. L. Stephens. 2021. Characteristics and metrics of resilient forests in the Sierra de San Pedro Mártir, Mexico. *Forest Ecology and Management* 482:118864.
- Naficy, C. E. 2017. A cross-scale assessment of historical fire severity patterns, landscape dynamics, and methodological challenges in mixed-severity fire regimes of the northern US Rockies. Dissertation. University of Colorado, Boulder, Colorado, USA.
- Naficy, C., A. Sala, E. G. Keeling, J. Graham, and T. H. DeLuca. 2010. Interactive effects of historical logging and fire exclusion on ponderosa pine forest structure in the northern Rockies. *Ecological Applications* 20:1851–1864.
- Ng, J., M. P. North, A. J. Arditti, M. R. Cooper, and J. A. Lutz. 2020. Topographic variation in tree group and gap structure in Sierra Nevada mixed-conifer forests with active fire regimes. *Forest Ecology and Management* 472:118220.
- Nigro, K., and N. Molinari. 2019. Status and trends of fire activity in southern California yellow pine and mixed conifer forests. *Forest Ecology and Management* 441:20–31.
- Norgaard, K. M. 2014. The politics of fire and the social impacts of fire exclusion on the Klamath. *Humboldt Journal of Social Relations* 36:77–101.
- North, M. P., B. M. Collins, H. D. Safford, and N. L. Stephenson. 2016. Montane forests. Pages 553–577 in H. A. Mooney and E. Zavaleta, editors. *Ecosystems of California*. University of California Press, Berkeley, California, USA.

- North, M., M. Hurteau, R. Fiegner, and M. Barbour. 2005a. Influence of fire and El Niño on tree recruitment varies by species in Sierran Mixed Conifer. *Forest Science* 51:187–197.
- North, M., B. Oakley, R. Fiegner, A. Gray, and M. Barbour. 2005b. Influence of light and soil moisture on Sierran mixed-conifer understory communities. *Plant Ecology* 177:13–24.
- North, M., et al. 2002. Vegetation and ecological characteristics of mixed-conifer and red fir forests at the Teakettle Experimental Forest. Technical Report PSW-GTR-186. Pacific Southwest Research Station, Forest Service, U.S. Department of Agriculture, Albany, California, USA.
- North, M. P., S. L. Stephens, B. M. Collins, J. K. Agee, G. Aplet, J. F. Franklin, and P. Z. Fulé. 2015. Reform forest fire management. *Science* 349:1280–1281.
- North, M., P. Stine, K. O'Hara, W. Zielinski, and S. Stephens. 2009. An ecosystem management strategy for Sierran mixed-conifer forests. General Technical Report PSW-GTR-220 (Second printing, with addendum). U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- Noss, R. F., J. F. Franklin, W. L. Baker, T. Schoennagel, and P. B. Moyle. 2006. Managing fire-prone forests in the western United States. *Frontiers in Ecology and the Environment* 4:481–487.
- O'Connor, C. D., D. A. Falk, A. M. Lynch, and T. W. Swetnam. 2014a. Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleno Mountains, Arizona, USA. *Forest Ecology and Management* 329:264–278.
- O'Connor, C. D., D. A. Falk, A. M. Lynch, and T. W. Swetnam. 2014b. Fire severity, size, and climate associations diverge from historical precedent along an ecological gradient in the Pinaleno Mountains, Arizona, USA. *Forest Ecology and Management* 329:264–278.
- O'Connor, C. D., D. A. Falk, A. M. Lynch, T. W. Swetnam, and C. P. Wilcox. 2017. Disturbance and productivity interactions mediate stability of forest composition and structure. *Ecological Applications* 27:900–915.
- Odion, D. C., and C. T. Hanson. 2006. Fire severity in conifer forests of the Sierra Nevada, California. *Ecosystems* 9:1177–1189.
- Odion, D. C., et al. 2014. Examining historical and current mixed-severity fire regimes in ponderosa pine and mixed-conifer forests of western North America. *PLoS ONE* 9: e87852.
- Parks, S. A., and J. T. Abatzoglou. 2020. Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985–2017. *Geophysical Research Letters*:e2020GL089858.
- Parks, S. A., L. M. Holsinger, M. H. Panunto, W. M. Jolly, S. Z. Dobrowski, and G. K. Dillon. 2018. High-severity fire: evaluating its key drivers and mapping its probability across western US forests. *Environmental Research Letters* 13:044037.
- Parks, S. A., C. Miller, C. R. Nelson, and Z. A. Holden. 2014. Previous fires moderate burn severity of subsequent wildland fires in two large western US wilderness areas. *Ecosystems* 17:29–42.
- Parks, S. A., C. Miller, M.-A. Parisien, L. M. Holsinger, S. Z. Dobrowski, and J. Abatzoglou. 2015. Wildland fire deficit and surplus in the western United States, 1984–2012. *Ecosphere* 6:1–13.
- Pawlikowski, N. C., M. Coppoletta, E. Knapp, and A. H. Taylor. 2019. Spatial dynamics of tree group and gap structure in an old-growth ponderosa pine-California black oak forest burned by repeated wildfires. *Forest Ecology and Management* 434:289–302.
- Peery, M. Z., G. M. Jones, R. J. Gutierrez, S. M. Redpath, A. B. Franklin, D. Simberloff, M. G. Turner, V. C. Radeloff, and G. C. White. 2019. The conundrum of agenda-driven science in conservation. *Frontiers in Ecology and the Environment* 17:80–82.
- Pellatt, M. G., and Z. Gedalof. 2014. Environmental change in Garry oak (*Quercus garryana*) ecosystems: the evolution of an eco-cultural landscape. *Biodiversity and Conservation* 23:2053–2067.
- Perry, D. A., P. F. Hessburg, C. N. Skinner, T. A. Spies, S. L. Stephens, A. H. Taylor, J. F. Franklin, B. McComb, and G. Riegel. 2011. The ecology of mixed severity fire regimes in Washington, Oregon, and Northern California. *Forest Ecology and Management* 262:703–717.
- Povak, N. A., V. R. Kane, B. M. Collins, J. M. Lydersen, and J. T. Kane. 2020. Multi-scaled drivers of severity patterns vary across land ownerships for the 2013 Rim Fire, California. *Landscape Ecology* 35:293–318.
- Prichard, S. J., P. F. Hessburg, R. W. Gray, N. A. Povak, R. B. Salter, C. Stevens-Rumann & P. Morgan. 2018. Final Report: evaluating the influence of prior burn mosaics on subsequent wildfire behavior, severity, and fire management options. Joint Fire Science Project 14_1_02_30. https://www.firescience.gov/projects/14-1-02-30/project/14-1-02-30_final_report.pdf
- Prichard, S. J., et al. 2021. Adapting western US forests to wildfires and climate change: 10 key questions. *Ecological Applications*, *in press*.
- Prichard, S. J., C. S. Stevens-Rumann, and P. F. Hessburg. 2017. Tamm Review: Shifting global fire regimes: Lessons from returns and research needs. *Forest Ecology and Management* 396:217–233.
- Rakhmatulina, E., G. Boisramé, S. L. Stephens, and S. Thompson. 2021. Hydrological benefits of restoring wildfire regimes in the Sierra Nevada persist in a warming climate. *Journal of Hydrology* 593:125808.
- Raphael, M. G., M. J. Wisdom, M. M. Rowland, R. S. Holthausen, B. C. Wales, B. G. Marcot, and T. D. Rich. 2001. Status and trends of habitats of terrestrial vertebrates in relation to land management in the interior Columbia river basin. *Forest Ecology and Management* 153:63–87.
- Reilly, M. J., C. J. Dunn, G. W. Meigs, T. A. Spies, R. E. Kennedy, J. D. Bailey, and K. Briggs. 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). *Ecosphere* 8:e01695.
- Reilly, M. J., M. Elia, T. A. Spies, M. J. Gregory, G. Sanesi, and R. Laforzezza. 2018. Cumulative effects of wildfires on forest dynamics in the eastern Cascade Mountains, USA. *Ecological Applications* 28:291–308.
- Reilly, M. J., V. J. Monleon, E. S. Jules, and R. J. Butz. 2019. Range-wide population structure and dynamics of a serotinous conifer, knobcone pine (*Pinus attenuata* L.), under an anthropogenically-altered disturbance regime. *Forest Ecology and Management* 441:182–191.
- Restaino, C., D. J. N. Young, B. Estes, S. Gross, A. Wuenschel, M. Meyer, and H. Safford. 2019. Forest structure and climate mediate drought-induced tree mortality in forests of the Sierra Nevada, USA. *Ecological Applications* 29:e01902.
- Reynolds, R. T., A. J. S. Meador, J. A. Youtz, T. Nicolet, M. S. Matonis, P. L. Jackson, D. G. DeLorenzo, and A. D. Graves. 2013. Restoring composition and structure in Southwestern frequent-fire forests: A science-based framework for improving ecosystem resiliency. General Technical Report RMRS-GTR-310. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Rhemtulla, J. M., R. J. Hall, E. S. Higgs, and S. E. Macdonald. 2011. Eighty years of change: vegetation in the montane

- ecoregion of Jasper National Park, Alberta, Canada. *Canadian Journal of Forest Research* 32:2010–2021.
- Riegel, G. N., R. F. Miller, C. N. Skinner, S. E. Smith, C. A. Farris, and K. E. Merriam. 2018. Northeastern plateaus bioregion. Pages 229–248 in J. W. van Wagtendonk, N. G. Sugihara, S. L. Stephens, A. E. Thode, K. E. Shaffer, and J. Fites-Kaufman, editors. *Fire in California's ecosystems*. Second edition. University of California Press, Berkeley, California, USA.
- Riggs, R. A., et al. 2015. Biomass and fire dynamics in a temperate forest-grassland mosaic: Integrating multi-species herbivory, climate, and fire with the FireBGCv2/GrazeBGC system. *Ecological Modelling* 296:57–78.
- Rivera-Huerta, H., H. D. Safford, and J. D. Miller. 2016. Patterns and trends in burned area and fire severity from 1984 to 2010 in the Sierra de San Pedro Mártir, Baja California, Mexico. *Fire Ecology* 12:52–72.
- Roccaforte, J. P., P. Z. Fulé, and W. W. Covington. 2008. Landscape-scale changes in canopy fuels and potential fire behaviour following ponderosa pine restoration treatments. *International Journal of Wildland Fire* 17:293–303.
- Rogeanu, M.-P., M.-A. Parisien, and M. D. Flannigan. 2016. Fire history sampling strategy of fire intervals associated with mixed- to full-severity fires in southern Alberta, Canada. *Forest Science* 62:613–622.
- Rollins, M. G. 2009. LANDFIRE: a nationally consistent vegetation, wildland fire, and fuel assessment. *International Journal of Wildland Fire* 18:235–249.
- Roos, C. I., et al. 2021. Native American fire management at an ancient wildland-urban interface in the Southwest United States. *Proceedings of the National Academy of Sciences USA* 118:e2018733118.
- Rummell, R. S. 1951. Some effects of livestock grazing on ponderosa pine forest and range in central Washington. *Ecology* 32:594–607.
- Safford, H. D., J. D. Miller, and B. M. Collins. 2015. Differences in land ownership, fire management objectives and source data matter: a reply to Hanson and Odion (2014). *International Journal of Wildland Fire* 24:286–293.
- Safford, H. D., J. Miller, D. Schmidt, B. Roath, and A. Parsons. 2008. BAER soil burn severity maps do not measure fire effects to vegetation: A comment on Odion and Hanson (2006). *Ecosystems* 11:1–11.
- Safford, H. D., and J. T. Stevens. 2017. Natural range of variation for yellow pine and mixed-conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. General Technical Report PSW-GTR-256. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- Savage, M., and T. W. Swetnam. 1990. Early 19th-century fire decline following sheep pasturing in a Navajo ponderosa pine forest. *Ecology* 71:2374–2378.
- Schneider, E. E., D. L. R. Affleck, and A. J. Larson. 2019. Tree spatial patterns modulate peak snow accumulation and snow disappearance. *Forest Ecology and Management* 441:9–19.
- Scholl, A. E., and A. H. Taylor. 2010. Fire regimes, forest change, and self-organization in an old-growth mixed-conifer forest, Yosemite National Park, USA. *Ecological Applications* 20:362–380.
- Shinneman, D. J., and W. L. Baker. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in Ponderosa pine landscapes of the Black Hills. *Conservation Biology* 11:1276–1288.
- Shive, K. L., H. K. Preisler, K. R. Welch, H. D. Safford, R. J. Butz, K. L. O'Hara, and S. L. Stephens. 2018. From the stand scale to the landscape scale: predicting the spatial patterns of forest regeneration after disturbance. *Ecological Applications* 28:1626–1639.
- Simpson, K. J., B. S. Ripley, P.-A. Christin, C. M. Belcher, C. E. R. Lehmann, G. H. Thomas, and C. P. Osborne. 2016. Determinants of flammability in savanna grass species. *Journal of Ecology* 104:138–148.
- Singer, J. A., R. Turnbull, M. Foster, C. Bettigole, B. R. Frey, M. C. Downey, K. R. Covey, and M. S. Ashton. 2019. Sudden aspen decline: a review of pattern and process in a changing climate. *Forests* 10:671.
- Skinner, C. N., A. H. Taylor, J. K. Agee, C. E. Briles, and C. L. Whitlock. 2018. Klamath mountains bioregion. Pages 171–194 in J. W. van Wagtendonk, N. G. Sugihara, S. L. Stephens, A. E. Thode, K. E. Shaffer, and J. Fites-Kaufman, editors. *Fire in California's ecosystems*. Second edition. University of California Press, Berkeley, California, USA.
- SNEP. 1996. Sierra Nevada Ecosystem Project final report to Congress: Status of the Sierra Nevada. Davis, Centers for Water and Wildland Resources, University of California, Davis, California, USA.
- Sowerwine, J., M. Mucioki, D. Sarna-Wojcicki, and L. Hillman. 2019. Reframing food security by and for Native American communities: a case study among tribes in the Klamath River basin of Oregon and California. *Food Security* 11:579–607.
- Spies, T. A., et al. 2017. Using an agent-based model to examine forest management outcomes in a fire-prone landscape in Oregon, USA. *Ecology and Society* 22:25.
- Spies, T. A., M. A. Hemstrom, A. Youngblood, and S. Hummel. 2006. Conserving old-growth forest diversity in disturbance-prone landscapes. *Conservation Biology* 20:351–362.
- Spies, T. A., P. F. Hessburg, C. N. Skinner, K. J. Puettmann, M. J. Reilly, R. J. Davis, J. A. Kertis, J. W. Long, and D. C. Shaw. 2018a. Chapter 3: Old growth, disturbance, forest succession, and management in the area of the Northwest Forest Plan. Page 95–243 in T. A. Spies, P. A. Stine, R. Gravenmier, J. W. Long, and M. J. Reilly, technical coordinators. *Synthesis of science to inform land management within the Northwest Forest Plan area*. PNW-GTR-966. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Spies, T. A., P. A. Stine, R. A. Gravenmier, J. W. Long, and M. J. Reilly. 2018b. Volume 1—Synthesis of science to inform land management within the Northwest forest plan area. PNW-GTR-966. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Spies, T. A., et al. 2019. Twenty-five years of the Northwest Forest Plan: what have we learned? *Frontiers in Ecology and the Environment* 17:511–520.
- Spies, T. A. 2010. Underestimating risks to the northern spotted owl in fire-prone forests: response to Hanson et al. *Conservation Biology* 24:330–333.
- Steel, Z. L., M. J. Koontz, and H. D. Safford. 2018. The changing landscape of wildfire: burn pattern trends and implications for California's yellow pine and mixed conifer forests. *Landscape Ecology* 33:1159–1176.
- Steel, Z. L., H. D. Safford, and J. H. Viers. 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere* 6:art8.
- Stephens, S. L., B. M. Collins, E. Biber, and P. Z. Fulé. 2016. U.S. federal fire and forest policy: emphasizing resilience in dry forests. *Ecosphere* 7:e01584.
- Stephens, S. L., B. M. Collins, C. J. Fettig, M. A. Finney, C. M. Hoffman, E. E. Knapp, M. P. North, H. Safford, and R. B. Wayman. 2018a. Drought, tree mortality, and wildfire in forests adapted to frequent fire. *BioScience* 68:77–88.

- Stephens, S. L., J. W. Kanem, J. D. Stuart. 2018*b*. North coast bioregion. Pages 149–170 in J. Van Wagtenonk, editor. *Fire in California's ecosystems*. Second edition. University of California Press, Berkeley, California, USA.
- Stephens, S. L., D. L. Fry, B. M. Collins, C. N. Skinner, E. Franco-Vizcaino, and T. J. Freed. 2010. Fire-scar formation in Jeffrey pine—mixed conifer forests in the Sierra San Pedro Mártir, Mexico. *Canadian Journal of Forest Research* 40:1497–1505.
- Stephens, S. L., and P. Z. Fulé. 2005. Western pine forests with continuing frequent fire regimes: Possible reference sites for management. *Journal of Forestry* 103:357–362.
- Stephens, S. L., et al. 2019. Is fire “for the birds”? How two rare species influence fire management across the US. *Frontiers in Ecology and the Environment* 17:391–399.
- Stephens, S. L., J. M. Lydersen, B. M. Collins, D. L. Fry, and M. D. Meyer. 2015. Historical and current landscape-scale ponderosa pine and mixed conifer forest structure in the Southern Sierra Nevada. *Ecosphere* 6:1–63.
- Stephens, S. L., J. T. Stevens, B. M. Collins, R. A. York, and J. M. Lydersen. 2018*c*. Historical and modern landscape forest structure in fir (*Abies*)-dominated mixed conifer forests in the northern Sierra Nevada, USA. *Fire Ecology* 14:1–14.
- Stephens, S. L., R. E. Martin, and N. E. Clinton. 2007. Prehistoric fire area and emissions from California's forests, woodlands, shrublands, and grasslands. *Forest Ecology and Management* 251:205–216.
- Stephens, S. L., A. L. Westerling, M. D. Hurteau, M. Z. Peery, C. A. Schultz, and S. Thompson. 2021. Undesirable outcomes in seasonally dry forests. *Frontiers in Ecology and the Environment* 19:87–88.
- Stephens, S. L., A. L. Westerling, M. D. Hurteau, Z. M. Peery, C. A. Schultz, and S. Thompson. 2020. Fire and climate change: conserving seasonally dry forests is still possible. *Frontiers in Ecology and the Environment* 18:354–360.
- Stevens, J. T., B. M. Collins, J. D. Miller, M. P. North, and S. L. Stephens. 2017. Changing spatial patterns of stand-replacing fire in California conifer forests. *Forest Ecology and Management* 406:28–36.
- Stevens, J. T., M. M. Kling, D. W. Schwilk, J. M. Varner, and J. M. Kane. 2020. Biogeography of fire regimes in western U.S. conifer forests: a trait-based approach. *Global Ecology and Biogeography* 29:944–955.
- Stevens, J. T., et al. 2016. Average stand age from forest inventory plots does not describe historical fire regimes in ponderosa pine and mixed-conifer forests of western North America. *PLoS ONE* 11:e0147688.
- Stevens-Rumann, C. S., K. B. Kemp, P. E. Higuera, B. J. Harvey, M. T. Rother, D. C. Donato, P. Morgan, and T. T. Veblen. 2018. Evidence for declining forest resilience to wildfires under climate change. *Ecology Letters* 21:243–252.
- Stevens-Rumann, C. S., and P. Morgan. 2019. Tree regeneration following wildfires in the western US: a review. *Fire Ecology* 15:15.
- Stevens-Rumann, C. S., S. J. Prichard, E. K. Strand, and P. Morgan. 2016. Prior wildfires influence burn severity of subsequent large fires. *Canadian Journal of Forest Research* 46:1375–1385.
- Stine, P., et al. 2014. The ecology and management of moist mixed-conifer forests in eastern Oregon and Washington: a synthesis of the relevant biophysical science and implications for future land management. PNW-GTR-897. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Stockdale, C. A., S. E. Macdonald, and E. Higgs. 2019*a*. Forest closure and encroachment at the grassland interface: a century-scale analysis using oblique repeat photography. *Ecosphere* 10:e02774.
- Stockdale, C. A., N. McLoughlin, M. Flannigan, and S. E. Macdonald. 2019*b*. Could restoration of a landscape to a pre-European historical vegetation condition reduce burn probability? *Ecosphere* 10:e02584.
- Stokes, M. A., and J. H. Dieterich. 1980. Proceedings of the fire history workshop. October 20–24, 1980, Tucson, Arizona. RM-GTR-81. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado, USA.
- Strahan, R. T., A. J. S. Meador, D. W. Huffman, and D. C. Laughlin. 2016. Shifts in community-level traits and functional diversity in a mixed conifer forest: a legacy of land-use change. *Journal of Applied Ecology* 53:1755–1765.
- Sugihara, N. G., J. W. van Wagtenonk, and J. Fites-Kaufman. 2018. Fire as an ecological process. Pages 58–74 in J. W. van Wagtenonk, N. G. Sugihara, S. L. Stephens, A. E. Thode, K. E. Shaffer, and J. A. Fites-Kaufman, editors. *Fire in California's ecosystems*. Second edition. University of California Press, Berkeley, California, USA.
- Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* 9:117–125.
- Swetnam, T. W., C. D. Allen, and J. L. Betancourt. 1999. Applied historical ecology: using the past to manage for the future. *Ecological Applications* 9:1189–1206.
- Swetnam, T., and C. Baisan. 1996. Historical fire regime patterns in the southwestern United States since 1700. Pages 11–32 in C. D. Allen, editor. *Fire Effects in Southwestern Forests*, Proceedings of the Second La Mesa Fire Symposium, March 29–31, 1994, Los Alamos, New Mexico. RM-GTR-286. U.S. Department of Agriculture, Rocky Mountain Forest and Range Experiment Station.
- Swetnam, T. W., C. H. Baisan, A. C. Caprio, P. M. Brown, R. Touchan, R. S. Anderson, and D. J. Hallett. 2009. Multi-millennial fire history of the Giant Forest, Sequoia National Park, California, USA. *Fire Ecology* 5:120–150.
- Swetnam, T. L., and P. M. Brown. 2010. Comparing selected fire regime condition class (FRCC) and LANDFIRE vegetation model results with tree-ring data. *International Journal of Wildland Fire* 19:1–13.
- Swetnam, T. W., J. Farella, C. I. Roos, M. J. Liebmann, D. A. Falk, and C. D. Allen. 2016. Multiscale perspectives of fire, climate and humans in western North America and the Jemez Mountains, USA. *Philosophical Transactions of the Royal Society B* 371:20150168.
- Taylor, A. H. 2000. Fire regimes and forest changes in mid and upper montane forests of the southern Cascades, Lassen Volcanic National Park, California, U.S.A. *Journal of Biogeography* 27:87–104.
- Taylor, A. H., C. Airey-Lauvaux, B. Estes, L. Harris, and C. N. Skinner. 2020. Spatial patterns of nineteenth century fire severity persist after fire exclusion and a twenty-first century wildfire in a mixed conifer forest landscape, Southern Cascades, USA. *Landscape Ecology* 35:2777–2790.
- Taylor, A. H., and C. N. Skinner. 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecological Applications* 13:704–719.
- Taylor, A. H., V. Trouet, C. N. Skinner, and S. Stephens. 2016. Socioecological transitions trigger fire regime shifts and modulate fire–climate interactions in the Sierra Nevada, USA, 1600–2015 CE. *Proceedings of the National Academy of Sciences USA* 113:13684–13689.
- Tepley, A. J., and T. T. Veblen. 2015. Spatiotemporal fire dynamics in mixed-conifer and aspen forests in the San Juan

- Mountains of southwestern Colorado, USA. *Ecological Monographs* 85:583–603.
- Thompson, J. R., T. A. Spies, and L. M. Ganio. 2007. Reburn severity in managed and unmanaged vegetation in a large wildfire. *Proceedings of the National Academy of Sciences USA* 104:10743–10748.
- Trant, A., E. Higgs, and B. M. Starzomski. 2020. A century of high elevation ecosystem change in the Canadian Rocky Mountains. *Scientific Reports* 10:9698.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171–197.
- Van Horne, M. L., and P. Z. Fulé. 2006. Comparing methods of reconstructing fire history using fire scars in a southwestern United States ponderosa pine forest. *Canadian Journal of Forest Research* 36:855–867.
- van Mantgem, P. J., D. A. Falk, E. C. Williams, A. J. Das, and N. L. Stephenson. 2020. The influence of pre-fire growth patterns on post-fire tree mortality for common conifers in western US parks. *International Journal of Wildland Fire* 29:513–518.
- van Wageningen, J. W., J. A. Fites-Kaufman, H. D. Safford, M. P. North, and B. M. Collins. 2018a. Sierra Nevada bioregion. Pages 249–278 in J. van Wageningen, N. G. Sugihara, S. L. Stephens, A. E. Thode, K. E. Shaffer, and J. Fites-Kaufman, editors. *Fire in California's ecosystems*. Second edition. University of California Press, Berkeley, California, USA.
- van Wageningen, J. W., N. G. Sugihara, S. L. Stephens, A. E. Thode, K. E. Shaffer, and J. Fites-Kaufman, editors. 2018b. *Fire in California's ecosystems*. Univ of California Press, Berkeley, California, USA.
- Veblen, T. T., and J. A. Donnegan. 2005. Historical range of variability for forest vegetation of the national forests of the Colorado Front Range. Final report. University of Colorado, Boulder, Colorado, USA.
- Veblen, T. T., and D. C. Lorenz. 1991. *The Colorado front range: a century of ecological change*. University of Utah Press, Salt Lake City, Utah USA.
- Walker, R. B., J. D. Coop, W. M. Downing, M. A. Krawchuk, S. L. Malone, and G. W. Meigs. 2019. How much forest persists through fire? High-resolution mapping of tree cover to characterize the abundance and spatial pattern of fire refugia across mosaics of burn severity. *Forests* 10:782.
- Walker, R. B., J. D. Coop, S. A. Parks, and L. Trader. 2018a. Fire regimes approaching historic norms reduce wildfire-facilitated conversion from forest to non-forest. *Ecosphere* 9:e02182.
- Walker, R. B., J. D. Coop, S. A. Parks, and L. Trader. 2018b. Fire regimes approaching historic norms reduce wildfire-facilitated conversion from forest to non-forest. *Ecosphere* 9:e02182.
- Wallin, D. O., F. J. Swanson, B. Marks, J. H. Cissel, and J. Kertis. 1996. Comparison of managed and pre-settlement landscape dynamics in forests of the Pacific Northwest, USA. *Forest Ecology and Management* 85:291–309.
- Warde, W., and J. W. Petranka. 1981. A correction factor table for missing point-center quarter data. *Ecology* 62:491–494.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase Western U.S. forest wildfire activity. *Science* 313:940–943.
- Whitlock, C., and P. J. Bartlein. 1997. Vegetation and climate change in northwest America during the past 125 kyr. *Nature* 388:57–61.
- Whitlock, C., C. N. Skinner, P. J. Bartlein, T. Minckley, and J. A. Mohr. 2004. Comparison of charcoal and tree-ring records of recent fires in the eastern Klamath Mountains, California, USA. *Canadian Journal of Forest Research* 34:2110–2121.
- Wiens, J. A., G. D. Hayward, H. D. Safford, and C. Giffen. 2012. *Historical environmental variation in conservation and natural resource management*. John Wiley & Sons, West Sussex, UK.
- Williams, M. A., and W. L. Baker. 2011. Testing the accuracy of new methods for reconstructing historical structure of forest landscapes using GLO survey data. *Ecological Monographs* 81:63–88.
- Williams, M. A., and W. L. Baker. 2012. Spatially extensive reconstructions show variable-severity fire and heterogeneous structure in historical western United States dry forests. *Global Ecology and Biogeography* 21:1042–1052.
- Wimberly, M. C., and R. S. H. Kennedy. 2008. Spatially explicit modeling of mixed-severity fire regimes and landscape dynamics. *Forest Ecology and Management* 254: 511–523.
- Winthers, E., et al. 2005. *Terrestrial ecological unit inventory technical guide*. General Technical Report WO-GTR-68. U.S. Department of Agriculture, Forest Service, Washington Office, Ecosystem Management Coordination Staff, Washington, D.C., USA.
- Wisdom, M. J. 2000. *Source habitats for terrestrial vertebrates of focus in the Interior Columbia Basin: Broad-scale trends and management implications*. PNW-GTR-485. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
- Wu, J., and O. L. Loucks. 1995. From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Quarterly Review of Biology* 70:439–466.
- Yocom Kent, L. 2014. An evaluation of fire regime reconstruction methods. Working Papers in Southwestern Ponderosa Pine Forest Restoration 32. Northern Arizona University, Flagstaff, Arizona, USA. <http://www.nwfirescience.org/sites/default/files/publications/doc.pdf>
- Yocom Kent, L. L., and P. Z. Fulé. 2015. Do rules of thumb measure up? Characteristics of fire-scarred trees and samples. *Tree-Ring Research* 71:78–82.
- Yocom Kent, L. L., et al. 2017. Climate drives fire synchrony but local factors control fire regime change in northern Mexico. *Ecosphere* 8:e01709.
- Yocom-Kent, L. L., P. Z. Fulé, W. A. Bunn, and E. G. Gdula. 2015. Historical high-severity fire patches in mixed-conifer forests. *Canadian Journal of Forest Research* 45:1587–1596.
- Young, D. J. N., J. T. Stevens, J. M. Earles, J. Moore, A. Ellis, A. L. Jirka, and A. M. Latimer. 2017. Long-term climate and competition explain forest mortality patterns under extreme drought. *Ecology Letters* 20:78–86.

SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2431/full>