ARTICLE

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The North American tree-ring fire-scar network

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Abstract

Fire regimes in North American forests are diverse and modern fire records are often too short to capture important patterns, trends, feedbacks, and drivers of variability. Tree-ring fire scars provide valuable perspectives on fire regimes, including centuries-long records of fire year, season, frequency, severity, and size. Here, we introduce the newly compiled North American tree-ring fire-scar network (NAFSN), which contains 2562 sites, >37,000 fire-scarred trees, and covers large parts of North America. We investigate the NAFSN in terms of geography, sample depth, vegetation, topography, climate, and human land use. Fire scars are found in most ecoregions, from boreal forests in northern Alaska and Canada to subtropical forests in southern Florida and Mexico. The network includes 91 tree species, but is dominated by gymnosperms in the genus *Pinus*. Fire scars are found from sea level to >4000-m elevation and across a range of topographic settings that vary by ecoregion. Multiple regions are densely sampled (e.g., >1000 fire-scarred trees), enabling new spatial analyses such as reconstructions of area burned. To demonstrate the potential of the network, we compared the climate space of the NAFSN to those of modern fires and forests; the NAFSN spans a climate space largely representative of the forested areas in North America, with notable gaps in warmer tropical climates. Modern fires are burning in similar climate spaces as historical fires, but disproportionately in warmer regions compared to the historical record, possibly related to under-sampling of warm subtropical forests or supporting

observations of changing fire regimes. The historical influence of Indigenous and non-Indigenous human land use on fire regimes varies in space and time. A 20th century fire deficit associated with human activities is evident in many regions, yet fire regimes characterized by frequent surface fires are still active in some areas (e.g., Mexico and the southeastern United States). These analyses provide a foundation and framework for future studies using the hundreds of thousands of annually- to sub-annually-resolved tree-ring records of fire spanning centuries, which will further advance our understanding of the interactions among fire, climate, topography, vegetation, and humans across North America.

INTRODUCTION

Fire regimes in forests of North America vary across space and time in response to a complex suite of environmental controls and human activities. In western North America, fires are increasing in size and severity, driven by both climate change and increased fuel loads resulting from anthropogenic fire exclusion (Abatzoglou & Williams, 2016; Covington & Moore, 1994; Hanes et al., 2019; Parks & Abatzoglou, 2020; Westerling et al., 2006). The direct impacts of these changing fire regimes include losses and alterations of forest cover, and vegetation type conversions at many sites (Coop et al., 2020; Girard et al., 2008; McLauchlan et al., 2020). Emissions from increasing wildfires are moving carbon from ecosystems into the atmosphere (Hurteau et al., 2019; Liang et al., 2018), with smoke affecting public health (Burke et al., 2021) and impacting air quality both nearby and far from active fires (Baars et al., 2011; Brey et al., 2018). In temperate forests of eastern North America, where recent large fires are relatively rare, historically recurrent fires were important in some locations and the lack of fire over the last century is driving ecosystem changes that include the loss of open forest communities and pyrophilic species, with a consequent decline in vegetation flammability (Hanberry et al., 2018; Nowacki & Abrams, 2008). In many locations in the southeastern United States, the Great Plains, and northern Mexico fire regimes have been maintained for centuries, often reflecting human land use practices, including intentional burning, and limited fire suppression (Allen & Palmer, 2011; Fule et al., 2011; Rother et al., 2020; Stambaugh et al., 2009; Villarreal et al., 2020). Despite this diversity in fire regime characteristics and influences, fire risk is projected to increase in much of North America due to climate change (Gao et al., 2021; Kitzberger et al., 2017; Krawchuk et al., 2009; Stephens et al., 2020), increasing lightning ignitions coupled with longer droughts (Fill et al., 2019; Romps et al., 2014), and increasing human ignitions coupled with fire suppression that increases fuel loads (Balch et al., 2017). However, uncertainties remain about the effects of climate change across the diversity of fire regimes in North America, particularly due to the variability, interactions, and complex nonlinear relationships between climate, fire, vegetation, topography, and human land use (Littell et al., 2018; Riley et al., 2019; Tepley et al., 2018). Our understanding of these mechanistic drivers of fire regimes is limited by the relatively short modern fire atlas and satellite records of fire that are entirely contained within a period highly influenced by humans.

Records of past fires that span centuries to millennia can be preserved in the annual growth rings of trees. Tree-ring fire scars provide spatially explicit records of nonlethal fire (i.e., the tree must survive the fire to record a scar) that can be dated to the year of burning using dendrochronology (Figure 1; Dieterich & Swetnam, 1984). In some circumstances, fire scars can also be used to estimate other information on past fires, such as fire intensity and spread direction (Bergeron & Brisson, 1990), or the seasonal timing of fires (Rother et al., 2018). Heat from the fire kills cambial cells to produce a scar that is covered by subsequent growth (Gutsell & Johnson, 1996; Smith et al., 2016), and in some cases, the scars can be completely internal, with no evidence of scarring on the outside of the trunk (e.g., Huffman, 2006; Lombardo et al., 2009; Taylor & Skinner, 1998). Fire-scarred trees are most common in low- to moderate-severity fire regimes, where many trees survive fires (Harley et al., 2013; Kipfmueller et al., 2017; Swetnam & Baisan, 1996), but they are also found in mixed- and high-severity regimes at the edges of high-severity fire patches (Guiterman et al., 2015; Heon et al., 2014; Heyerdahl et al., 2019; Margolis et al., 2007). The strength of fire-scar
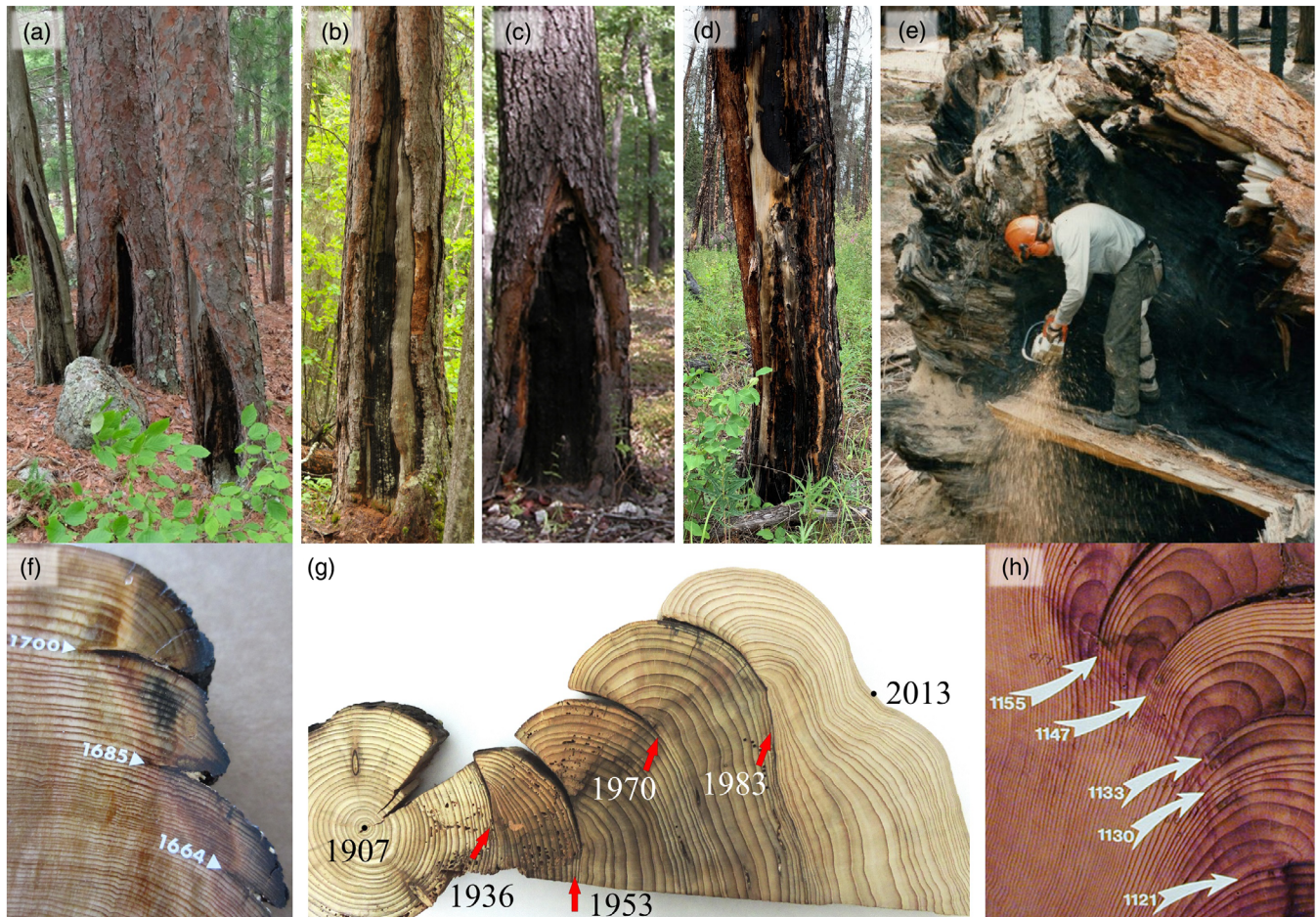
FIGURE 1 Tree-ring fire scars: (a) on multiple red pine (*Pinus resinosa*) in Minnesota, USA (image by L. B. Johnson), (b) on western larch (*Larix occidentalis*) in Montana, USA (image by C. E. Naficy), (c) on black oak (*Quercus velutina*) in Missouri, USA (image by M. Stambaugh), (d) on jack pine (*P. banksiana*) in Alberta, Canada (image by E. Whitman), (e) being sampled with a chainsaw from a dead giant sequoia (*Sequoiadendron giganteum*) in California, USA (image by T. W. Swetnam), (f) dated on a cross section of ponderosa pine (*P. ponderosa*) from New Mexico, USA (image by E. Q. Margolis), (g) dated on an oyamel (*Abies religiosa*) from Puebla, Mexico (image by J. Cerano-Paredes), and (h) dated on a giant sequoia from California, USA (image by A. Caprio).

records comes from the annual to sub-annual precision that enables compiling many point records into networks that span scales from individual trees, to landscapes, to regions, and to continents (Falk et al., 2011; Swetnam et al., 2016; Trouet et al., 2010). These spatially distributed, multicentury records of fire provide valuable, long-term context for modern fire records derived from satellites and mapped fire atlases that generally span from 1984 to present. Exceptional, multimillennial fire histories have been developed from giant sequoia (*Sequoiadendron giganteum*; Swetnam, 1993) and 200 million-year-old fire scars have even been found in late Triassic petrified wood in Arizona (Byers et al., 2020). Combining tree-ring records of fire with modern records, as well as longer Indigenous oral histories, and charcoal and pollen records from bogs, lakes, soils, or glaciers that span 10,000 years or more, enables analyses of patterns and drivers of fire regimes over the Holocene (e.g.,

Allen et al., 2008; Fule et al., 2011; Higuera et al., 2010, 2021; Hoffman et al., 2017; Larson et al., 2021; Roos & Guiterman, 2021).

The ability of trees to record a history of fires has been recognized scientifically for over a century by iconic ecologists, naturalists, and foresters including Frederick Clements, Aldo Leopold, and Gifford Pinchot (Clements, 1910; Leopold, 1924; Swetnam & Baisan, 1996). The first crossdated fire-history study was published by Harold Weaver (1951) using cross sections of ponderosa pine (*Pinus ponderosa*) from northern Arizona that were dated by the founder of dendrochronology, Andrew Douglass. The first fire-history workshop was convened in 1980 at the Laboratory of Tree-Ring Research in Tucson, AZ, to discuss the newly emerging field (Stokes, 1980). For over 40 years, tree-ring fire-history research has expanded in terms of number and spatial coverage of sites and

researchers across North America and around the world. New tools have been developed to facilitate analysis of the growing volume of fire history data—including graphical user interface software, FHAES (Fire History Analysis Exploration System; Sutherland et al., 2014), and a tree-ring fire-history R package, *burnr* (Malevich et al., 2018)—which has advanced the field through analyses of large fire scar networks to address important new research questions (Harley et al., 2018).

Tree-ring fire-scar networks enable the exploration of mechanistic drivers of spatiotemporal variability in fire dynamics and place modern changes in a long-term context. Fire-scar networks were vital for increasing the understanding of climate drivers of fire regimes. This includes the effects of equatorial Pacific Ocean sea surface temperatures associated with large-scale climate modes, such as the El Niño-Southern Oscillation, on fire regimes in the United States (Beckage et al., 2003; Heyerdahl et al., 2008; Swetnam & Betancourt, 1990, 1998) and synchronizing fire occurrences in parts of North and South America (Kitzberger et al., 2001), as well as identifying the North Pacific jet stream as a driver of wildfire extremes in California (Wahl et al., 2019). Guyette et al. (2012) identified major climate drivers of historical fire frequency for the United States using the physical chemistry fire frequency model and a network of 170 fire history sites. Fire-scar networks have also revealed important contexts for changing vegetation and landscape dynamics (Dewar et al., 2021; Lafon et al., 2017; O'Connor et al., 2017) and human influences on fire regimes (Collins & Stephens, 2007; Guyette et al., 2002; Kipfmueller et al., 2021; Kitchen, 2015; Swetnam et al., 2016). Regional fire-scar networks were key to identifying the anomaly of 20th century fire exclusion in large parts of the United States (Guyette et al., 2002; Swetnam & Baisan, 1996), thereby shaping national fire policies. Insights such as these, realized only as data were compiled over expanding geographic scales, attest to the potential of a continent-wide fire-scar synthesis initiative. A North American tree-ring fire-scar network that spans multiple centuries and covers the broad diversity of climate, forest biomes, topography, and human influences, is necessary to identify patterns, trends, and drivers of fire as a fundamental ecological process (McLauchlan et al., 2020). Such evidence and understanding are key for predicting future fire activity and effects, and for informing management and policy decisions in an era of rapid change (Guyette et al., 2014; Hessburg et al., 2019).

In this paper, we present a newly compiled continental-scale network of tree-ring fire-scar collections, the North American tree-ring fire-scar network (NAFSN). We analyze the spatiotemporal patterns of the NAFSN (e.g., using state-space analyses) for the following key components and influences on fire regimes: (1) geography, (2) vegetation, (3) sample depth, (4) topography, (5) climate, and (6) humans. For each topic, we describe background, analyses, findings, and interpretations, including future directions. We include an example application of the NAFSN to place the climate space of modern fires in a historical context. By analyzing key influences on fire regimes, we illustrate the potential of the NAFSN to advance our understanding of the past, present, and future role of fire in forested ecosystems, including promoting future research on the spatiotemporal relationships between fire, climate, vegetation, and humans across multiple scales.

COMPILING THE TREE-RING FIRE-SCAR NETWORK

The NAFSN builds on previous efforts to compile and synthesize tree-ring fire-history data. The largest existing data source is the International Multiproxy Paleofire Database (IMPD; https://www.ncei.noaa.gov/products/paleoclimatology/fire-history). The IMPD and other data compilations provide coverage across the western United States and northern Mexico (e.g., Marlon et al., 2012; Swetnam et al., 2016; Yocom Kent et al., 2017), while other North American regions remain sparsely represented. The tree-ring fire-history community, largely represented here in our authorship, added >1750 sites and many of those are located outside of the western United States, making the network truly North American in scope.

We compiled data from all available tree-ring fire-scar sites or plots (hereafter "sites," discussed further below) in North America (Canada, United States, and Mexico, and Indigenous Nations). We included completed studies going back to 1980, as well as dated sites from ongoing studies. We did not limit sites by the number of trees, or the area sampled, although these attributes were quantified when available. We only included records from fire-scarred trees and excluded tree-ring fire history derived from tree ages. Tree ages are important for determining fire severity, and are commonly used to study high-severity fire regimes, but unlike fire scars, tree ages often do not indicate the exact year a fire occurred, and therefore have different data structures and analysis methods (Margolis et al., 2007). All fire-scar sites in the NAFSN are crossdated to provide annually precise dates.

The NAFSN currently includes 2562 sites and >37,000 fire-scarred trees. The metadata include site name, contributor, geographic coordinates, tree species of fire-scar samples, area sampled, number of trees, years of first and last tree ring, years of first and last fire scar, and published references (https://doi.org/10.5066/P9PT90QX). We included all known dated fire-scar collections as of August 2020. Area sampled was the least reported metric (64% of sites). Eight

hundred of the NAFSN sites are publicly available on the IMPD, primarily representing western North America. We added 1762 sites to the network, which includes 491 sites compiled by the Fire and Climate Synthesis (FACS) project focused on the western United States (Swetnam, Falk, Sutherland, et al., 2011). One goal of the NAFSN project is to increase the number and spatial representation of sites publicly available, which is ongoing through facilitation of the process to contribute data to the IMPD.

GEOGRAPHY

The use of fire scars in fire-history studies, fire-regime analysis, and fire climatology is deeply rooted in geography; all of the themes of the NAFSN described hereafter are inherently spatial. To describe the basic geography of the network, we mapped the site locations and calculated the density of sites and fire-scarred trees within 10,000-km^2 hexels (Figure 2). We also compared the NAFSN site locations with other available data sets that have potential for cross-disciplinary analysis, including paleo-charcoal, paleo-pollen, and tree-ring width sites (e.g., Marlon et al., 2008, 2012; Appendix S1: Figures S1–S3).

The NAFSN sites are broadly distributed across large areas of North America (Figure 2a). Variability in sampling intensity is evident in both the density of sites (Figure 2b) and the density of sampled trees (Figure 2c). Several areas of particularly high sampling density are found in ponderosa pine and dry mixed conifer forests of the western United States, including: (1) The Jemez Mountains of northern New Mexico (1645 trees at 117 sites), (2) the southern Cascades/northern Sierra Nevada of northern California (1502 trees at 115 sites), (3) the Sky Islands of southeastern Arizona (1426 trees at 234 sites), (4) the Colorado Front Range (1352 trees at 95 sites), (5) the Blue Mountains of eastern Oregon (1151 trees at 61 sites), and (6) the San Juan Mountains of southwestern Colorado (1135 trees at 43 sites). Areas of high sample density in boreal and northern forest regions include a ca. 150-km-long transect in northwestern Quebec (1269 trees at 93 sites), the Lake of the Woods along the Ontario/Manitoba border (1227 trees at 8 sites), the Boundary Waters Canoe Area Wilderness of northern Minnesota and Quetico Provincial Park of southwestern Ontario (596 trees at 103 sites), and 778 trees at 241 sites in Alaska. In the eastern United States, fire scars were sampled from more than 1800 trees along the Appalachian Mountains and more than 600 trees in the Ozarks of southeastern Missouri and northern Arkansas. In Mexico, almost 3000 trees have been sampled at more than 100 sites. There are notable spatial gaps or low densities of sample sites in some forested regions, including

sections of the eastern United States, southern Mexico, and boreal Canada (Figure 2).

The area sampled and the number of sampled trees in a site varies across North America. For sites where area sampled was reported ($n = 1628$), the median area sampled per site is 3.2 ha (mean = 199.2 ha; range = 0.0015–75,000 ha). Small sample areas are generally associated with sampling designs using networks of small (1–2 ha) plots, whereas larger sample areas often indicate "targeted" designs where trees were sampled opportunistically across large areas (Farris et al., 2013). The median number of fire-scarred trees in a site is eight (mean = 14.8; range = 1–250). Although a site with a single tree may seem too small for inclusion, a single giant sequoia, ponderosa pine, or longleaf pine (*Pinus palustris*) can provide a rich record of 30 or more fire scars (e.g., Guiterman et al., 2019; Huffman, 2006; Swetnam et al., 2009).

The spatial distribution of fire-scar sites across North America provides insights into factors that affect fire-scar formation, preservation, and sampling. Most areas with high sample density are in dry conifer forests of western North America where a seasonally warm and dry climate historically promoted low- to moderate-severity fire, and tree species are well-suited to recording and preserving fire scars (Dieterich & Swetnam, 1984; Keeley et al., 2011). In contrast, sampling density is lower in noncoastal plain regions of the eastern United States, where forests are dominated by angiosperm tree species that compartmentalize fire scars less effectively and decay quickly (Smith & Sutherland, 1999). Moreover, few mature forests remain in this region following centuries of extensive Euro-American land-clearing, logging, and settlement (see *Vegetation* section for further discussion). In areas such as boreal and subalpine landscapes where fires typically burn at high severity and kill most mature trees over large areas, substantial effort may be required to find fire-scarred trees, and those trees typically record few fires (Heon et al., 2014; O'Connor et al., 2014). Finally, the fire-scarred trees must produce annual rings that can be crossdated to provide annually resolved fire dates. Crossdating is typically not a limitation in much of North America, as illustrated by the spatial distribution of existing tree-ring width chronologies (Appendix S1: Figure S1), but there may be problems in certain regions where tree growth continues year-round (e.g., tropical Mexico), or with certain species (e.g., Coast redwood, *Sequoia sempervirens*; Brown & Swetnam, 1994). Future sampling to fill spatial gaps in the southeastern United States, northwestern Canada, and southern Mexico would provide valuable new data on fire regimes in under-studied ecosystems and coupled human-natural systems.

The variability in sample area and sample density among NAFSN sites reflects variation in study design as well as underlying variability in the topography, species
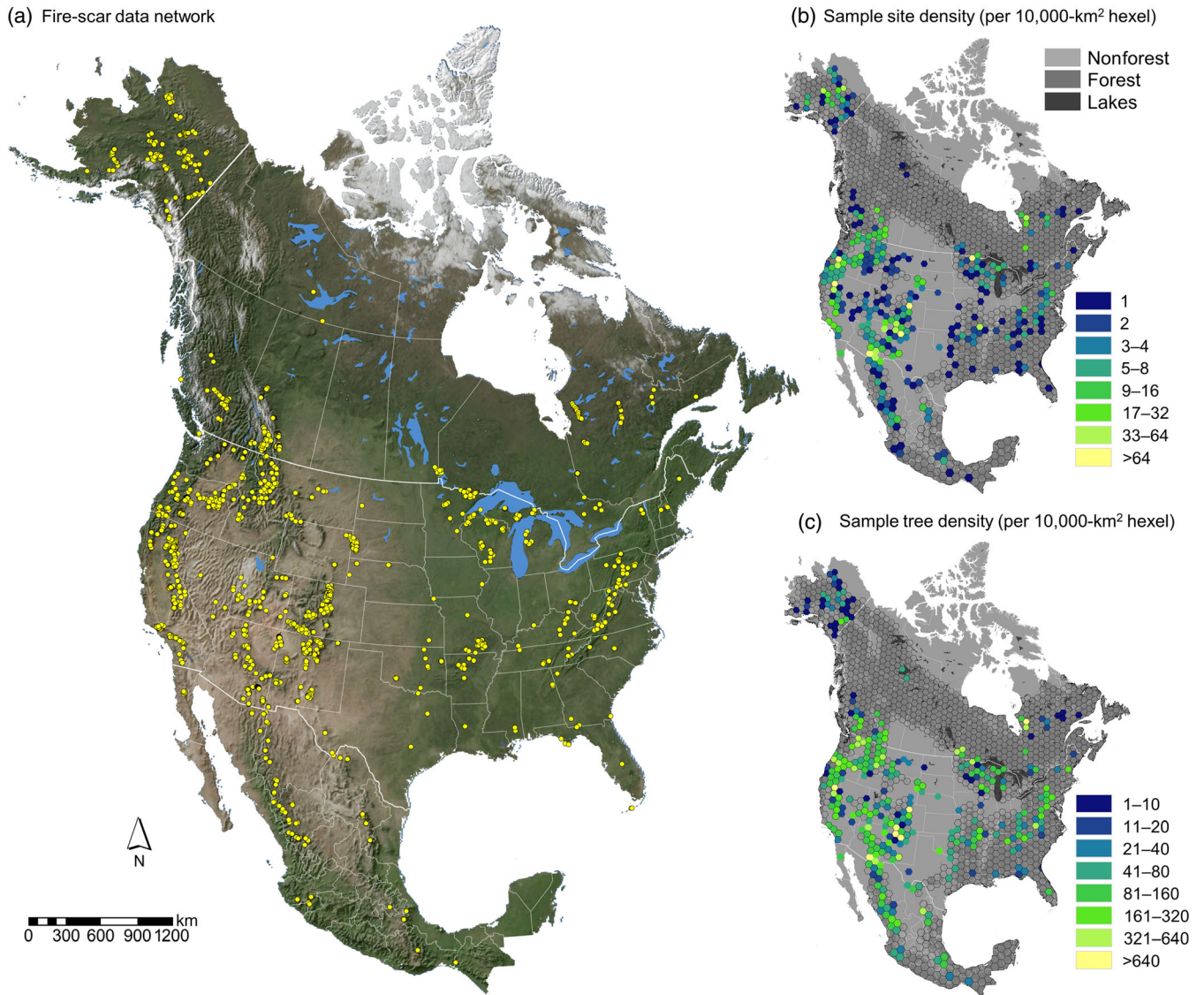
(a) Fire-scar data network

(b) Sample site density (per 10,000-km² hexel)

(c) Sample tree density (per 10,000-km² hexel)

FIGURE 2 Distribution of fire-scar sample sites (a) across North America. The number of sample sites (b) and sampled trees (c) was calculated per 10,000-km² hexel. Gray shading in (b) and (c) represents current forest cover based on 1-km MODIS imagery. Hexel outlines are shown only if at least 10% of the hexel area is forested. Some sample sites fall within hexels with <10% forest cover; these are color-coded by their sample-site and sample-tree density, but the hexel outline is not shown. Aerial imagery is from the NASA Earth Observation Blue Marble (https://neo.sci.gsfc.nasa.gov/view.php?datasetId=BlueMarbleNG-TB).

composition, wood preservation, land use, and fire regimes across North America. For instance, in a relatively homogeneous landscape with a frequent fire regime, if the vegetation is dominated by trees that easily record and preserve fire scars, it may be possible to characterize attributes of the fire regime, such as mean fire interval or fire season, with a small number of sites or relatively few trees (Van Horne & Fule, 2006). More intensive sampling is needed, however, to address more specific questions, such as the relationships among fire, climate, and tree establishment (Brown & Wu, 2005), the spatial extent of individual fires (Farris et al., 2010; Hessl et al., 2007; Huffman et al., 2015; Marschall et al., 2019; O'Connor et al., 2014; Swetnam, Falk, Hessl, &

Farris, 2011), landscape variability in fire regime metrics (Kernan & Hessl, 2010), or uncertainty in estimates of fire regime metrics for a given degree of sampling effort (Farris et al., 2013; Van Horne & Fule, 2006). A higher density of sample sites is typically needed in more topographically complex landscapes, or when seeking to quantify variation in fire regimes across biophysical gradients (Caprio & Swetnam, 1995; Heyerdahl et al., 2011; Huffman et al., 2020; Kellogg et al., 2007; Kitchen, 2012; Margolis & Balmat, 2009; Odion et al., 2014; Taylor & Skinner, 1998). To address questions of spatial scaling of fire-regime metrics, spatially explicit tree locations are valuable (McKenzie et al., 2006; McKenzie & Kennedy, 2012). Different sample designs are likely necessary to meet

different study objectives, but where possible, standardized sampling (e.g., small plot reconstructions, along with recording individual tree locations) will facilitate future meta-analyses and data comparisons, making it a priority for the fire-history community.

Although the network is composed of sites collected with different methods and objectives, which can pose some challenges for meta-analyses, the common standard of crossdating that results in annually resolved fire dates is one reason that many of the potential limitations can be overcome. Tree ring fire scars are unequivocal point records of fire occurrence, which allows them to be combined and analyzed across scales (e.g., Falk et al., 2011; Swetnam & Baisan, 1996). This is why tree-ring fire-scar network analyses have provided important insights into fire–climate relationships, as described above, in addition to the broad spatial scales over which many components of the climate system operate. Analyses across large areas will require different techniques (e.g., filtering to including fires recorded by $>x$% of trees) applied to the different components of a fire regime to minimize the differences and possible limitations of the original data. Not all fire regime metrics are equally comparable across the network. For example, fire interval analyses may need careful assessment of covariates such as area sampled (Falk & Swetnam, 2003) or vegetation type for valid comparisons. Statistical assessments of sample-size relationships or collector's curves can help quantify, model, and correct for differences among sampling procedures or changing sample depth to ensure robust comparisons across sites and through time (e.g., Swetnam et al., 2016). Overall, these challenges can be addressed with multiple methods, including validations of the fire-scar record with modern fire data.

The increasing number of regions with high sample densities presents new opportunities to advance our understanding of scaling properties of fire regimes (Lertzman et al., 1998; McKenzie & Kennedy, 2012). An important question, even for well-sampled ecoregions, is what is an appropriate spatial scale of inference beyond the immediate stand or vegetation patch where trees were sampled? This can be tested through combinations of fire history, stand reconstructions, and modeling (e.g., Kennedy & McKenzie, 2010; Maxwell et al., 2014). The answer to this question undoubtedly depends on fire size and frequency and varies among landscapes within the continent, with important implications for ongoing debates in fire science and management (e.g., Fulé et al., 2014; Lafon et al., 2017; Matlack, 2013; Oswald et al., 2020). Additionally, the large scope of this collection provides the opportunity for studies of fundamental scaling properties of fire regimes, such as relationships between fire frequency and area—similar to species–area relationships (Arabas

et al., 2006; Falk et al., 2007; Falk & Swetnam, 2003; McKenzie et al., 2006). Such relationships may provide critical information for effective fire management, especially in frequent fire regions where prescribed fires or lightning ignited wildfires are needed to maintain habitats (e.g., Fill et al., 2015; Huffman et al., 2017; Noss et al., 2015).

Comparing the fire-scar network to other continental paleodata networks suggests possible directions for future syntheses and collaborations (Appendix S1: Figures S1–S3). For example, the Global Charcoal Database v3 includes 211 lake-sediment charcoal sites in North America (Marlon et al., 2015). Twenty (9%) of these sites are within 10 km of a fire-scar site, 27 (13%) sites are within 15 km, and 40 (19%) sites are within 20 km. Thus, without collecting additional data there may be numerous opportunities to combine tree-ring and lake-sediment records of fire. Combining the centuries-long annual to sub-annual resolution tree-ring fire-scar data with the multimillennial length lake sediment and alluvial charcoal data can inform a more complete understanding of patterns and drivers of fire regime changes (Allen et al., 2008; Beaty & Taylor, 2009; Bigio et al., 2010; Higuera et al., 2010, 2021; Leys et al., 2019; Waito et al., 2018; Whitlock et al., 2004). There are also 254 fire-scar sites located within 10 km of a lake-sediment pollen site in the Neotoma Paleoecology Database (https://www.neotomadb.org/; Appendix S1: Figure S3), providing the potential to evaluate fire history within the context of long-term vegetation change. Some potential challenges for combining tree-ring and sediment records include different temporal resolutions (e.g., annual to sub-annual vs. multidecadal to centennial, although annually resolved "varved" lake sediments do exist), different spatial resolutions (systematic grids covering thousands of hectares vs. single sediment cores), potential differences in ecological settings (e.g., mid-elevation montane forests vs. high-elevation alpine lakes). Many of these challenges can be addressed with careful site selection, analysis methods, and calibration with modern fires (e.g., Allen et al., 2008).

VEGETATION

Fire is a fundamental driver of plant evolution and ecology (Bond & Keeley, 2005; Mutch, 1970), promoting a diverse suite of adaptations for survival and reproduction (Keeley et al., 2011; Pausas et al., 2004; Poulos et al., 2018), and shaping global patterns of terrestrial vegetation (Bond et al., 2005; McLauchlan et al., 2020; Noss et al., 2015). Across a wide range of North American ecosystems, studies of fire scars have demonstrated how different vegetation patterns and processes are linked ecologically and evolutionarily to particular fire regimes (Heinselman, 1973; Johnston et al., 2016; Myers, 1985;

O'Connor et al., 2017; Stephens et al., 2003; Tande, 1979; Wright & Agee, 2004). Such studies also demonstrate how fire regimes have changed in association with human land use and climate, shedding light on attendant vegetation shifts (Bergeron, 1991; Brown & Sieg, 1999; Guyette et al., 2002; Huffman et al., 2004; Iniguez et al., 2016; Larson et al., 2021; North et al., 2005; Savage & Swetnam, 1990; Taylor et al., 2016). In addition to the effects of fire on vegetation, fire regimes themselves are strongly modulated by vegetation composition and structure, creating fire-vegetation feedbacks (e.g., Platt et al., 2016) that are increasingly recognized as important ecological processes (Hoctor et al., 2006) as well as important determinants of forest resilience and, conversely, vulnerability under climate change (Hurteau et al., 2019; Kitzberger et al., 2016; Liang et al., 2017; Odion et al., 2010; Strahan et al., 2016). Fire-scar analysis can provide critical insights into a full range of fire-vegetation feedbacks, including fuel limitations (Erni et al., 2017; Guyette et al., 2002; Scholl & Taylor, 2010; Taylor & Skinner, 2003) and the development and maintenance of alternate vegetation types (Flatley et al., 2015; Guiterman et al., 2018), thus contributing to the scientific foundation for restoring fire-dependent ecological communities (Swetnam et al., 1999). We anticipate that the NAFSN will provide opportunities to develop new insights into the importance of fire-vegetation interactions across scales and disciplines. To illustrate some of these opportunities, we characterize the forest types and tree species of the NAFSN at continental and ecoregional scales.

Ecoregions are areas in which local ecological types recur predictably on comparable sites (Bailey, 1995), and generally represent geographic areas that integrate broad similarities in climate and biogeographic affinity. We used North American Level 1 Ecoregions (https://www.epa.gov/eco-research/ecoregions), recognizing a trade-off between accuracy at the continental scale and high variability in forest types and ecology at the landscape to local scales. We constrained the spatial extent of our analysis to areas mapped as forest based on a 500-m resolution MODIS vegetation product (Friedl & Sulla-Menashe, 2019). We used the resulting forested portions of ecoregions to define areas of interest for vegetation analyses, as well as for subsequent analyses in the paper (e.g., the topographic and climate spaces of fire regimes). A small percentage of sites (1.4%) were in areas not mapped as forests. Some of these represent inaccuracies or mismatches of spatial resolution in the MODIS product, but others may represent shifts to nonforest following recent high-severity fires or other human land use. Broad groupings of gymnosperm and angiosperm fire-scarred trees were compared to current forest cover from the North American Land Cover Monitoring System (http://www.cec.org/north-american-environmental-atlas/land-cover-30m-2015-landsat-and-rapideye/) to look for potential differences between the present forest cover and the forest type sampled in the fire-scar record. To describe the patterns and variability of fire-scarred tree species across North America, we determined the relative proportion of species sampled for all sites and by ecoregion. Samples at each study site were also grouped by phylum, genus, and species to examine patterns by ecoregion.

Tree-ring fire-scar sites are present across a broad range of gymnosperm and angiosperm dominated forests in North America (Figure 3a). Fire-scar sites occur in 13 of 15 ecoregions, ranging from boreal forests in northern Alaska and Canada to subtropical forests in southern Mexico (Figure 3b, Table 1). The Northwestern Forested Mountains ecoregion contains nearly half (46%) of the total number of fire-scar sites (1182 sites) and has the second highest density of sites (6.6 per 10,000 km^2; Table 1). The highest density of sites (9.5 per 10,000 km^2) is in the Southern Semi-arid Highlands in the US/Mexico borderlands, the second smallest ecoregion. The Northern Forests, Taiga, Temperate Sierras, and Eastern Temperate Forests ecoregions contain 170–258 sites (Table 1). The North American Deserts, Mediterranean California, Hudson Plain, Great Plains, Marine West Coast Forest, Tropical Wet Forests, and Tundra have the fewest sites (2–73 sites).

The NAFSN includes 91 species of fire-scarred trees, but only a small number were commonly sampled. The 10 most common species were sampled at 75% of the sites, and 71 species (78% of the total) were sampled at 25 or fewer sites (Figure 4; Appendix S1: Table S1). Most sites in the network (73%) contain fire-scarred gymnosperms from the genus *Pinus* (Figure 3a). *Pinus* species ($n = 39$) account for 43% of the total tree species and were sampled in all ecoregions except for Tundra (Figure 4). Ponderosa pine was the most sampled species in the NAFSN and was present at 39% of all sites (1005 out of 2562). Other gymnosperm genera represented by three or more species include *Abies*, *Juniperus*, *Tsuga*, *Larix*, and *Picea*. The following gymnosperm species are important regionally: Douglas-fir (*Pseudotsuga menziesii*), black spruce (*Picea mariana*), lodgepole pine (*P. contorta*), southwestern white pine (*P. strobiformis*), pitch pine (*P. rigida*), red pine (*P. resinosa*), shortleaf pine (*P. echinata*), bigcone Douglas-fir (*Pseudotsuga macrocarpa*), and Table Mountain pine (*P. pungens*; Figure 4). Fire-scarred angiosperms were less commonly sampled (24 species at 8% of the sites), but are important regionally (e.g., Great Plains). *Quercus* was the most-commonly sampled angiosperm genus, represented by 12 species sampled at 122 sites. Other angiosperm genera included *Populus* ($n = 52$ sites) and *Carya* ($n = 11$ sites).
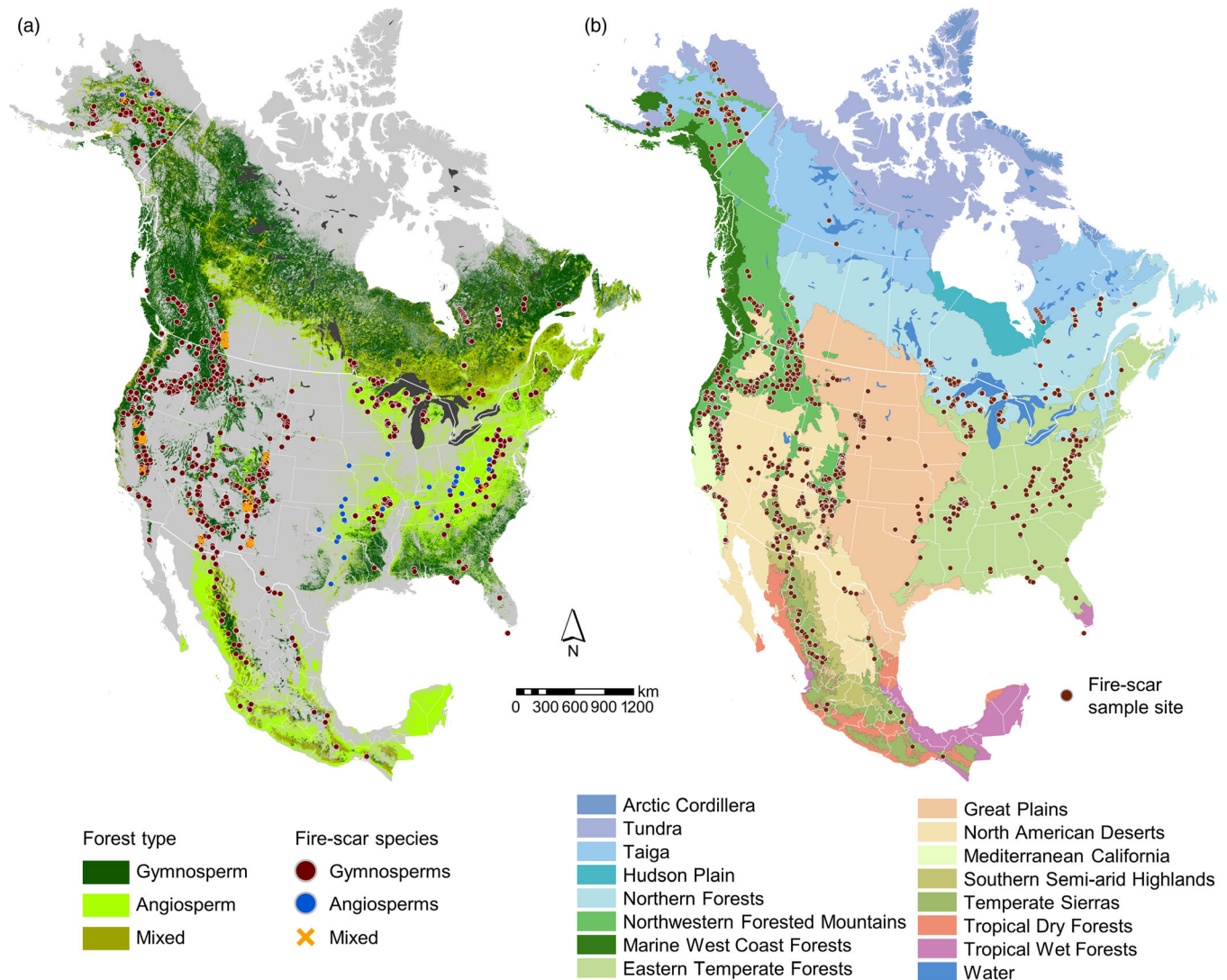
FIGURE 3 The North American tree-ring fire-scar network mapped with (a) gymnosperm and angiosperm forests and (b) level 1 ecoregions. The fire-scar sites in (a) are coded by the same forest classes, which highlights areas where the current mapped forest class differs from the species with fire scars (e.g., angiosperm forest cover with gymnosperm fire-scarred species in the eastern United States). North American Level 1 Ecoregions (https://www.epa.gov/eco-research/ecoregions).

An interesting mismatch exists in multiple regions between the general forest type of the current dominant tree species and the species of fire-scarred trees (e.g., the eastern United States and the southern Great Lakes regions; Figure 3a). Although current forests in large parts of these regions are dominated by angiosperms, the fire-scar collections are dominated by gymnosperms. This mismatch has multiple probable causes. First, gymnosperms are less common than they were historically due to widespread logging and fire exclusion, especially where *Pinus* communities were maintained by frequent fire (Nowacki & Abrams, 2008). Second, isolated individuals or patches of gymnosperms are the best recorders of fire in angiosperm-dominated landscapes, because of the relatively poor preservation of scars by angiosperms, making gymnosperms the primary target for sampling

(Lafon et al., 2017; Marschall et al., 2019). A more subtle change in species composition from fire-tolerant to fire-intolerant gymnosperms has also occurred in response to over a century of fire exclusion in many western forests (Hagmann et al., 2021; Johnston et al., 2016; Margolis & Malevich, 2016; Merschel et al., 2014; Metlen et al., 2018). In these locations, fire scars are present on the more fire-tolerant species, despite their reduced and declining proportion in the current forest.

The spatial pattern of fire-scar samples in the NAFSN is largely determined by broad biogeographic patterns of vegetation and fire regimes. Conifers, and particularly pines, are common in seasonally warm, surface fire-prone ecoregions and dry topographic positions such as exposed uplands and ridgetops (e.g., Fule et al., 2011; Lafon et al., 2017; Marschall et al., 2019). The distribution

TABLE 1 Tree-ring fire-scar site information for North American ecoregions. Ecoregions are sorted by descending fire-scar site density

Level 1 ecoregion	No. sites	Area (km²)	Site density (no./10,000 km²)
Southern Semi-arid Highlands	256	270,340	9.47
Northwestern Forested Mountains	1181	1,788,950	6.60
Temperate Sierras	224	634,485	3.53
Mediterranean California	63	198,975	3.17
Northern Forests	258	2,363,825	1.09
Hudson Plain	34	334,530	1.02
Taiga	255	2,799,230	0.91
Eastern Temperate Forests	170	2,578,435	0.66
North American Deserts	73	2,027,460	0.36
Marine West Coast Forests	12	692,970	0.17
Great Plains	32	3,543,875	0.09
Tropical Wet Forests	2	311,070	0.06
Tundra	2	2,856,850	0.01
Arctic Cordillera	0	168,520	0
Tropical Dry Forests	0	333,170	0
All ecoregions	2562		

of dry conifer forests, which includes ponderosa pine and the associated frequent fire regimes, is a primary reason for the high density of sites in the Northwestern Forested Mountains ecoregion and other ecoregions of western North America (Figures 2 and 3). Other factors, such as naturally low tree cover or conversion to agriculture, contribute to the low sampling density in the Tundra, North American Deserts, and Great Plains ecoregions. This means that few fire-scar records exist for some of the most fire-dependent vegetation on the continent, such as the expansive grasslands of the Great Plains. Fire-scar sites are also rare in some regions with abundant conifer forests, such as the Eastern Temperate Forest ecoregion, where current forests are relatively young due to centuries of extensive human land use. Stumps of pine species such as longleaf pine, which dominated the southeastern Coastal Plain before logging, can contain numerous fire scars (Huffman, 2006; Huffman et al., 2004; Rother et al., 2020), but most stumps were removed or have been consumed by prescribed fires, and in some stands stumps rarely contain scars because of the historically low intensity, frequent fires (Huffman et al., 2004; Rother et al., 2020; Stambaugh, Guyette, & Marschall, 2011). Finally, there are more fire-scar records from the Taiga and Northern Forests than might be expected given that these forest types are generally expected to burn at high severity and consequently produce relatively few surviving trees to record fire (e.g., de Groot et al., 2013). In these forests, fire scars can sometimes be found on scattered surviving trees within high-severity patches or along fire

boundaries where fire intensity drops as a result of a fuel break (e.g., less productive surficial deposits) or an increase in soil moisture along the edges of peatlands or lakes (Bergeron, 1991; Heon et al., 2014; Rogeau et al., 2016). In boreal ecoregions, islands and lakeshore landscapes are areas where mixed fire severities and fuel breaks can result in abundant fire scars (Bergeron, 1991).

Plant traits also have a large influence on the distribution of sites and species in the NAFSN. The predominance of pine species such as ponderosa, longleaf, pitch, and red pine among the fire-scar sample sites reflects the presence of traits that may promote relatively frequent and low-intensity fires (Mutch, 1970; Platt et al., 2016), including high energy content in the litter and dead branches (Reid & Robertson, 2012), concentrations of flammable chemicals, especially terpenes (Varner et al., 2015), and long pyrogenic needles that minimize fuel bulk density and fire intensity (Schwilk & Caprio, 2011). Many pines and other conifers also have traits suiting them to record and preserve fire scars, such as thick, insulating bark (Keeley, 2012), and resinous wood and secondary compounds (e.g., terpenes) that provide resistance to decay after scarring (Smith et al., 2016; Verrall, 1938) and postmortem. These traits enable pines to survive and preserve fire injuries more often than angiosperms, leading them to be the most represented fire-scarred trees even in angiosperm-dominated ecoregions (e.g., the Eastern Temperate Forests; Figure 3a). *Quercus* and other angiosperm genera are more susceptible to disease and rapid decay (Lafon et al., 2017; McEwan
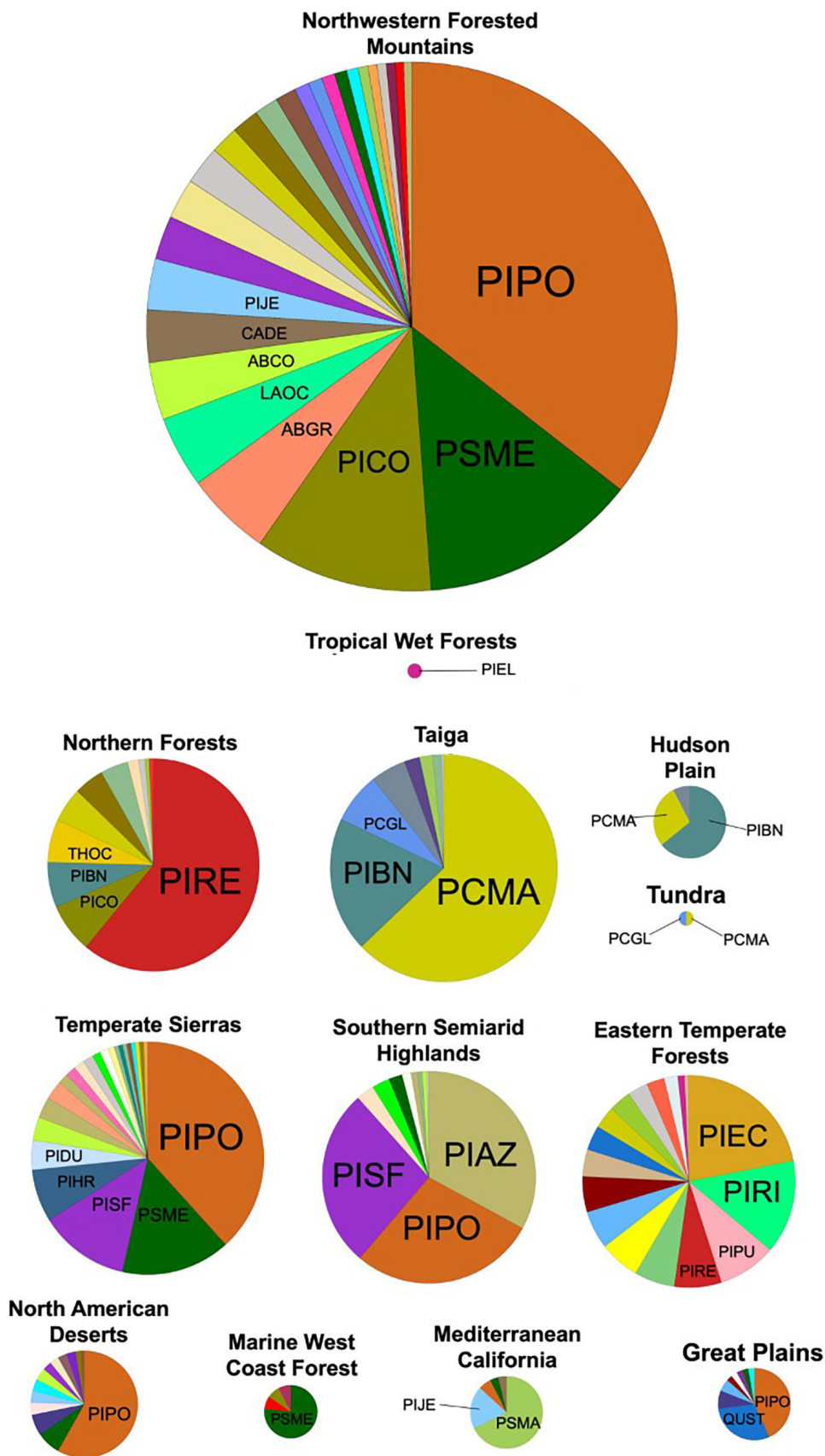
FIGURE 4 Proportion of fire-scarred tree species (four-letter species codes) sampled by site for North American ecoregions. The pie chart size is scaled by the relative number of sites in each ecoregion. See Appendix S1: Table S1 for the full species names and the count of all species.

et al., 2007). Additionally, many hardwood species lack the long lifespans ideal for reconstruction of historical fire, although there are important exceptions (Shumway et al., 2001; Stambaugh, Sparks, et al., 2011; Wolf, 2004).

The presence of fire-scarred trees across different ecoregions, genera, and species in the NAFSN indicates that fire was historically an important ecological component of diverse ecosystems across North America, even in areas where fire scars were previously thought to have been uncommon. The dataset revealed a remarkably high diversity of tree species that can be used for fire-scar analysis. Recent advances in the use of new species, including *Pinus* species in Mexico and angiosperms in eastern North America, indicate great potential for expanding the fire scar network. It is likely that fire-scarred trees and remnants exist in ecosystems and regions that lack the widely sampled conifers, such as near-coastal forests containing knobcone pine (*P. attenuata*) in California, or sagebrush and other nonforested ecosystems where forested islands contain conifers that can record fire scars. In addition, fire-scar sites in locations that currently do not contain forests due to recent, repeated high-severity fires (e.g., the Southern Semi-arid Highlands) provide important context for increasing disturbance-catalyzed vegetation changes (Coop et al., 2020) and projected future changes (Keyser et al., 2020; O'Connor et al., 2020). Further innovative uses of tree-rings and fire scars to address pressing vegetation questions have the potential to further unravel complex feedbacks between fire regimes, vegetation, and human influence in a changing climate.

SAMPLE DEPTH

The multicentennial to millennial length of tree-ring fire-scar records is a primary reason they are valuable for understanding patterns and drivers of variability of fire regimes (Marlon et al., 2012; Swetnam, 1993; Taylor et al., 2016). The potential temporal depth of fire-scar records across North American forests is dependent on numerous factors previously discussed, such as species composition and age, wood preservation, or logging and land use history. The location of research programs focused on fire-scar analysis, with strong roots in the western United States and more recent expansion elsewhere, also influences the sample depth of fire-history studies. Recent high-intensity fires, or even low-intensity fires burning during drought can kill fire-scarred trees, can burn off fire scars on live trees, or consume dead wood containing the oldest fire records (Heyerdahl & McKay, 2008). Given the diversity and overlap of these variables across North America, diversity in the length of

fire-scar records is considerable. Here, we evaluate the NAFSN with respect to the sample depth and temporal extent of fire history data by ecoregion to identify areas of particular value to focus future sampling to better identify fundamental properties of North American fire history.

Fire-scar dates range from 1237 Before the Common Era to 2017 Common Era (CE). The earliest fire scars were recorded in giant sequoia trees in the Sierra Nevada of California (Swetnam, 1993; Swetnam et al., 2009). Ten percent of the sites (243) have fire scars dating to 1500 CE or earlier (Figure 5a), most of which are located in western ecoregions; 647 (25%) have fire scars prior to 1600 CE, including numerous sites in the Northern Forests and Eastern Temperate Forests ecoregions; and 1297 (51%) sites have fire scars earlier than the year 1700 CE and span much of North America. The Northwestern Forested Mountains has the oldest records (Figure 5a,b), largely due to giant sequoia sites. Multiple other ecoregions demonstrate the potential for fire records back to the 1400s (e.g., North American Deserts and the Temperate Sierras), even with relatively few sites. Although tree-ring and fire records tend to be shorter in the eastern and northern ecoregions, the interval between the start of the tree-ring record and the first fire scar at sites throughout the network was similar (Figure 5b), potentially indicating a property of fire-scar formation in surface fire regimes that should be investigated further. The notable exception is in the Taiga, where the length of the fire-scar records is relatively short, even where the tree ages extended multiple centuries. The year of the most recent fire per site varies within and among ecoregions. Fire declined in some ecoregions ca. 1900 CE (e.g., Northwestern Forested Mountains and Northern Forests), whereas other regions have relatively continuous fire records up to the present (e.g., Southern Semi-arid Highlands of Mexico; Figure 5b). When summed across the NAFSN, a peak in the most recent fire year occurred ca. 1900 CE, coincident with land use changes and widespread fire exclusion. Another peak ca. 2000 CE (Figure 5c) represents uninterrupted fire regimes and recent increases in fire activity (see *Humans* section for further discussion of patterns and drivers of fire regime changes).

Variation in the length of the fire-scar records reflects spatial patterns of many variables that influence fire regimes (e.g., climate, species traits, and land-use history). Records are longer in drier ecoregions where sites and favorable tree species for fire scar sampling and wood preservation were associated with frequent, low-severity fire regimes (e.g., Mediterranean California, Temperate Sierras, North American Deserts, and Northwestern Forested Mountains). In contrast, records are
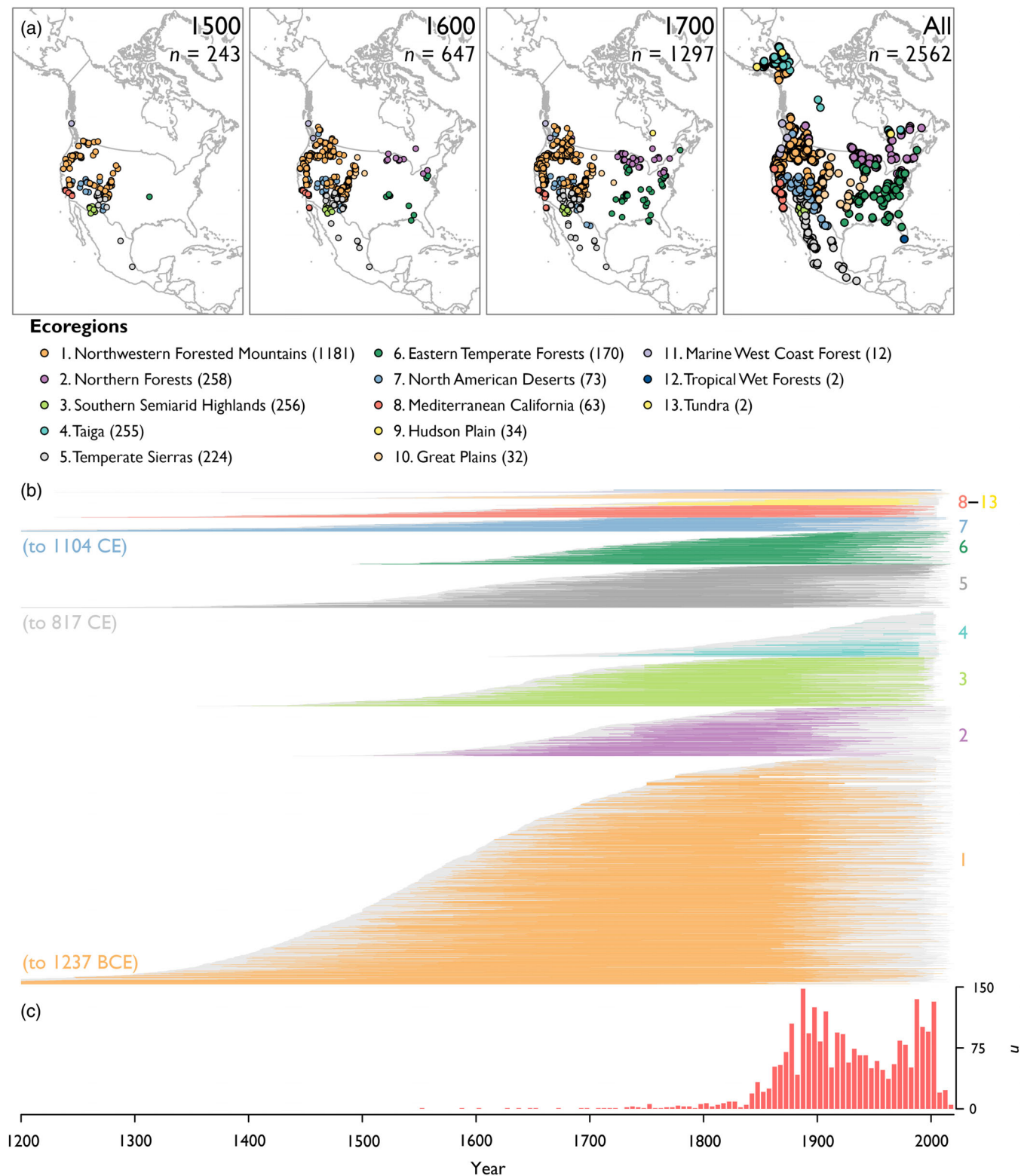
FIGURE 5 Sample depth of the North American tree-ring fire-scar network in time and space by ecoregion. (a) Maps of the spatial distribution of the network in time. Sites are color coded by ecoregion. (b) Sample depth through time of fire-scar sites by ecoregion back to 1200 Common Era (CE). The tree-ring record is light gray, and the fire-scar record is colored by ecoregion. Ecoregions with <50 sites are not numbered. The earliest fire date for sites extending <1200 CE is noted for each ecoregion. (c) Histogram of the most recent fire year for all North American fire-scar sites.

shorter in wetter ecoregions where decomposition is more rapid (Eastern Temperate Forests) and where mixed- or high-severity fire regimes are more common (e.g., Taiga, Northern Forests). Although older records (>400 years old) do exist in these wetter environments, a strategic approach may be required to find them. The difference between the length of the tree-ring record and the fire-scar record in the Taiga may be the result of a higher-severity regime. It could also represent a changing fire regime driven by climate change or changing human ignitions, or an incomplete fire record related to the species sampled (e.g., spruce vs. pine). There is great potential to expand the spatial and temporal coverage of fire history in the Taiga and Northern Forests (Figures 3a and 5), although challenges include the rarity of long-lived species, remoteness, relatively poor preservation of wood, greater potential for high-severity fire that creates fewer fire scars, and the recent increase in fire activity that destroys wood containing fire scars.

The broad spatial coverage of the NAFSN back to 1700 CE and earlier provides new opportunities for continental-scale analysis of fire regimes and drivers of spatiotemporal variability in fire regimes. Increased coverage in Canada and Alaska is ongoing and should be prioritized to better understand these important regions where climate change is rapidly increasing fire activity (Whitman et al., 2019). Targeting areas with the potential for longer records (i.e., prior to 1700 CE) in eastern North America would be beneficial for studying the changes in ecosystems and fire regimes related to European colonization and displacement and decline of Native American populations and cultural practices (Guyette et al., 2002; Kipfmueller et al., 2021; Stambaugh et al., 2018). Characterizing the environmental conditions of existing older sites in undersampled regions (e.g., topography or geologic features such as exposed rock that can reduce rates of wood decay or moderate fire behavior) could be fruitful to systematically target potential new areas for older fire records. Similar systematic or spatial modeling approaches could also be used to extend fire records prior to the Spanish influence in southern North America ca. 1500–1600 CE. Finally, it is important to recognize that we are on the "tip of the iceberg" in terms of the potential for tree-ring fire-scar records in much of North America, even in well-sampled regions or heavily logged forests (e.g., Taylor, 2004). For example, a recent collection from the cold and dry Taos Plateau of northern New Mexico, a region with a long dendropyrochronological history, is revealing some of the longest, most-interesting fire histories in the region (i.e., multiple sites with replicated fire scars back to the 1400s and individual scars in the 1100s).

TOPOGRAPHY

Topography is a primary influence on fire regimes and fire-scar formation through direct effects on the physics of fire behavior and indirectly through effects on vegetation and fuels (Agee, 1993; Rothermel, 1983). Slope, aspect, elevation, and topographic roughness directly and indirectly influence fire frequency, severity, and fire size (Cansler & McKenzie, 2014; Dillon et al., 2011; Heyerdahl et al., 2001; Iniguez et al., 2008; Kellogg et al., 2007; Kitchen, 2012; Stambaugh & Guyette, 2008; Taylor & Skinner, 1998). For example, flatter areas on ridge tops or valley bottoms may be more likely to burn with lower intensity or at longer intervals (e.g., Romme & Knight, 1981; Van de Water & North, 2010), whereas steeper slopes can increase the probability of high-severity fire (Swanson, 1981), leaving fewer surviving trees. Slope also affects the process and pattern of fire-scar formation. In flat terrain, fire scars are commonly found on the leeward side of trees, in relation to the direction of the flaming front, due to increased heat and residence time that can be explained by fluid dynamics and heat transfer (Gutsell & Johnson, 1996; Rothermel, 1983). In sloped terrain, fire scars commonly form on the upslope side of the tree, regardless of the direction of the wind or the flaming front (Yocom Kent & Fulé, 2015). This is due to multiple processes, including increased convective heating and upslope vortices, and the effect of gravity on downslope movement of fuel that accumulates on the upslope side of the tree and increases heat and the residence time of burning. Elevation likewise affects productivity, fuel loads, and plant species composition, and thus influences fire intensity and creates patterns of fire-scarred trees along elevational gradients (Guyette et al., 2012). Topographic complexity overall, measured at multiple spatial scales, is reflected in spatiotemporal patterns of fire scars (Kellogg et al., 2007; Kennedy & McKenzie, 2010; McKenzie & Kennedy, 2012). The broad range of topographic conditions represented by the NAFSN provides new opportunities to explore the effects of topography on fire regimes and fire-scar formation.

We characterized topographic variables associated with the NAFSN to identify patterns and variability in the fire-history record across North America. We derived topographic data for North America from a mosaic of 90-m resolution digital elevation models from Mexico, the conterminous United States, Canada, and Alaska. For Mexico and the conterminous United States, we used Shuttle Radar Topography Mission (SRTM) data (https://www2.jpl.nasa.gov/srtm/). Due to a lack of high latitude SRTM data for Canada and Alaska, we used 90-m resolution Multi-Error-Removed Improved-Terrain digital elevation data (Yamazaki et al., 2017). We used the combined elevation data to derive two additional topographic variables, slope angle and slope aspect. We then

extracted values for the three topographic variables for the point location of all fire-scar sites. In some cases, there may be considerable variation in topographic conditions within individual fire-scar sites, and future fine-scale studies of fire-topography interactions using NAFSN will be important for understanding cross-scale influences of topographic conditions on historical fire regimes. The analysis presented herein offers a preliminary look at topographic influences on the continental-scale fire-scar record.

To compare the topography of sampled fire-scar sites with the background topography of forests across North America, we derived a topographic state space. The topographic state space of North American forests was produced by extracting elevation, slope angle, and slope aspect from 330,000 random points within the MODIS North American forested area (described in *Vegetation* section). The topographic variables were then compared between NAFSN sites and the random points to identify the topographic conditions with relatively high or low numbers of fire scar sites.

Tree-ring fire-scar sites in North America are found across a broad range of topographic settings. Fire scars are present in flat and steep terrain, across all slope aspects, and from sea level to more than 4000 m above sea level (asl; Figure 6a). When compared to the background forested landscape, fire-scar sites are found in greater abundance on steeper slopes (between 10° and 30°) and at higher elevations (between 1000 and 3000 m asl, Figure 6a,b). Fire-scar sites in low-elevation, flat, forested areas of eastern and northern North America are rare in the NAFSN, although there were large areas of forest in this topographic setting (Figure 6b). Fire-scar sites are located more often on southerly aspects and less on northerly aspects than North American forests (Figure 6c).

The topography of forests and fire-scar sites indicates important variability within and among North American ecoregions. Fire-scar sites at relatively high elevations are concentrated in four ecoregions in southwestern North America: Mediterranean California, North American Deserts, Southern Semi-arid Highlands, and the Temperate Sierras (Figure 7). There is a unique bimodal distribution in the elevation of fire-scar sites in the Northern Forests ecoregion, which represents low-elevation sites in the glaciated Great Lakes region and ridgetop sites in the Appalachian Mountains of the northeastern United States. The slope angle of fire scar sites (typically between 0° and 30°) is relatively similar among ecoregions, except where steeper terrain was rare (e.g., Taiga and Hudson Plain, Figure 7). The slope aspect of fire-scar sites is highly variable among ecoregions. The pattern of fire-scar sites on south-facing slopes in the full network (Figure 6c) is

concentrated in four ecoregions: Northwestern Forested Mountains, Northern Forests, Temperate Sierras, and Hudson Plain (Figure 7). In contrast, the North American Deserts, Mediterranean California, Southern Semi-arid Highlands, and the Great Plains show the opposite pattern, higher concentrations of fire-scar sites on north-facing slopes when compared to the slope aspect of forests in those ecoregions.

The topographic patterns and variability in the NAFSN are a function of (1) the pattern of fire-scarred trees on the landscape and (2) where fire scars were sampled. It is not possible to determine whether patterns in a certain topographic variable indicate a pattern in the location of fire-scarred trees or a pattern in the sampling; both are present in the data. For example, in some ecoregions (e.g., Northwestern Forested Mountains) some of the wetter, north-facing slopes were historically more likely to burn at higher severity or longer intervals and have fewer fire-scarred trees; conversely the adjacent drier, south-facing slopes were less likely to burn at high-severity and have more fire-scarred trees (e.g., Margolis & Balmat, 2009; Marschall et al., 2016; Taylor & Skinner, 1998). In this example, if the goal of sampling is to capture the longest record with the most fire scars in an area, then a south-facing slope would be preferred. Random or spatially systematic samples of fire scars across large, topographically diverse areas (e.g., Farris et al., 2010; Heyerdahl et al., 2011; Merschel et al., 2018; Scholl & Taylor, 2010) can be used to objectively characterize and better assess topographic variables associated with fire-scar formation. Spatially systematic samples can also illuminate cross-scale patterns on landscapes (Falk et al., 2007; Kernan & Hessl, 2010; McKenzie & Kennedy, 2012). Increased understanding of topographic controls on fire-scar formation at multiple scales would increase confidence in the extrapolation of fire-scar derived fire regime metrics across topographically complex landscapes.

The ecoregion-level analysis revealed interesting patterns of variability in topography associated with fire-scar sites. These likely reflect regional differences in the patterns and drivers of fire regimes (e.g., influences of climate, vegetation, and humans). For example, in cooler, wetter, flatter environments, such as the Great Lakes sites within the Northern Forests ecoregion, topography likely amplified human impacts on fire regimes at south and southwest-facing sites that were edaphically more amenable to frequent surface fire (Larson et al., 2021). North American Deserts ecoregion, fire-scar sites are concentrated at circa 2500 m asl, 1000 m higher than the peak density of forests. This likely represents the confluence of multiple bio-climatic phenomena unique to this semi-arid region that affect fire regimes and tree growth.
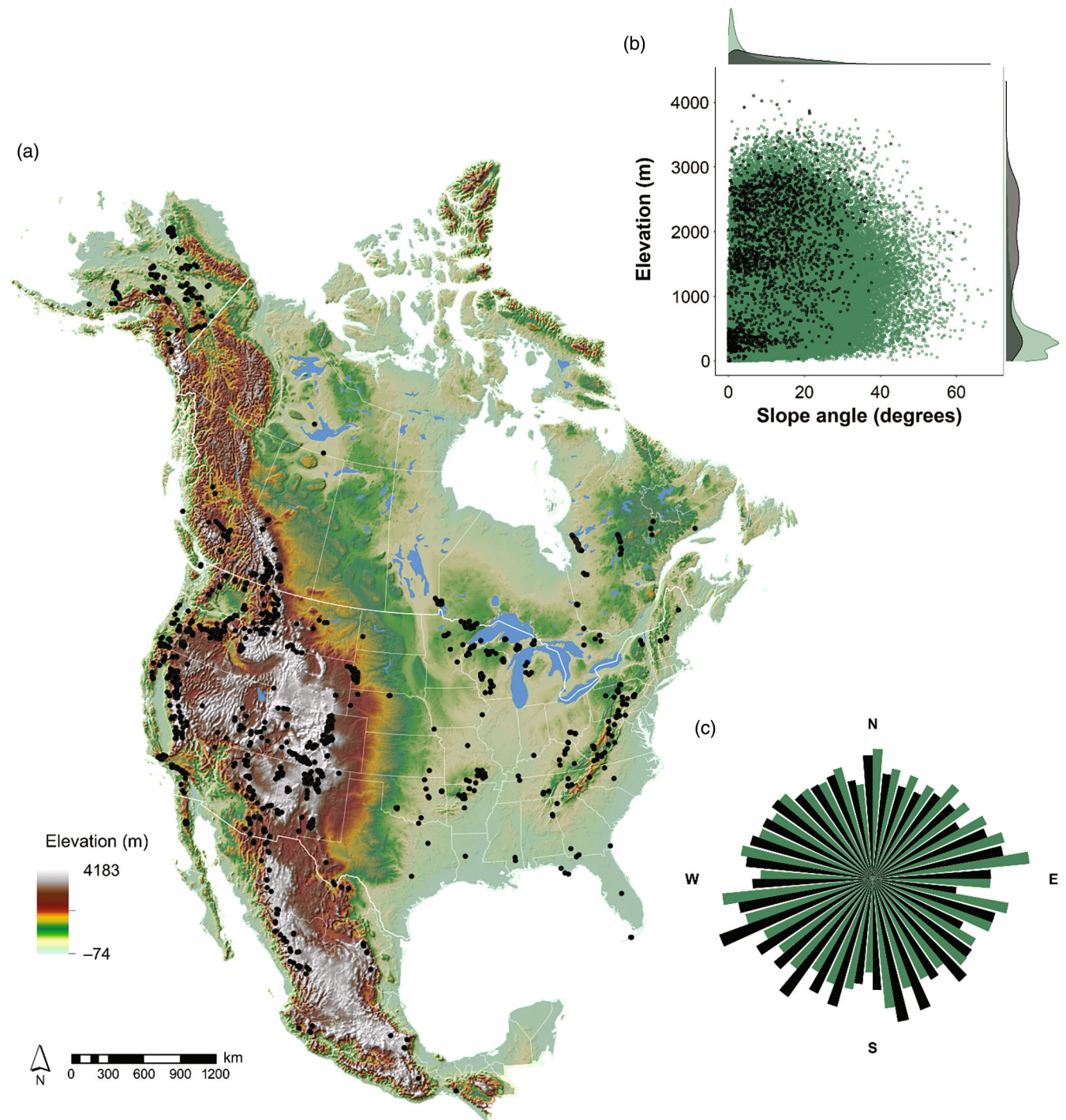
FIGURE 6 (a) Elevation and fire-scar sites (black points) in North America. (b) Slope angle versus elevation of random points (green) in North American forests and tree-ring fire-scar sites (black). (c) Slope aspect of random points in North American forests (green) and tree-ring fire-scar sites (black). Aspect class bar length is percent of total sites. The random points were located in forested areas of North America to represent the potential topographic state space of fire scars.

These relatively high-elevation fire-scar sites indicate the zone where moisture is sufficient to produce enough fuel to support recurring fire, yet still sufficiently arid to dry out the fuels so they can burn frequently (Martin, 1982; North et al., 2009). In addition, forests located below this zone of peak density of NAFSN sites may have fewer

trees that can be crossdated, because of abundant missing or false rings associated with opportunistic growth during the summer North American monsoon rains (Meko & Baisan, 2001).

The topographic patterns revealed in the NAFSN have practical utility to guide future research. Gaps in
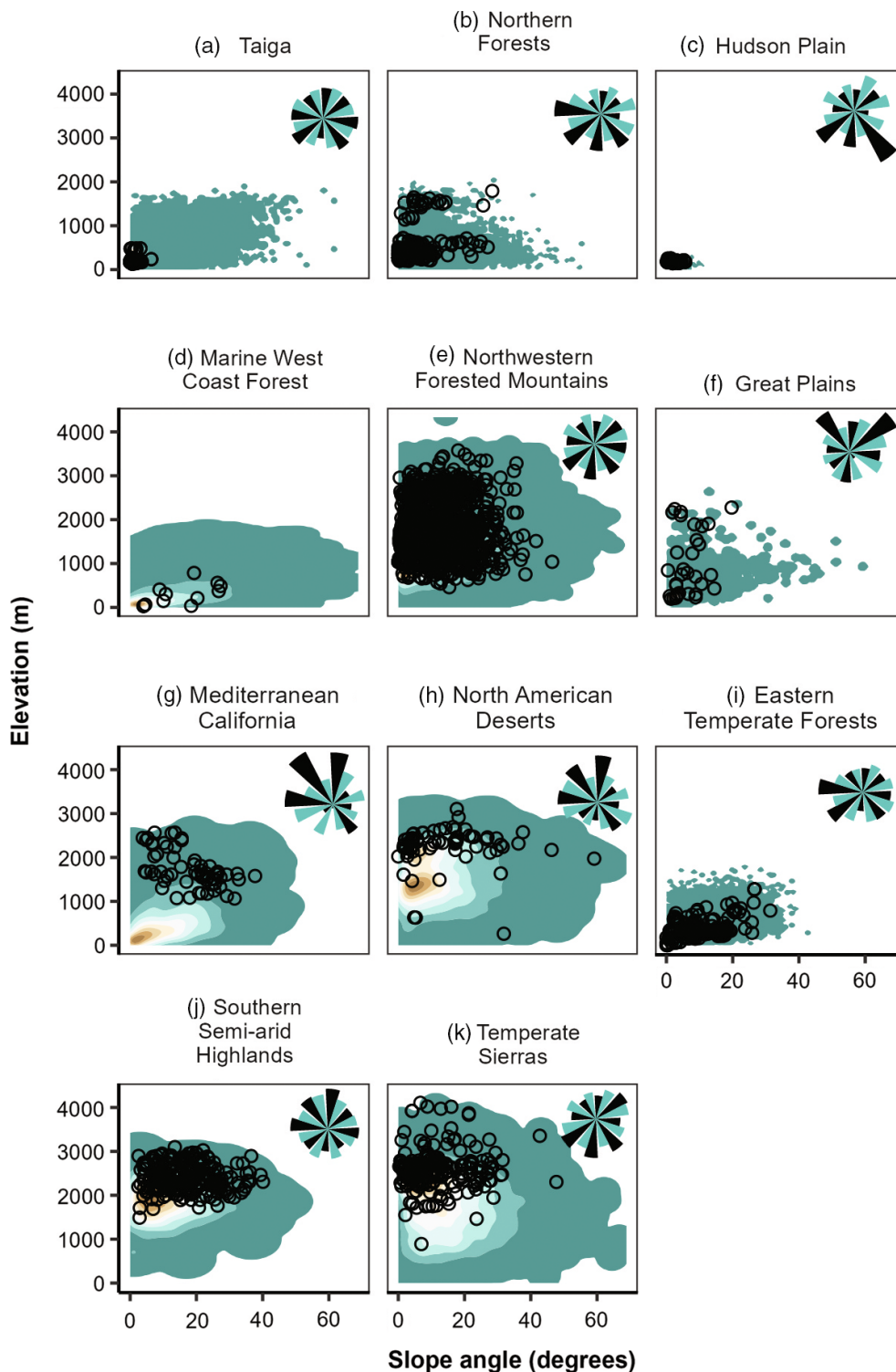
FIGURE 7 (a–k) Slope, elevation, and slope aspect (inset windroses) for random points in forests (colored) and tree-ring fire-scar sites (black) for North American ecoregions. For slope and elevation, the colored surface represents the possible topographic space derived from two-dimensional kernel density estimation scaled from 0.0 to 1.0, (green to brown), with 1 corresponding to the highest point densities. For slope aspect, the green bars of the windrose represent the proportion of random points in 16 aspect classes (north on top) and the black bars are proportions of fire-scarred sites in each aspect class. Slope and elevation were analyzed for ecoregions with more than two fire-scar sites. Slope aspect was analyzed for ecoregions with more than 30 sites. Ecoregion panels are arranged by decreasing latitude.

topographic space may indicate targets for future sampling and may represent new, unrecognized fire regimes (e.g., within the under-sampled flat, low-elevation forests, especially in dissected coastal regions, or on different aspects). Some of these areas may be where human populations are currently concentrated; while this creates challenges related to finding old wood with fire scars, information on historical fires in these areas will be important for contextualizing the growing fire problems in the wildland urban interface. Ecoregional patterns of topographic variables where fire scars are most likely to be found, or refinements of these patterns for a specific study area, can also be used to systematically map and model potential fire-scar locations and develop predictive frameworks for hypothesis testing. Future research could also link topography and fire regime characteristics (e.g., fire frequency or severity) based on mechanisms of fire behavior that were not part of this synthesis. For example, topographic controls may be superseded by extreme fire behavior in a warming climate, leading to "no-analog" patterns of fire frequency and severity being reflected in the fire-scar record (McKenzie & Kennedy, 2012). Capitalizing on the new network and its diversity in fire regimes and topography could provide valuable insights on the role of topographic variability in historical and future fire occurrence and severity, especially in the context of changing fuel structures and warming climate.

CLIMATE

Climate is an important driver of fire regimes that regulates fuels and fire behavior on time scales ranging from seasons within individual years to millennia. Weather and climate variations directly influence the length and severity of the fire season (Parisien et al., 2014; Parks et al., 2018; Westerling, 2016; Westerling et al., 2006), the progression of individual fires (Wang et al., 2017), fire frequency (Guyette et al., 2012), and the variability and efficiency of lightning ignitions (Romps et al., 2014; Veraverbeke et al., 2017). Climatic influences can also include lagging relationships that develop over multiple years. For example, antecedent wet conditions in fuel-limited systems often result in greater abundance and continuity of herbaceous and fine fuels that increase the probability of fire spread in subsequent dry years (Dewar et al., 2021; Howard et al., 2021; Littell et al., 2009, 2018; Margolis et al., 2017; Pohl et al., 2006; Swetnam & Betancourt, 1998). Prolonged, multiseason or multiyear drought can also increase fire occurrence in cooler, wetter, climate-limited systems (e.g., subalpine and boreal forests; Flannigan et al., 2009; Gedalof et al., 2005;

Schoennagel et al., 2007). Over longer time scales of centuries to millennia, climate affects not only fire regimes (Marlon et al., 2008; Marlon et al., 2012; Swetnam, 1993), but also the spatial distribution of vegetation itself (e.g., Nolan et al., 2018), thus modulating the fuelscapes that fires burn. For example, sparser fuels in a warmer drier future may reduce total area burned in some regions, even though wildfire is forecasted to increase globally (Kennedy et al., 2021; Mckenzie & Littell, 2017). Increased understanding of the effects of ocean–atmosphere teleconnections (e.g., the El Niño–Southern Oscillation; Beckage et al., 2003; Swetnam & Betancourt, 1990, 1998; Trouet et al., 2010; Yocom et al., 2010) and jet stream dynamics (Wahl et al., 2019) on fire regimes can provide forecasting opportunities and mechanisms to model future climate-driven changes in fire regimes (Westerling et al., 2003).

To enhance our mechanistic understanding of how climate influences fire regimes across the continent, we summarized the climate space of North American forests, compared this to the climate space of NAFSN sites and to that of modern fires recorded by satellites. The climate-space analysis was conducted at continental and eco-regional scales (Figure 3b). Using a state-space or climate-space approach, as we did with topography, allowed us to better understand climate domains that may be more or less common in the NAFSN than would be expected from the background climate of forests. The characterization of modern fires enabled us to ask whether there is a consistent climate domain that supports surface-fire regimes across North America, and whether that has changed through time. We acknowledge that comparisons between tree-ring fire-scar sites—areas that have burned in the past—and satellite-derived fire records are imperfect due to limitations of both records (e.g., Farris et al., 2010), but think that it is informative.

We analyzed four annual climate variables that influence modern fire occurrence: (1) mean annual temperature (in degrees Celsius; MAT), (2) mean annual precipitation (in millimeters; MAP), (3) the Hargreaves climatic moisture deficit (in millimeters; CMD), and (4) actual evapotranspiration (in millimeters; AET) calculated as the Hargreaves reference evapotranspiration minus CMD. We used ClimateNA (Wang et al., 2016) to extract 1-km resolution annual data for the period 1981–2010 and calculated mean values of each variable to represent climatic normals. We square-root transformed MAP because the raw values were highly skewed. We then extracted the climate normals for these four variables at each of the 2562 NAFSN sites to compare with 335,375 randomly selected points in forested areas and the centroids of 366,581 satellite detected modern forest fire perimeters (see Appendix S1 for data sources used to assemble the modern North American fire atlas).

To represent and compare the climate space of North American forests and the NAFSN we plotted MAP versus MAT and AET versus CMD for the random points in the forest layer and the fire scar sites. We made similar comparisons for each of the 11 individual ecoregions with >2 fire-scar sites. We used a two-dimensional kernel density estimation to calculate probability density functions for the random "background" forest points. To facilitate comparison between ecoregions, density estimates were scaled from 0 to 1, with the value 1 representing the area in the climate space with the highest density of points. Additionally, we drew convex hulls enclosing 95% of the fire-scar sites and modern forest fire sites.

The climate space of the NAFSN is largely representative of the core climate space of existing forested areas (Figure 8a; Appendix S1: Figure S4). The major gaps in the NAFSN are in the hottest (MAT > ∼18°C) and driest (MAP < ∼20 mm/year, CMD > 1000 mm/year) climates (Figure 8a; Appendix S1: Figure S4), as well as in areas with AET >1000 mm/year, likely corresponding to the southeastern United States and southern Mexico. Among ecoregions, there is variability in the degree to which the fire-scar sites represent the climate space of forests (Figure 8). For example, fire scar collections represent the majority of the climate domain of the Northwestern Forested Mountains, Eastern Temperate Forests, Northern Forests, and Taiga ecoregions. In contrast, fire scars are lacking from portions of the forested climate space in the Great Plains, Marine West Coast Forest, North American Deserts, Southern Semi-arid Highlands, and Temperate Sierras (Figure 8; Appendix S1: Figure S4). In most cases (e.g., Temperate Sierras and Great Plains), fire scars were not sampled in the warmest range of forests. In other cases, sampling was concentrated at the climatic edge of the range of forests (e.g., Southern Semi-arid Highlands). It is worth noting that the climate space of the NAFSN extends beyond the climate space of existing forests in the Southern Semi-arid Highlands (Figure 8h; Appendix S1: Figure S4), and to a lesser degree in the Temperate Sierras. This may indicate recent forest loss due to high-severity fire (see discussion in *Vegetation* section), or that fire scars were found in areas with little representation regionally, for example, small high-elevation bands of forest in the Temperate Sierras.

The core climate space of modern fires overlaps with the fire-scar record of historical fires (Figure 8; Appendix S1: Figure S4). The exception is in warmer climates (e.g., MAT > ∼20°C), where there are modern fires but few fire-scar sites. This is likely due to undersampling of fire scars in these warmer climates and ecoregions (e.g., Tropical Wet and Tropical Dry Forests), but in some locations could also indicate changing fire regimes, or differences in fire regimes recorded by fire scars versus the

modern satellite records. Despite the differences in the warmer climate space, there is broad similarity between the core climate spaces of North American forests, historical fire regimes represented by fire-scar sites, and modern fires (Figure 8; Appendix S1: Figure S4). This suggests a common range of climate variables associated with fire occurrence, both historically and for modern fires. There are also interesting differences, particularly within and among ecoregions, between historical and modern fires. For example, there is less overlap between modern fires and NAFSN sites in the Northern Forests, Eastern Temperate Forests, and Semi-Arid Highlands ecoregions compared to other ecoregions. These findings suggest abundant possibilities for future research, from analyses of fire-climate associations utilizing the new, continental data set, to consideration of changes in the driving factors of fire regimes over time, to opportunities for expanding the network via more intensive and extensive sampling of underrepresented climates and ecoregions.

The overlap between the core climate space of forests, modern fires, and historical fires in North America is broadly consistent with previous work exploring the climate space of fire regimes; while many terrestrial vegetation types can support fire, fire is most abundant where temperature and moisture gradients optimize a combination of fuel availability, flammability, and ignition (Archibald et al., 2013; Guyette et al., 2012; Krawchuk & Moritz, 2011; Parisien & Moritz, 2009; Whitman et al., 2015). However, the NAFSN tends toward lower values of moisture and temperature (and CMD and AET) than that represented by the full spectrum of North American forests (Figure 8a). The NAFSN sites in the drier climate space are likely more conducive to fire if fuel is not limiting. The low number of NAFSN sites in the warmer portion of the climate space of forests is likely due to a combination of factors. The highest concentrations of these undersampled, warmer, forested climate spaces occur in lower latitude subtropical forest ecoregions in Mexico (Figures 3b and 8a). Mexico is an expanding frontier for dendrochronology (e.g., Arizpe et al., 2020; Cerano-Paredes et al., 2019; Fulé et al., 2005; Yocom Kent et al., 2017) and should be a focus of future work for multiple reasons, but also contains climatic conditions and species where crossdating can be challenging, where human land use has removed old trees that may have had evidence of fire, or where fires within the life spans of trees were infrequent to nonexistent. In addition, parts of Mexico may have similarities to the future climates, vegetation, and fire regimes for more northern latitudes (Gomez-Pineda et al., 2020). Because we used modern climate data to describe the climate space of the NAFSN, it is also possible that some differences between
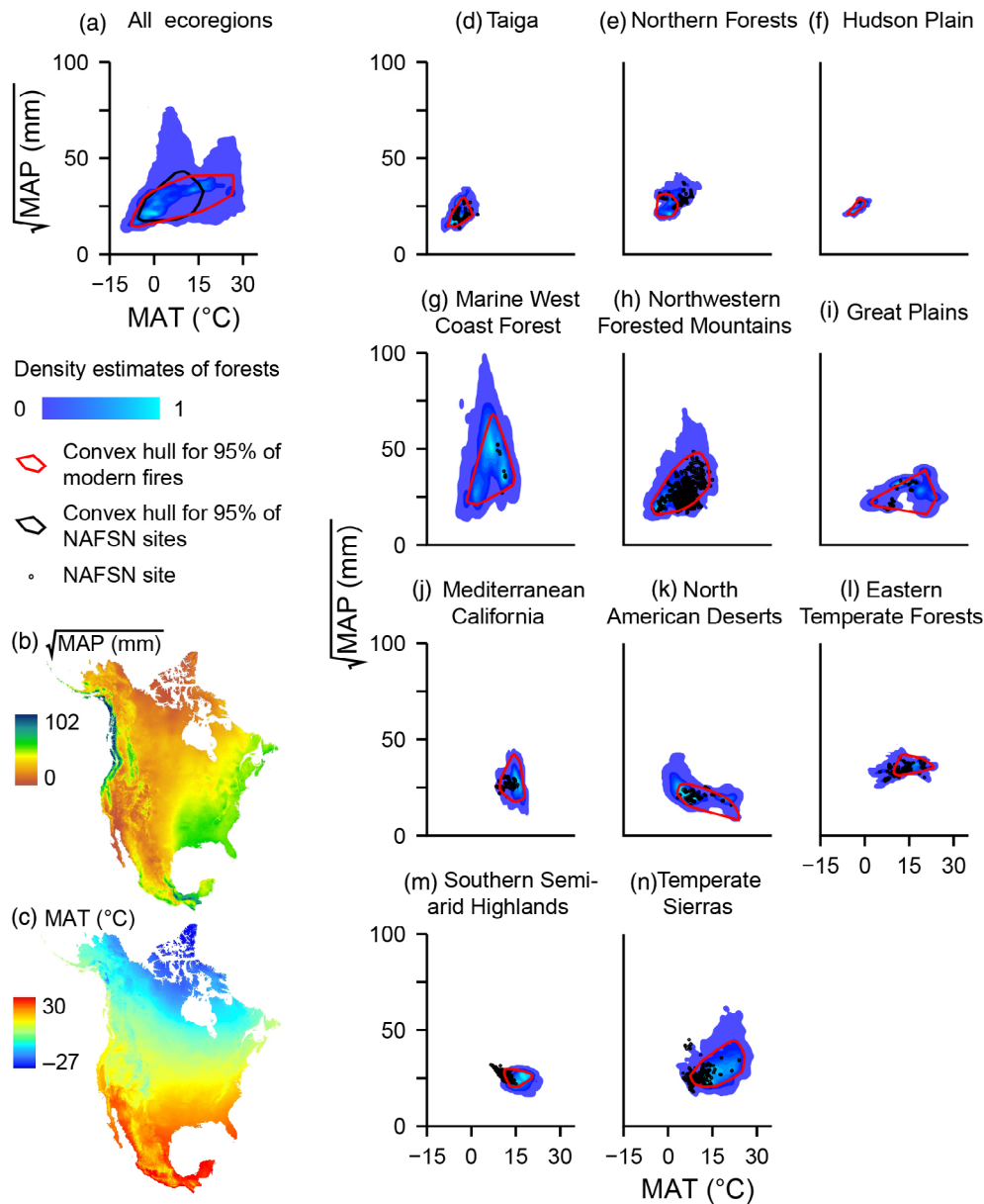
FIGURE 8   (a–n) Climate space of forests, the North American fire-scar network (NAFSN) sites, and modern fires in terms of mean annual precipitation (MAP; square root transformed) and mean annual temperature (MAT) by ecoregion. Forests: Density estimates of the forested climate space were derived using 2D kernel density estimation and scaled from 0.0 to 1.0 (blue to cyan), with 1 corresponding to the highest densities. The NAFSN sites: Black convex hull enclosing 95% of the sites in all ecoregions and black dots by ecoregion. Modern fires: Red convex hulls enclosing 95% of the fire locations. Also shown are maps of MAP (square-root transformed) and MAT (1981–2010). Ecoregion panels are arranged by decreasing latitude.

modern and historical fires could be related to climate shifts to warmer conditions compared to prior centuries when the fires recorded in the NAFSN were burning. Lastly, microsite climates that were conducive to historical fires and fire scars, such as dry ridges in otherwise mesic areas, may not be reflected by the coarse climate data in the analysis.

Our climate analyses highlight interesting patterns and tantalizing research potential, as well as potential limitations of the NAFSN. Insights provided by the fire-scar network have applicability primarily across the sampled range of forest types and climate spaces it represents. This calls for research efforts to fill data gaps (e.g., sites in warmer or wetter climates), but acknowledges that some regions and forest types may not contain tree-ring fire-scar records, necessitating other approaches such as paleo-charcoal (Girardin et al., 2019), forest age structure-derived fire history (Drobyshev et al., 2017; Johnson & Larsen, 1991; Van Wagner, 1978), or the use of precisely dateable anatomical indicators of fire exposure (Arbellay et al.,

2014a, 2014b). We also note that we characterized the NAFSN in the context of contemporary climate space, whereas historical fires may have burned under different climate conditions centuries ago. Next steps include building upon existing tree-ring fire-climate network analyses (e.g., Kitzberger et al., 2007; Trouet et al., 2010) to conduct regional and continental assessments of the historical climatic drivers of fire using historical climate data, such as the tree-ring based North American Drought Atlas (Cook et al., 2004) or the many new seasonal paleo-climatic reconstructions (e.g., Stahle et al., 2020). As complete fire chronologies from NAFSN sites become available for analysis, there is great potential to develop a deeper understanding of the relationships between climate, ecoregional variation, and fire regimes.

HUMANS

Humans have influenced fire regimes across the globe for millennia (Bond & Keeley, 2005; Bowman et al., 2009, 2011; Guyette et al., 2002). In North America, evidence of human presence extends to the Pleistocene with the earliest evidence during the Last Glacial Maximum circa 24 kyr BP (Bourgeon et al., 2017). Throughout the Holocene, Indigenous peoples managed ecosystems with fire for multiple benefits, affecting pyrodiversity and biodiversity (Bowman et al., 2016; Huffman, 2013; Lake & Christianson, 2019; Roos et al., 2021; Stewart, 2002). In some places, Indigenous fire use has adapted to changing ecological, climatological, and social factors through the present, whereas in others, fire use declined due to Indigenous population decline, land dispossession, and cultural suppression after European contact (Lake & Christianson, 2019). European exploration and settlement altered fire regimes via land clearing, intensive agriculture, and livestock grazing, and as a consequence, fire regime changes have continued with increased industrialization and fire exclusion policies (Borman, 2005; Guyette et al., 2002; Pyne, 1997; Waito et al., 2018). Humans have profoundly modified basic components of fire regimes, including fire frequency, ignition source, seasonality, size, and severity, at a continental scale (Balch et al., 2017) to the point of overriding fire–climate relationships in many areas (Chavardès et al., 2018; Higuera et al., 2015; Parks et al., 2015; Platt et al., 2015; Syphard et al., 2017; Wahl et al., 2019). Although the effect of humans on fire regimes is complex and highly variable across North America, evidence suggests that contemporary anthropogenic activities generally limit fire activity across much of the continent (Parisien et al., 2016).

We explored the potential human influences on fire regimes recorded in the NAFSN in terms of (1) Indigenous territories and influences, (2) spatiotemporal variability in human population, (3) the timing of land use transitions, and (4) the last fire year recorded by fire scars. We use these topics to identify patterns of human-related processes that affected past fire regimes, influence current patterns of fire and vegetation, and will continue to affect future fire regimes.

Across North America, fire-scar records commonly pre-date European colonization, back to a time when a complex geography of intersecting Indigenous territories existed (Larson et al., 2021; Stephens et al., 2003; Swetnam et al., 2016). We mapped a spatial database of >600 North American Indigenous territories (www. native-land.ca, Figure 9a) to generate hypotheses related to Indigenous influences on fire regimes. Many territories overlap in space and time under an ongoing dynamic of cultural change. In some cases, fire-scarred trees recorded fires that occurred prior to European contact and some surely reflect fire use by Indigenous peoples across these territories, in practices related to hunting, agricultural land clearing, culturally important plants, pest management, warfare and signaling, and clearing areas for travel (e.g., Huffman, 2013; Lewis & Ferguson, 1988; Pyne, 1997; Roos et al., 2021). The majority of records, however, cover time periods of Indigenous displacement and increased Euro-American influences prior to the 20th century (Figure 5). Fire regime changes coincident with this transition are often indicative of anthropogenic factors that may override the climatic influence. Post-colonial fire regimes may contrast with earlier periods due to European influences or mirror historical conditions through the adoption of Indigenous land use practices by settlers (Pyne, 2000; Roos et al., 2021).

Fire-scar sites exist across a range of human population densities before and after European contact. Regions with the highest documented pre-contact human populations are located on the west coast and in south central Mexico and smaller areas with high densities including Chesapeake Bay, upstate New York, and the upper Rio Grande Valley (Driver & Massey, 1957; Figure 9b). Inland Alaska, northern Canada, the Ohio River Valley, and the Great Basin are thought to represent the regions of lowest pre-contact populations. Since European arrival, increases in human population have largely been focused in the eastern half of the United States, southern Canada, the west coast of North America, and scattered regions in the western and central United States (CIESIN, 2016, Figure 9c). Many areas with high current human populations have a history of fire recorded in the NAFSN, indicating the potential for fire burning through modern communities, as we are increasingly observing (e.g., recent large wildfires in California, Oregon, British Colombia, and Tennessee). In this
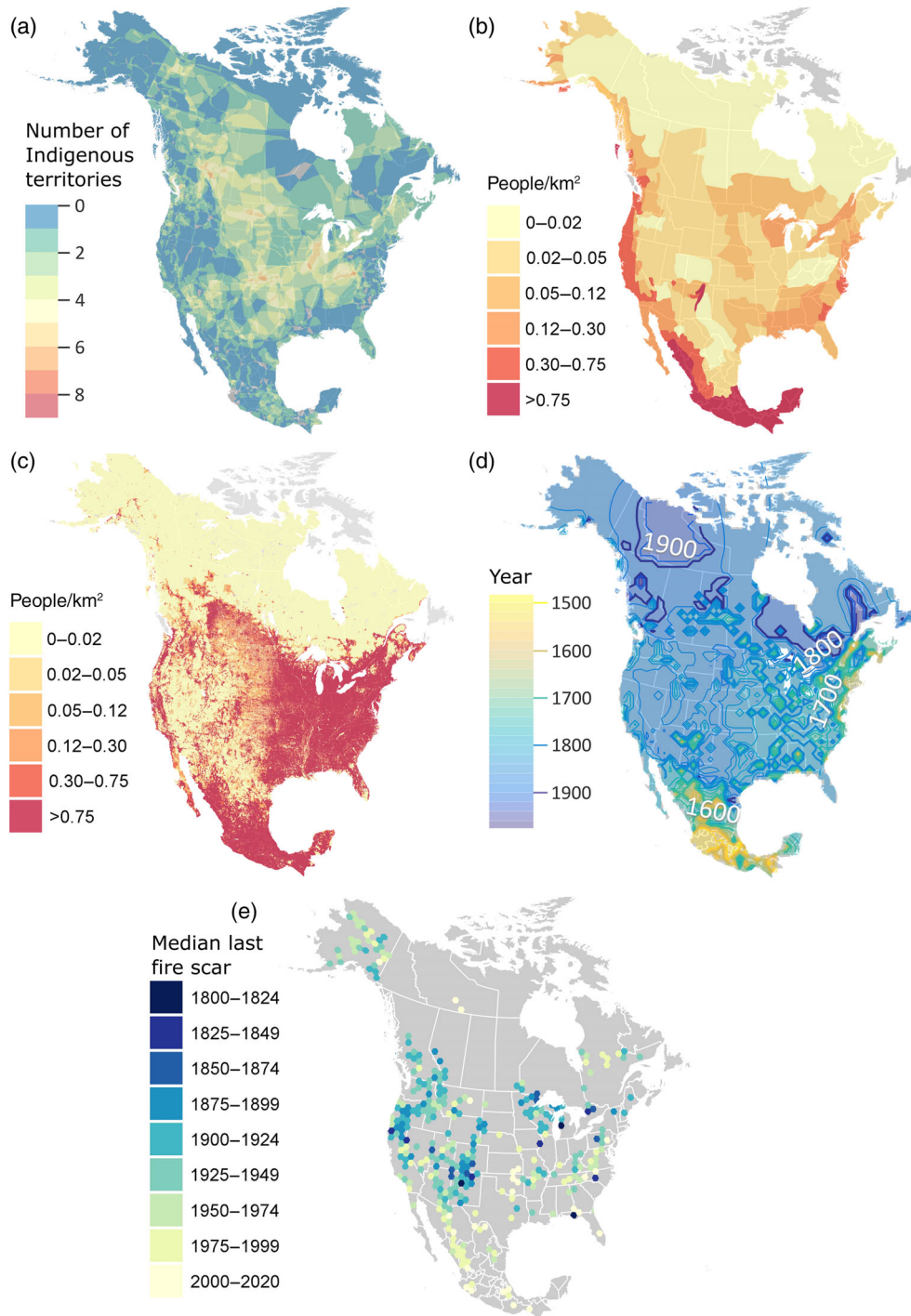
FIGURE 9 Maps of human factors linked to the North American tree-ring fire-scar network. (a) Territories of >600 North American Indigenous tribes (https://native-land.ca), (b) pre-European contact human population density estimates (Driver & Massey, 1957), (c) current (2020) human population density (source: CIESIN, 2020), (d) contour map depicting the year of land use transitions with possible influences on fire regimes (see text for sources), and (e) most recent fire calculated as the median most recent fire-scar year of sites within 10,000-km² hexels. Only hexels containing a fire-scar site with a minimum of two fire-scarred trees are displayed.

context, fire-scar data will be increasingly informative for urban planning, land management, and health and safety concerns (e.g., smoke exposure, wildfire risk mitigation). Increasing populations and associated anthropogenic activities continue to influence and modify fire regimes, both directly through the ignition and suppression of fires, and indirectly through the alteration of the amount and spatial arrangement of fuels.

Major human demographic changes may be reflected in the fire-scar record. We mapped the spatiotemporal

variability of the timing of major land use transitions across North America (Figure 9d) to frame hypotheses regarding fire regime changes that could be tested with the NAFSN. The map was created using direct reports or by proximal information including: land cession dates, treaty dates from Canada, railway establishment timing from Canada and the United States, post office establishment dates from the western United States, timing of smallpox outbreaks across North America, and timing of European settlement or disruption of traditional Indigenous practices (see Appendix S1: Table S2 for data sources). This land-use transition map reflects the complex historical events that followed initial European contact in the late-15th century. Contours were interpolated by inverse distance weighting using multiple data sources at a 100-km^2 spatial resolution. In cases of overlapping lines of evidence, the minimum date was selected.

Broadly, current-day Mexico was the first area to experience widespread land-use transition, in an already densely populated area, during the establishment of New Spain throughout the 16th century (Figure 9b,d). The gradual establishment of colonies by Spain along the East Coast and Gulf of Mexico also occurred farther north in eastern North America by England and France in the 17th century, with subsequent intrusions within the continent in the Midwest and Great Lakes. While European settlement in the western half of what is now the United States and Canada mostly came later (as recently as the early 20th century in some localities), substantial areas of Spanish colonization predated this westward wave of establishment, notably in parts of what is now California and the southwestern United States. In addition, impacts on Indigenous peoples and associated fire regimes generally preceded the advancing front of settlement and associated colonial policies of relocation, acculturation, and fire exclusion, primarily through the spread of introduced diseases that decimated populations and entire cultures before settlers arrived in large numbers (Jones, 2017; Lake & Christianson, 2019; Murphy et al., 2007). Northern areas were generally the most recently settled by non-Indigenous peoples, although these settlements were relatively small and sparse. The land-use transition map attempts to characterize phenomena affecting patterns of interactions with the land (and by extension, fire regimes), although at any given location many other factors or events may have affected fire regimes through time (e.g., agrarian reforms, urban development, and fire suppression policies). Future studies of human effects on historical fire regimes in North America could consider (i.e., map) these and other factors to paint a more complete picture of fire regime change through time.

To explore one aspect of the spatiotemporal variability of human influence on North American fire regimes, fire regime decline, we mapped the year of the most recent fire scar recorded by the NAFSN sites. We acknowledge multiple limitations of using this metric. First, it may not represent the actual last fire at a site, because of the wide range of fire-scar sample collection years, or different sampling strategies (e.g., dead wood vs. live trees) in the NAFSN, which can result in different lengths of tree-ring records. In other cases, the last fire date may be a modern fire that was purposely sampled for corroboration with fire-scar records (e.g., Farris et al., 2010). Therefore, these data may not always represent the actual timing of a major disruption in the fire regime, such as the onset of 20th century fire exclusion. We did, however, find general patterns in the aggregate of all last fire dates in relatively large spatial areas (10,000-km^2 hexels, minimum of 2 sites per hexel). We then calculated the median year of the most recent fire scar as a measure of central tendency within these hexels.

The date of the most recent fire scar varies spatially across North America. The contrast at the US/Mexico border is perhaps the most obvious feature (Figure 9e), which can be attributed to different land use history primarily related to the timing of intensive livestock grazing (Fulé et al., 2012). Fires were largely eliminated by 1900 throughout the southwestern United States primarily due to widespread overgrazing that removed fine fuels and inhibited fire spread (Allen, 2007; Dewar et al., 2021; Fulé et al., 2012), while fires continued to burn across many sites in northern Mexico until the mid-1900s, and in some cases without disruption to the present (Arizpe et al., 2020; Fule et al., 2011; Heyerdahl & Alvarado, 2003; Meunier et al., 2014; Poulos et al., 2013; Skinner et al., 2008; Yocom Kent et al., 2017). It was not until the redistribution of lands to communal *ejidos* in 1934 and 1940 (Lopez & Bernardino Mata, 1992) and subsequent increased livestock grazing, that fire frequency decreased across many sites in Mexico (Heyerdahl & Alvarado, 2003; Poulos et al., 2013). There are also concentrations of most recent fire scars ca. 1900 in the western United States and the Great Lakes region. The latter is likely related to the restriction of Indigenous populations coincident with Euro-American settlement (Kipfmueller et al., 2021). Interestingly, in some regions where the most recent fire scar dates are close to the present, European settlement was the earliest (in the 15th–17th centuries); this encompasses areas with intact traditional fire use (e.g., in Mexico; Martínez-Torres et al., 2016) or where prescribed and resource benefit fires are a priority for local stakeholders (e.g., the southeastern and south-central United States; Rother et al., 2020). Future research using the full fire-scar record

will help identify the timing of shifting fire regimes, including increasing fire (e.g., Stambaugh et al., 2018), and the role of humans, or other factors in driving these changes.

The NAFSN shows tremendous potential to advance our understanding of the roles that humans have played in shaping fire regimes and ecosystems of North America. Local to regional studies have demonstrated the ability to use fire-scar data to identify human influence on historical fire regimes (Guiterman et al., 2019; Hoffman et al., 2017; Huffman et al., 2004; Kitchen, 2015; Roos et al., 2021; Stambaugh et al., 2018; Swetnam et al., 2016; Taylor et al., 2016). To better understand the anthropogenic component of historical fire regimes, it is necessary to disentangle the spatiotemporal variability caused by climate and vegetation, the other major drivers of fire regime change, from that of human activities (Bowman et al., 2020; Fulé et al., 2012; Whitlock & Knox, 2002). With this network, new opportunities become available for the multidisciplinary examination of historical fire regimes and their associated cultural phenomena. The key to disentangling the influence on fire regimes of humans from climate lies in the emerging methodologies that allow the analysis and interpretation of tree-ring based fire histories in the context of other forms of knowledge and historical ecology data. Specifically, these include multiproxy approaches that incorporate different lines of evidence of human land use (e.g., palaeoecological and archeological data; Whitlock et al., 2010, Carter et al., 2021), multidisciplinary approaches that draw on expertise from, among others, anthropology and human geography, and collaborative methodologies that engage directly with Indigenous fire knowledge keepers and scholars (Lake et al., 2017; Roos et al., 2021). Recognizing the nuanced contributions of people to fire regimes across North America will rely on future research that is place-based, scale-appropriate, and reflects the spatiotemporal variability of the relationship between people and fire (McWethy et al., 2013).

CONCLUSIONS AND FUTURE DIRECTIONS

The NAFSN and our broad analyses of the key influences on fire regimes, (1) vegetation, (2) topography, (3) climate, and (4) humans, provide a foundation and framework for many new opportunities to advance fire research. Future analyses of the NAFSN will facilitate increased understanding of the patterns and drivers of spatiotemporal variability in fire regimes, including relationships between fire, climate, humans, topography, and vegetation at local to continental scales. Great potential exists for future analyses of the full fire-scar data sets

containing >300,000 annually to sub-annually resolved fire records over the past several hundred years. These newly compiled data will provide insights into important fire-related topics, including: climate influences on fire regimes (Guyette et al., 2012; Kitzberger et al., 2017); changing fire severity and fire-catalyzed vegetation type conversion (Coop et al., 2020; Guiterman et al., 2018); cross-scale spatial analyses (Falk et al., 2007; Kennedy & McKenzie, 2010), including area burned reconstructions that can place current fire trends and the fire deficit in a multicentury context (Farris et al., 2010; Swetnam, Falk, Hessl, & Farris, 2011); broader context on topographic controls of fire occurrence and severity (Heyerdahl et al., 2001; Kellogg et al., 2007); and deeper insights into human influences on past, present, and future fire regimes, including Indigenous burning and European settlement (Howard et al., 2021; Stambaugh et al., 2018; Taylor et al., 2016). Fire scars can also record sub-annual (or seasonal) variability in fire occurrence, an understudied topic that can inform seasonal fire–climate relationships (Margolis et al., 2017), identify human influences on fire regimes (Kitchen, 2015; Rother et al., 2020; Seklecki et al., 1996), and possibly detect other patterns, drivers, and trends related to modern changes in fire season (e.g., Westerling et al., 2006). Furthermore, analysis of data in the fire-scar network can reveal previously unrecognized changes in other variables and processes, such as climate, vegetation, or human land use (Swetnam & Brown, 2011), because of strong interdependencies with fire regimes (Taylor et al., 2016).

The potential to build upon the NAFSN and collect new fire scar samples to fill important data gaps identified in this paper may have a shrinking window of opportunity. Tree-ring fire-scar collections and analyses commonly are limited more by institutional factors and resources, such as the limited pool of skilled scientists and resources, than by the availability of fire-scarred trees. Nonetheless, there is urgency to sample and extract tree-ring records of fire from the great, ephemeral, old-wood in "unread" forest libraries across North America. Increasing fire activity, climate- and insect-induced mortality of old trees, logging, decay, and development are erasing old tree-ring fire records that have existed for centuries. These threats highlight the need to collect and securely archive tree-ring records of fire, as well as other tree-ring records, including for climate or forest stand reconstructions, which will be essential for future studies. Gaps in geographic, ecoregional, or climatic and topographic state space identified in this paper can be the beginning of a road map for fire-scar collections to fill spatial, temporal, and knowledge gaps before the records are lost.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The fire-scar site metadata (Margolis & Guiterman, 2022) analyzed in this study are available in a USGS data release (https://doi.org/10.5066/P9PT90QX). The full tree-ring fire-scar records for the NAFSN sites have varying stages of availability. The current repository for tree-ring fire-scar data is the IMPD, where 800 sites in the NAFSN are publicly available and >300 additional sites are being processed as part of the NASFN effort (https://doi.org/10.25921/pef0-zz47). The compilation of the NAFSN has engaged the broad community of fire-history researchers to expand the data available through the IMPD, which is ongoing. The site-level metadata structure that we developed, which links directly to the specific tree-ring fire-scar data files, has increased the utility of the fire-scar data for network analyses. We also recommend that all future submissions to the IMPD contain tree-level metadata, which greatly expands the research potential by facilitating re-grouping of fire-scar trees as appropriate for different research questions. By utilizing the expanded NAFSN, researchers and others (e.g., fire managers) will have better access to locally relevant data on fire history, including fire-regime metrics, or area and species sampled. We are also developing new tools and resources that build on existing software (e.g., Malevich et al., 2018; Sutherland et al., 2014) to facilitate online exploration, data queries and extraction, and analyses of the IMPD fire-history archive to promote the use within and beyond ecological fields of study.

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REFERENCES

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* 113: 11770–5.

Agee, J. K. 1993. *Fire Ecology of Pacific Northwest Forests.* Washington, DC: Island Press.

Allen, C. D. 2007. "Interactions across Spatial Scales among Forest Dieback, Fire, and Erosion in Northern New Mexico Landscapes." *Ecosystems* 10: 797–808.

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: 115–30.

Allen, M. S., and M. W. Palmer. 2011. "Fire History of a Prairie/Forest Boundary: More Than 250 Years of Frequent Fire in a North American Tallgrass Prairie." *Journal of Vegetation Science* 22: 436–44.

Arabas, K. B., K. S. Hadley, and E. R. Larson. 2006. "Fire History of a Naturally Fragmented Landscape in Central Oregon." *Canadian Journal of Forest Research* 36: 1108–20.

Arbellay, E., M. Stoffel, E. K. Sutherland, K. T. Smith, and D. A. Falk. 2014a. "Resin Duct Size and Density as Ecophysiological Traits in Fire Scars of *Pseudotsuga menziesii* and *Larix occidentalis.*" *Annals of Botany* 114: 973–80.

Arbellay, E., M. Stoffel, E. K. Sutherland, K. T. Smith, and D. A. Falk. 2014b. "Changes in Tracheid and Ray Traits in Fire Scars of North American Conifers and their Ecophysiological Implications." *Annals of Botany* 114: 223–32.

Archibald, S., C. E. Lehmann, J. L. Gomez-Dans, and R. A. Bradstock. 2013. "Defining Pyromes and Global Syndromes of Fire Regimes." *Proceedings of the National Academy of Sciences of the United States of America* 110: 6442–7.

Arizpe, A. H., D. A. Falk, C. A. Woodhouse, and T. W. Swetnam. 2020. "Widespread Fire Years in the US–Mexico Sky Islands Are Contingent on Both Winter and Monsoon Precipitation." *International Journal of Wildland Fire* 29: 1072–87.

Baars, H., A. Ansmann, D. Althausen, R. Engelmann, P. Artaxo, T. Pauliquevis, and R. Souza. 2011. "Further Evidence for Significant Smoke Transport from Africa to Amazonia." *Geophysical Research Letters* 38: 1-6.

Bailey, R. G. 1995. *Description of Ecoregions of the United States.* Asheville, NC: U.S. Department of Agriculture, Forest Service.

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 of the United States of America* 114: 2946–51.

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: 347–58.

Beckage, B., W. J. Platt, M. G. Slocum, and B. Pank. 2003. "Influence of the El Nino Southern Oscillation on Fire Regimes in the Florida Everglades." *Ecology* 84: 3124–30.

Bergeron, Y. 1991. "The Influence of Island and Mainland Lakeshore Landscapes on Boreal Forest-Fire Regimes." *Ecology* 72: 1980–92.

Bergeron, Y., and J. Brisson. 1990. "Fire Regime in Red Pine Stands at the Northern Limit of the Species Range." *Ecology* 71: 1352–64.

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." *The Holocene* 20: 1047–61.

Bond, W., and J. Keeley. 2005. "Fire as a Global 'Herbivore': The Ecology and Evolution of Flammable Ecosystems." *Trends in Ecology & Evolution* 20: 387–94.

Bond, W. J., F. I. Woodward, and G. F. Midgley. 2005. "The Global Distribution of Ecosystems in a World without Fire." *New Phytologist* 165: 525–38.

Borman, M. M. 2005. "Forest Stand Dynamics and Livestock Grazing in Historical Context." *Conservation Biology* 19: 1658–62.

Bourgeon, L., A. Burke, and T. Higham. 2017. "Earliest Human Presence in North America Dated to the Last Glacial Maximum: New Radiocarbon Dates from Bluefish Caves, Canada." *PLoS One* 12: e0169486.

Bowman, D. M. J. S., J. Balch, P. Artaxo, W. J. Bond, M. A. Cochrane, C. M. D'Antonio, R. DeFries, et al. 2011. "The Human Dimension of Fire Regimes on Earth." *Journal of Biogeography* 38: 2223–36.

Bowman, D. M. J. S., D. M. J. S. Bowman, J. K. Balch, P. Artaxo, W. J. Bond, J. M. Carlson, M. A. Cochrane, et al. 2009. "Fire in the Earth System." *Science* 324: 481–4.

Bowman, D. M. J. S., C. A. Kolden, J. T. Abatzoglou, F. H. Johnston, G. R. van der Werf, and M. Flannigan. 2020. "Vegetation Fires in the Anthropocene." *Nature Reviews Earth & Environment* 1: 500–15.

Bowman, D. M., G. L. Perry, S. I. Higgins, C. N. Johnson, S. D. Fuhlendorf, and B. P. Murphy. 2016. "Pyrodiversity Is the Coupling of Biodiversity and Fire Regimes in Food Webs." *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 371: 20150169.

Brey, S. J., M. Ruminski, S. A. Atwood, and E. V. Fischer. 2018. "Connecting Smoke Plumes to Sources Using Hazard Mapping System (HMS) Smoke and Fire Location Data over North America." *Atmospheric Chemistry and Physics* 18: 1745–61.

Brown, P. M., and C. H. Sieg. 1999. "Historical Variability in Fire at the Ponderosa Pine—Northern Great Plains Prairie Ecotone, Southeastern Black Hills, South Dakota." *Ecoscience* 6: 539–47.

Brown, P. M., and T. W. Swetnam. 1994. "A Cross-Dated Fire History from Coast Redwood near Redwood National Park, California." *Canadian Journal of Forest Research* 24: 21–31.

Brown, P. M., and R. Wu. 2005. "Climate and Disturbance Forcing of Episodic Tree Recruitment in a Southwestern Ponderosa Pine Landscape." *Ecology* 86: 3030–8.

Burke, M., A. Driscoll, S. Heft-Neal, J. Xue, J. Burney, and M. Wara. 2021. "The Changing Risk and Burden of Wildfire in the United States." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2011048118.

Byers, B. A., L. DeSoto, D. Chaney, S. R. Ash, A. B. Byers, J. B. Byers, and M. Stoffel. 2020. "Fire-Scarred Fossil Tree from the Late Triassic Shows a Pre-Fire Drought Signal." *Scientific Reports* 10: 20104.

Cansler, C., and D. McKenzie. 2014. "Climate, Fire Size, and Biophysical Setting Control Fire Severity and Spatial Pattern in the Northern Cascade Range, USA." *Ecological Applications* 24: 1037–56.

Caprio, A. C., and T. W. Swetnam. 1995. "Historic Fire Regimes along an Elevational Gradient on the West Slope of the Sierra

Nevada, California." In *Proceedings: Symposium on Fire in Wilderness and Park Management. USDA Forest Service General Technical Report INT-GTR-320*, edited by J. K. Brown, R. W. Mutch, C. W. Spoon, and R. H. Wakimoto, 173–9. Ogden, UT: USDA Forest Service.

Carter, V. A., A. Brunelle, M. J. Power, R. J. DeRose, M. F. Bekker, I. Hart, S. Brewer, et al. 2021. "Legacies of Indigenous Land Use Shaped Past Wildfire Regimes in the Basin-Plateau Region, USA." *Communications Earth & Environment* 2: 72.

Cerano-Paredes, J., J. Villanueva-Díaz, L. Vázquez-Selem, R. Cervantes-Martínez, V. O. Magaña-Rueda, V. Constante-García, G. Esquivel-Arriaga, and R. D. Valdez-Cepeda. 2019. "Climatic Influence on Fire Regime (1700 to 2008) in the Nazas Watershed, Durango, Mexico." *Fire Ecology* 15: 9.

Chavardès, R. D., L. D. Daniels, Z. Gedalof, and D. W. Andison. 2018. "Human Influences Superseded Climate to Disrupt the 20th Century Fire Regime in Jasper National Park, Canada." *Dendrochronologia* 48: 10–9.

CIESIN. 2016. *Documentation for the Gridded Population of the World, Version 4 (GPWv4)*. Palisades, NY: Center for International Earth Science Information Network (CIESIN), NASA Socioeconomic Data and Applications Center.

Clements, F. E. 1910. *The Life History of Lodgepole Burn Forests*. Washington, DC: USDA Forest Service.

Collins, B. M., and S. L. Stephens. 2007. "Managing Natural Wildfires in Sierra Nevada Wilderness Areas." *Frontiers in Ecology and the Environment* 5: 523–7.

Cook, E. R., C. A. Woodhouse, and C. M. Eakin. 2004. "Long-Term Aridity Changes in the Western United States." 306: 1015–8.

Coop, J. D., S. A. Parks, C. S. Stevens-Rumann, S. D. Crausbay, P. E. Higuera, M. D. Hurteau, A. Tepley, et al. 2020. "Wildfire-Driven Forest Conversion in Western North American Landscapes." *BioScience* 70: 659–73.

Covington, W. W., and M. M. Moore. 1994. "Southwestern Ponderosa Forest Structure." *Journal of Forestry* 92: 39–47.

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: 331–52.

Dieterich, J. A., and T. W. Swetnam. 1984. "Dendrochronology of a Fire-Scarred Ponderosa Pine." *Forest Science* 30: 238–47.

Dillon, G. K., Z. A. Holden, P. Morgan, M. A. Crimmins, E. K. Heyerdahl, and C. H. Luce. 2011. "Both Topography and Climate Affected Forest and Woodland Burn Severity in Two Regions of the Western US, 1984 to 2006." *Ecosphere* 2: 1–33.

Driver, H. E., and W. C. Massey. 1957. "Comparative Studies of North American Indians." *Transactions of the American Philosophical Society* 47: 165–456.

Drobyshev, I., Y. Bergeron, M. P. Girardin, S. Gauthier, C. Ols, and J. Ojal. 2017. "Strong Gradients in Forest Sensitivity to Climate Change Revealed by Dynamics of Forest Fire Cycles in the Post Little Ice Age Era." *Journal of Geophysical Research: Biogeosciences* 122: 2605–16.

Erni, S., D. Arseneault, M. A. Parisien, and Y. Begin. 2017. "Spatial and Temporal Dimensions of Fire Activity in the Fire-Prone Eastern Canadian Taiga." *Global Change Biology* 23: 1152–66.

Falk, D. A., E. K. Heyerdahl, P. M. Brown, C. Farris, P. Z. Fule, D. McKenzie, T. W. Swetnam, A. H. Taylor, and M. L. Van Horne. 2011. "Multi-Scale Controls of Historical Forest-Fire Regimes: New Insights from Fire-Scar Networks." *Frontiers in Ecology and the Environment* 9: 446–54.

Falk, D. A., C. Miller, D. McKenzie, and A. E. Black. 2007. "Cross-Scale Analysis of Fire Regimes." *Ecosystems* 10: 809–23.

Falk, D. A., and T. W. Swetnam. 2003. "Scaling Rules and Probability Models for Surface Fire Regimes in Ponderosa Pine Forests." In *Fire, Fuel Treatments, and Ecological Restoration: Conference Proceedings*, edited by P. N. Omi and L. A. Joyce, 301–17. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station.

Farris, C. A., C. H. Baisan, D. A. Falk, M. L. Van 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: 1021–33.

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: 1598–614.

Fill, J. M., C. N. Davis, and R. M. Crandall. 2019. "Climate Change Lengthens Southeastern USA Lightning-Ignited Fire Seasons." *Global Change Biology* 25: 3562–9.

Fill, J. M., W. J. Platt, S. M. Welch, J. L. Waldron, and T. A. Mousseau. 2015. "Updating Models for Restoration and Management of Fiery Ecosystems." *Forest Ecology and Management* 356: 54–63.

Flannigan, M., B. Stocks, M. Turetsky, and M. Wotton. 2009. "Impacts of Climate Change on Fire Activity and Fire Management in the Circumboreal Forest." *Global Change Biology* 15: 549–60.

Flatley, W. T., C. W. Lafon, H. D. Grissino-Mayer, and L. B. LaForest. 2015. "Changing Fire Regimes and Old-Growth Forest Succession along a Topographic Gradient in the Great Smoky Mountains." *Forest Ecology and Management* 350: 96–106.

Friedl, M., and D. Sulla-Menashe. 2019. "MCD12Q1 MODIS/Terra + Aqua Land Cover Type Yearly L3 Global 500 m SIN Grid V006." NASA EOSDIS Land Processes DAAC.

Fule, P. Z., M. Ramos-Gomez, C. Cortes-Montano, and A. M. Miller. 2011. "Fire Regime in a Mexican Forest under Indigenous Resource Management." *Ecological Applications* 21: 764–75.

Fulé, P. Z., T. W. Swetnam, P. M. Brown, D. A. Falk, D. L. Peterson, C. D. Allen, G. H. Aplet, 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: 825–30.

Fulé, P. Z., J. Villanueva-Diaz, and M. Ramos-Gomez. 2005. "Fire Regime in a Conservation Reserve in Chihuahua, Mexico." *Canadian Journal of Forest Research* 35: 320–30.

Fulé, P. Z., L. L. Yocom, C. C. Montano, D. A. Falk, J. Cerano, and J. Villanueva-Diaz. 2012. "Testing a Pyroclimatic Hypothesis on the Mexico-United States Border." *Ecology* 93: 1830–40.

Gao, P., A. J. Terando, J. A. Kupfer, J. Morgan Varner, M. C. Stambaugh, T. L. Lei, and J. Kevin Hiers. 2021. "Robust Projections of Future Fire Probability for the Conterminous United States." *Science of the Total Environment* 789: 147872.

Gedalof, Z., D. L. Peterson, and N. J. Mantua. 2005. "Atmospheric, Climatic, and Ecological Controls on Extreme Wildfire Years

in the Northwestern United States." *Ecological Applications* 15: 154–74.

Girard, F., S. Payette, and R. Gagnon. 2008. "Rapid Expansion of Lichen Woodlands within the Closed-Crown Boreal Forest Zone over the Last 50 Years Caused by Stand Disturbances in Eastern Canada." *Journal of Biogeography* 35: 529–37.

Girardin, M. P., J. Portier, C. C. Remy, A. A. Ali, J. Paillard, O. Blarquez, H. Asselin, S. Gauthier, P. Grondin, and Y. Bergeron. 2019. "Coherent Signature of Warming-Induced Extreme Sub-Continental Boreal Wildfire Activity 4800 and 1100 Years BP." *Environmental Research Letters* 14: 124042.

Gomez-Pineda, E., C. Saenz-Romero, J. M. Ortega-Rodriguez, A. Blanco-Garcia, X. Madrigal-Sanchez, R. Lindig-Cisneros, L. Lopez-Toledo, M. E. Pedraza-Santos, and G. E. Rehfeldt. 2020. "Suitable Climatic Habitat Changes for Mexican Conifers along Altitudinal Gradients under Climatic Change Scenarios." *Ecological Applications* 30: e02041.

de Groot, W. J., M. D. Flannigan, and A. S. Cantin. 2013. "Climate Change Impacts on Future Boreal Fire Regimes." *Forest Ecology and Management* 294: 35–44.

Guiterman, 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: 943–59.

Guiterman, C. H., E. Q. Margolis, C. H. Baisan, D. A. Falk, C. D. Allen, and T. W. Swetnam. 2019. "Spatiotemporal Variability of Human-Fire Interactions on the Navajo Nation." *Ecosphere* 10: e02932.

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.

Gutsell, S. L., and E. A. Johnson. 1996. "How Fire Scars Are Formed: Coupling a Disturbance Process to its Ecological Effect." *Canadian Journal of Forest Research* 26: 166–74.

Guyette, R. P., R. M. Muzika, and D. C. Dey. 2002. "Dynamics of an Anthropogenic Fire Regime." *Ecosystems* 5: 472–86.

Guyette, R. P., M. C. Stambaugh, D. C. Dey, and R.-M. Muzika. 2012. "Predicting Fire Frequency with Chemistry and Climate." *Ecosystems* 15: 322–35.

Guyette, R. P., F. R. Thompson, J. Whittier, M. C. Stambaugh, and D. C. Dey. 2014. "Future Fire Probability Modeling with Climate Change Data and Physical Chemistry." *Forest Science* 60: 862–70.

Hagmann, R. K., P. F. Hessburg, S. J. Prichard, N. A. Povak, P. M. Brown, P. Z. Fule, R. E. Keane, et al. 2021. "Evidence for Widespread Changes in the Structure, Composition, and Fire Regimes of Western North American Forests." *Ecological Applications* 31: e02431.

Hanberry, B. B., D. C. Bragg, and T. F. Hutchinson. 2018. "A Reconceptualization of Open Oak and Pine Ecosystems of Eastern North America Using a Forest Structure Spectrum." *Ecosphere* 9: e02431.

Hanes, C. C., X. Wang, P. Jain, M.-A. Parisien, J. M. Little, and M. D. Flannigan. 2019. "Fire-Regime Changes in Canada over the Last Half Century." *Canadian Journal of Forest Research* 49: 256–69.

Harley, G. L., C. H. Baisan, P. M. Brown, D. A. Falk, W. T. Flatley, H. D. Grissino-Mayer, A. Hessl, et al. 2018. "Advancing Dendrochronological Studies of Fire in the United States." *Fire* 1: 1–6.

Harley, G. L., H. D. Grissino-Mayer, and S. P. Horn. 2013. "Fire History and Forest Structure of an Endangered Subtropical Ecosystem in the Florida Keys, USA." *International Journal of Wildland Fire* 22: 394–404.

Heinselman, M. L. 1973. "Fire in the Virgin Forests of the Boundary Waters Canoe Area, Minnesota." *Quaternary Research* 3: 329–82.

Heon, J., D. Arseneault, and M. A. Parisien. 2014. "Resistance of the Boreal Forest to High Burn Rates." *Proceedings of the National Academy of Sciences of the United States of America* 111: 13888–93.

Hessburg, P. F., C. L. Miller, S. A. Parks, N. A. Povak, A. H. Taylor, P. E. Higuera, S. J. Prichard, et al. 2019. "Climate, Environment, and Disturbance History Govern Resilience of Western North American Forests." *Frontiers in Ecology and Evolution* 7: 239.

Hessl, A., J. Miller, J. Kernan, D. Keenum, and D. McKenzie. 2007. "Mapping Paleo-Fire Boundaries from Binary Point Data: Comparing Interpolation Methods." *The Professional Geographer* 59: 87–104.

Heyerdahl, E. K., and E. Alvarado. 2003. In *Influence of Climate and Land Use on Historical Surface Fires in Pine-Oak Forests, Sierra Madre Occidental, Mexico*, edited by T. T. Veblen, B. H. Baker, G. Montenegro, and T. W. Swetnam, 196–217. New York: Springer.

Heyerdahl, E. K., P. M. Brown, S. G. Kitchen, and M. H. Weber. 2011. *Multicentury Fire and Forest Histories at 19 Sites in Utah and Eastern Nevada*. Gen. Tech. Rep. RMRS-GTR-261. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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: 660–78.

Heyerdahl, E. K., R. A. Loehman, and D. A. Falk. 2019. "A Multi-Century History of Fire Regimes along a Transect of Mixed-Conifer Forests in Central Oregon, U.S.A." *Canadian Journal of Forest Research* 49: 76–86.

Heyerdahl, E. K., and S. J. McKay. 2008. "Condition of Live Fire-Scarred Ponderosa Pine Twenty-One Years after Removing Partial Cross-Sections." *Tree-Ring Research* 73: 149–53.

Heyerdahl, E. K., D. McKenzie, L. D. Daniels, A. E. Hessl, J. S. Littell, and N. J. Mantua. 2008. "Climate Drivers of Regionally Synchronous Fires in the Inland Northwest (1651–1900)." *International Journal of Wildland Fire* 17: 40–9.

Higuera, P. E., J. T. Abatzoglou, J. S. Littell, and P. Morgan. 2015. "The Changing Strength and Nature of Fire-Climate Relationships in the Northern Rocky Mountains, U.S.A., 1902–2008." *PLoS One* 10: e0127563.

Higuera, P. E., B. N. Shuman, and K. D. Wolf. 2021. "Rocky Mountain Subalpine Forests Now Burning More than any Time in Recent Millennia." *Proceedings of the National Academy of Sciences of the United States of America* 118: e2103135118.

Higuera, P. E., C. Whitlock, and J. A. Gage. 2010. "Linking Tree-Ring and Sediment-Charcoal Records to Reconstruct Fire Occurrence and Area Burned in Subalpine Forests of Yellowstone National Park, USA." *The Holocene* 21: 327–41.

Hoctor, T. S., R. F. Noss, L. D. Harris, and K. A. Whitney. 2006. "Spatial Ecology and Restoration of the Longleaf Pine Evosystem." In *The Longleaf Pine Ecosystem*, edited by S. Jose, E. J. Jokela, and D. L. Miller, 377–402. New York: Springer.

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: 2903–15.

Howard, L. F., G. D. Cahalan, K. Ehleben, B. A. Muhammad El, H. Halza, and S. DeLeon. 2021. "Fire History and Dendroecology of Catoctin Mountain, Maryland, USA, with Newspaper Corroboration." *Fire Ecology* 17: 8.

Huffman, J. M. 2006. "Historical Fire Regimes in Southeastern Pine Savannas." PhD dissertation, Louisiana State University.

Huffman, M. R. 2013. "The Many Elements of Traditional Fire Knowledge: Synthesis, Classification, and Aids to Cross-Cultural Problem Solving in Fire-Dependent Systems around the World." *Ecology and Society* 18: 3.

Huffman, D. W., M. L. Floyd, D. P. Hanna, J. E. Crouse, P. Z. Fulé, A. J. Sánchez Meador, and J. D. Springer. 2020. "Fire Regimes and Structural Changes in Oak-Pine Forests of the Mogollon Highlands Ecoregion: Implications for Ecological Restoration." *Forest Ecology and Management* 465: 118087.

Huffman, J. M., W. J. Platt, H. Grissino-Mayer, and C. J. Boyce. 2004. "Fire History of a Barrier Island Slash Pine (*Pinus elliottii*) Savanna." *Natural Areas Journal* 24: 258–68.

Huffman, D. W., A. J. Sánchez Meador, M. T. Stoddard, J. E. Crouse, and J. P. Roccaforte. 2017. "Efficacy of Resource Objective Wildfires for Restoration of Ponderosa Pine (*Pinus ponderosa*) Forests in Northern Arizona." *Forest Ecology and Management* 389: 395–403.

Huffman, D. W., T. J. Zegler, and P. Z. Fule. 2015. "Fire History of a Mixed Conifer Forest on the Mogollon Rim, Northern Arizona, USA." *International Journal of Wildland Fire* 24: 680–9.

Hurteau, M. D., S. Liang, A. L. Westerling, and C. Wiedinmyer. 2019. "Vegetation-Fire Feedback Reduces Projected Area Burned under Climate Change." *Scientific Reports* 9: 2838.

Iniguez, J. M., T. W. Swetnam, and C. H. Baisan. 2016. "Fire History and Moisture Influences on Historical Forest Age Structure in the Sky Islands of Southern Arizona, USA." *Journal of Biogeography* 43: 85–95.

Iniguez, J. M., T. W. Swetnam, and S. R. Yool. 2008. "Topography Affected Landscape Fire History Patterns in Southern Arizona, USA." *Forest Ecology and Management* 256: 295–303.

Johnson, E. A., and C. P. S. Larsen. 1991. "Climatically Induced Change in Fire Frequency in the Southern Canadian Rockies." *Ecology* 72: 194–201.

Johnston, J. D., J. D. Bailey, and C. J. Dunn. 2016. "Influence of Fire Disturbance and Biophysical Heterogeneity on Pre-Settlement Ponderosa Pine and Mixed Conifer Forests." *Ecosphere* 7: e01581.

Jones, E. E. 2017. "Spatiotemporal Analysis of Old World Diseases in North America, A.D. 1519–1807." *American Antiquity* 79: 487–506.

Keeley, J. E. 2012. "Ecology and Evolution of Pine Life Histories." *Annals of Forest Science* 69: 445–53.

Keeley, J. E., J. G. Pausas, P. W. Rundel, W. J. Bond, and R. A. Bradstock. 2011. "Fire as an Evolutionary Pressure Shaping Plant Traits." *Trends in Plant Science* 16: 406–11.

Kellogg, L.-K. B., D. McKenzie, D. L. Peterson, and A. E. Hessl. 2007. "Spatial Models for Inferring Topographic Controls on Historical Low-Severity Fire in the Eastern Cascade Range of Washington, USA." *Landscape Ecology* 23: 227–40.

Kennedy, M. C., R. R. Bart, C. L. Tague, and J. S. Choate. 2021. "Does Hot and Dry Equal More Wildfire? Contrasting Short- and Long-Term Climate Effects on Fire in the Sierra Nevada, CA." *Ecosphere* 12: e03657.

Kennedy, M. C., and D. McKenzie. 2010. "Using a Stochastic Model and Cross-Scale Analysis to Evaluate Controls on Historical Low-Severity Fire Regimes." *Landscape Ecology* 25: 1561–73.

Kernan, J. T., and A. E. Hessl. 2010. "Spatially Heterogeneous Estimates of Fire Frequency in Ponderosa Pine Forests of Washington, USA." *Fire Ecology* 6: 117–35.

Keyser, A. R., D. J. Krofcheck, C. C. Remy, C. D. Allen, and M. D. Hurteau. 2020. "Simulated Increases in Fire Activity Reinforce Shrub Conversion in a Southwestern US Forest." *Ecosystems* 23: 1702–13.

Kipfmueller, K. F., E. R. Larson, L. B. Johnson, and E. A. Schneider. 2021. "Human Augmentation of Historical Red Pine Fire Regimes in the Boundary Waters Canoe Area Wilderness." *Ecosphere* 12: e03673.

Kipfmueller, K. F., E. A. Schneider, S. A. Weyenberg, and L. B. Johnson. 2017. "Historical Drivers of a Frequent Fire Regime in the Red Pine Forests of Voyageurs National Park, MN, USA." *Forest Ecology and Management* 405: 31–43.

Kitchen, S. G. 2012. "Historical Fire Regime and Forest Variability on Two Eastern Great Basin Fire-Sheds (USA)." *Forest Ecology and Management* 285: 53–66.

Kitchen, S. G. 2015. "Climate and Human Influences on Historical Fire Regimes (AD 1400–1900) in the Eastern Great Basin (USA)." *The Holocene* 26: 397–407.

Kitzberger, T., D. A. Falk, A. L. Westerling, and T. W. Swetnam. 2017. "Direct and Indirect Climate Controls Predict Heterogeneous Early-Mid 21st Century Wildfire Burned Area across Western and Boreal North America." *PLoS One* 12: e0188486.

Kitzberger, T., G. L. W. Perry, J. Paritsis, J. H. Gowda, A. J. Tepley, A. Holz, and T. T. Veblen. 2016. "Fire–Vegetation Feedbacks and Alternative States: Common Mechanisms of Temperate Forest Vulnerability to Fire in Southern South America and New Zealand." *New Zealand Journal of Botany* 54: 247–72.

Kitzberger, T., P. M. Brown, E. K. Heyerdahl, T. W. Swetnam, and T. T. and Veblen. 2007. "Contingent Pacific-Atlantic Ocean Influence on Multicentury Wildfire Synchrony over Western North America." *Proceedings of the National Academy of Sciences of the United States of America* 104:543–8.

Kitzberger, T., T. W. Swetnam, and T. T. Veblen. 2001. "Inter-Hemispheric Synchrony of Forest Fires and the El Nino-Southern Oscillation." *Global Ecology and Biogeography* 10: 315–26.

Krawchuk, M. A., and M. A. Moritz. 2011. "Constraints on Global Fire Activity Vary across a Resource Gradient." *Ecology* 92: 121–32.

Krawchuk, M. A., M. A. Moritz, M. A. Parisien, J. Van Dorn, and K. Hayhoe. 2009. "Global Pyrogeography: The Current and Future Distribution of Wildfire." *PLoS One* 4: e5102.

Lafon, C. W., A. T. Naito, H. Grissino-Mayer, S. P. Horn, and T. A. Waldrop. 2017. *Fire History of the Appalachian Region: a Review and Synthesis.* Gen. Tech. Rep. SRS-219. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station.

Lake, F. K., and A. C. Christianson. 2019. "Indigenous Fire Stewardship." In *Encyclopedia of Wildfires and Wildland-Urban Interface (WUI) Fires* 1–9. Cham, Switzerland: Springer.

Lake, F. K., V. Wright, P. Morgan, M. McFadzen, D. McWethy, and C. Stevens-Rumann. 2017. "Returning Fire to the Land: Celebrating Traditional Knowledge and Fire." *Journal of Forestry* 115: 343–53.

Larson, E. R., K. F. Kipfmueller, and L. B. Johnson. 2021. "People, Fire, and Pine: Linking Human Agency and Landscape in the Boundary Waters Canoe Area Wilderness and beyond." *Annals of the American Association of Geographers* 111: 1–25.

Leopold, A. 1924. "Grass, Brush, Timber, and Fire in Southern Arizona." *Journal of Forestry* 22: 1–10.

Lertzman, K., J. Fall, and B. Dorner. 1998. "Three Kinds of Heterogeneity in Fire Regimes: At the Crossroads of Fire History and Landscape Ecology." *Northwest Science* 72: 4–23.

Lewis, H. T., and T. A. Ferguson. 1988. "Yards, Corridors, and Mosaics: How to Burn a Boreal Forest." *Human Ecology* 16: 57–77.

Leys, B., D. Griffin, E. R. Larson, and M. L. KK. 2019. "Century-Scale Fire Dynamics in a Savanna Ecosystem." *Fire* 2: 51.

Liang, S., M. D. Hurteau, and A. L. Westerling. 2017. "Potential Decline in Carbon Carrying Capacity under Projected Climate-Wildfire Interactions in the Sierra Nevada." *Scientific Reports* 7: 2420.

Liang, S., M. D. Hurteau, and A. L. Westerling. 2018. "Large-Scale Restoration Increases Carbon Stability under Projected Climate and Wildfire Regimes." *Frontiers in Ecology and the Environment* 16: 207–12.

Littell, J. S., D. McKenzie, D. L. Peterson, and A. L. Westerling. 2009. "Climate and Wildfire Area Burned in Western U.S. Ecoprovinces, 1916–2003." *Ecological Applications* 19: 1003–21.

Littell, J. S., D. McKenzie, H. Y. Wan, and S. A. Cushman. 2018. "Climate Change and Future Wildfire in the Western United States: An Ecological Approach to Nonstationarity." *Earth's Future* 6: 1097–111.

Lombardo, K. J., T. W. Swetnam, A. Baker, and M. I. Borchert. 2009. "Using Bigcone Douglas-Fir Fire Scars and Tree Rings to Reconstruct Interior Chaparral Fire History." *Fire Ecology* 5: 35–56.

Lopez, E., and G. Bernardino Mata. 1992. *Análisis Crítico de la Nueva Reforma Agraria*. Chapingo: Universidad Autónoma Chapingo.

Malevich, S. B., C. H. Guiterman, and E. Q. Margolis. 2018. "Burnr: Fire History Analysis and Graphics in R." *Dendrochronologia* 49: 9–15.

Margolis, E. Q., and J. Balmat. 2009. "Fire History and Fire-Climate Relationships along a Fire Regime Gradient in the Santa Fe Municipal Watershed, NM, USA." *Forest Ecology and Management* 258: 2416–30.

Margolis, E. Q., and C. Guiterman. 2022. "North American Tree-Ring Fire-Scar Site Descriptions: U.S. Geological Survey Data Release." https://doi.org/10.5066/P9PT90QX.

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.

Margolis, E. Q., T. W. Swetnam, and C. D. Allen. 2007. "A Stand-Replacing Fire History in Upper Montane Forests of the Southern Rocky Mountains." *Canadian Journal of Forest Research* 37: 2227–41.

Margolis, E. Q., C. A. Woodhouse, and T. W. Swetnam. 2017. "Drought, Multi-Seasonal Climate, and Wildfire in Northern New Mexico." *Climatic Change* 142: 433–46.

Marlon, J. R., P. J. Bartlein, C. Carcaillet, D. G. Gavin, S. P. Harrison, P. E. Higuera, F. Joos, M. J. Power, and I. C. Prentice. 2008. "Climate and Human Influences on Global Biomass Burning over the Past Two Millennia." *Nature Geoscience* 1: 697–702.

Marlon, J. R., P. J. Bartlein, D. G. Gavin, C. J. Long, R. Anderson, C. E. Briles, K. J. Brown, et al. 2012. "Long-Term Perspective on Wildfires in the Western USA." *Proceedings of the National Academy of Sciences of the United States of America* 109: E535–43.

Marlon, J. R., R. Kelly, A. L. Daniau, B. Vannière, M. J. Power, P. Bartlein, P. Higuera, et al. 2015. "Reconstructions of Biomass Burning from Sediment Charcoal Records to Improve Data-Model Comparisons." *Biogeosciences Discussions* 12: 53.

Marschall, J. M., M. C. Stambaugh, B. C. Jones, and E. Abadir. 2019. "Spatial Variability of Historical Fires across a Red Pine–Oak Landscape, Pennsylvania, USA." *Ecosphere* 10: e02978.

Marschall, J., M. Stambaugh, B. Jones, R. Guyette, P. Brose, and D. Dey. 2016. "Fire Regimes of Remnant Pitch Pine Communities in the Ridge and Valley Region of Central Pennsylvania, USA." *Forests* 7: 224.

Martin, R. E. 1982. "Fire History and Its Role in Succession." In *Forest Succession and Stand Development Research in the Northwest. Symposium Proceedings* 92–9. Corvallis, OR: Oregon State University.

Martínez-Torres, H. L., A. Castillo, M. I. Ramírez, and D. R. Pérez-Salicrup. 2016. "The Importance of the Traditional Fire Knowledge System in a Subtropical Montane Socio-Ecosystem in a Protected Natural Area." *International Journal of Wildland Fire* 25: 911–21.

Matlack, G. R. 2013. "Reassessment of the Use of Fire as a Management Tool in Deciduous Forests of Eastern North America." *Conservation Biology* 27: 916–26.

Maxwell, R. S., A. H. Taylor, C. N. Skinner, H. D. Safford, R. E. Isaacs, C. Airey, and A. B. Young. 2014. "Landscape-Scale Modeling of Reference Period Forest Conditions and Fire Behavior on Heavily Logged Lands." *Ecosphere* 5: 1–28.

McEwan, R. W., T. F. Hutchinson, R. P. Long, D. R. Ford, and B. C. McCarthy. 2007. "Temporal and Spatial Patterns in Fire Occurrence during the Establishment of Mixed-Oak Forests in Eastern North America." *Journal of Vegetation Science* 18: 655–64.

McKenzie, D., A. E. Hessl, and L.-K. B. Kellogg. 2006. "Using Neutral Models to Identify Constraints on Low-Severity Fire Regimes." *Landscape Ecology* 21: 139–52.

McKenzie, D., and M. C. Kennedy. 2012. "Power Laws Reveal Phase Transitions in Landscape Controls of Fire Regimes." *Nature Communications* 3: 726.

Mckenzie, D., and J. S. Littell. 2017. "Climate Change and the Eco-Hydrology of Fire: Will Area Burned Increase in a Warming Western USA?" *Ecological Applications* 27: 26–36.

McLauchlan, K. K., P. E. Higuera, J. Miesel, B. M. Rogers, J. Schweitzer, J. K. Shuman, A. J. Tepley, et al. 2020. "Fire as a Fundamental Ecological Process: Research Advances and Frontiers." *Journal of Ecology* 108: 2047–69.

McWethy, D. B., P. E. Higuera, C. Whitlock, T. T. Veblen, D. M. J. S. Bowman, G. J. Cary, S. G. Haberle, et al. 2013. "A Conceptual Framework for Predicting Temperate Ecosystem Sensitivity to Human Impacts on Fire Regimes." *Global Ecology and Biogeography* 22: 900–12.

Meko, D. M., and C. H. Baisan. 2001. "Pilot Study of Latewood-Width of Conifers as an Indicator of Variability of Summer Rainfall in the North American Monsoon Region." *International Journal of Climatology* 21: 697–708.

Merschel, A. G., E. K. Heyerdahl, T. A. Spies, and R. A. Loehman. 2018. "Influence of Landscape Structure, Topography, and Forest Type on Spatial Variation in Historical Fire Regimes, Central Oregon, USA." *Landscape Ecology* 33: 1195–209.

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: 1670–88.

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., W. H. Romme, and P. M. Brown. 2014. "Climate and Land-Use Effects on Wildfire in Northern Mexico, 1650–2010." *Forest Ecology and Management* 325: 49–59.

Murphy, A., J. Abrams, T. Daniel, and V. Yazzie. 2007. "Living among Frequent-Fire Forests: Human History and Cultural Perspectives." *Ecology and Society* 12: 17.

Mutch, R. W. 1970. "Wildland Fires and Ecosystems—A Hypothesis." *Ecology* 51: 1046–51.

Myers, R. L. 1985. "Fire and the Dynamic Relationship between Florida Sandhill and Sand Pine Scrub Vegetation." *Bulletin of the Torrey Botanical Club* 112: 241–52.

Nolan, C., J. T. Overpeck, J. R. M. Allen, P. M. Anderson, J. L. Betancourt, H. A. Binney, S. Brewer, et al. 2018. "Past and Future Global Transformation of Terrestrial Ecosystems under Climate Change." *Science* 361: 920–3.

North, M., M. Hurteau, R. Fiegener, and M. Barbour. 2005. "Influence of Fire and El Nino on Tree Recruitment Varies by Species in Sierran Mixed Conifer." *Forest Science* 51: 187–97.

North, M. P., K. M. Van de Water, S. L. Stephens, and B. M. Collins. 2009. "Climate, Rain Shadow, and Human-Use Influences on Fire Regimes in the Eastern Sierra Nevada, California, USA." *Fire Ecology* 5: 20–34.

Noss, R. F., W. J. Platt, B. A. Sorrie, A. S. Weakley, D. B. Means, J. Costanza, R. K. Peet, and D. Richardson. 2015. "How Global Biodiversity Hotspots May Go Unrecognized: Lessons from the North American Coastal Plain." *Diversity and Distributions* 21: 236–44.

Nowacki, G. J., and M. D. Abrams. 2008. "The Demise of Fire and "Mesofication" of Forests in the Eastern United States." *BioScience* 58: 123–38.

O'Connor, C. D., D. A. Falk, and G. M. Garfin. 2020. "Projected Climate-Fire Interactions Drive Forest to Shrubland Transition on an Arizona Sky Island." *Frontiers in Environmental Science* 8: 137.

O'Connor, C. D., D. A. Falk, A. M. Lynch, and T. W. Swetnam. 2014. "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: 264–78.

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: 900–15.

Odion, D. C., C. T. Hanson, A. Arsenault, W. L. Baker, D. A. Dellasala, R. L. Hutto, W. Klenner, 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.

Odion, D. C., M. A. Moritz, and D. A. DellaSala. 2010. "Alternative Community States Maintained by Fire in the Klamath Mountains, USA." *Journal of Ecology* 98: 96–105.

Oswald, W. W., D. R. Foster, B. N. Shuman, E. S. Chilton, D. L. Doucette, and D. L. Duranleau. 2020. "Conservation Implications of Limited Native American Impacts in Pre-Contact New England." *Nature Sustainability* 3: 241–6.

Parisien, M.-A., C. Miller, S. A. Parks, E. R. DeLancey, F.-N. Robinne, and M. D. Flannigan. 2016. "The Spatially Varying Influence of Humans on Fire Probability in North America." *Environmental Research Letters* 11: 075005.

Parisien, M.-A., and M. A. Moritz. 2009. "Environmental Controls on the Distribution of Wildfire at Multiple Spatial Scales." *Ecological Monographs* 79: 127–54.

Parisien, M. A., S. A. Parks, M. A. Krawchuk, J. M. Little, M. D. Flannigan, L. M. Gowman, and M. A. Moritz. 2014. "An Analysis of Controls on Fire Activity in Boreal Canada: Comparing Models Built with Different Temporal Resolutions." *Ecological Applications* 24: 1341–56.

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 to 2017." *Geophysical Research Letters* 47: 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, 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: art275.

Pausas, J. G., R. A. Bradstock, D. A. Keith, J. Keeley, and G. F. Network. 2004. "Plant Functional Traits in Relation to Fire in Crown-Fire Ecosystems." *Ecology* 85: 1085–100.

Platt, W. J., D. P. Ellair, J. M. Huffman, S. E. Potts, and B. Beckage. 2016. "Pyrogenic Fuels Produced by Savanna Trees Can Engineer Humid Savannas." *Ecological Monographs* 86: 352–72.

Platt, W. J., S. L. Orzell, and M. G. Slocum. 2015. "Seasonality of Fire Weather Strongly Influences Fire Regimes in South Florida Savanna-Grassland Landscapes." *PLoS One* 10: e0116952.

Pohl, K. A., K. S. Hadley, and K. B. Arabas. 2006. "Decoupling Tree-Ring Signatures of Climate Variation, Fire, and Insect Outbreaks in Central Oregon." *Tree-Ring Research* 62: 37–50.

Poulos, H., A. Barton, J. Slingsby, and D. Bowman. 2018. "Do Mixed Fire Regimes Shape Plant Flammability and Post-Fire Recovery Strategies?" *Fire* 1(3): 39.

Poulos, H. M., J. Villanueva Díaz, J. Cerano Paredes, A. E. Camp, and R. G. Gatewood. 2013. "Human Influences on Fire

Regimes and Forest Structure in the Chihuahuan Desert Borderlands." *Forest Ecology and Management* 298: 1–11.

Pyne, S. 1997. *Fire in America: a Cultural History of Wildland and Rural Fire*. Seattle, WA: Univeristy of Washinton Press.

Pyne, S. 2000. *Vestal Fire: An Environmental History, Told through Fire, of Europe and Europe's Encounter with the World*. Seattle, WA: University of Washington Press.

Reid, A. M., and K. M. Robertson. 2012. "Energy Content of Common Fuels in Upland Pine Savannas of the South-Eastern US and their Application to Fire Behaviour Modelling." *International Journal of Wildland Fire* 21: 591–5.

Riley, K. L., A. P. Williams, S. P. Urbanski, D. E. Calkin, K. C. Short, and C. D. O'Connor. 2019. "Will Landscape Fire Increase in the Future? A Systems Approach to Climate, Fire, Fuel, and Human Drivers." *Current Pollution Reports* 5: 9–24.

Rogeau, 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: 613–22.

Romme, W. H., and D. H. Knight. 1981. "Fire Frequency and Subalpine Forest Succession along a Topographic Gradient in Wyoming." *Ecology* 62: 319–26.

Romps, D. M., J. T. Seeley, D. Vollaro, and J. Molinari. 2014. "Climate Change. Projected Increase in Lightning Strikes in the United States Due to Global Warming." *Science* 346: 851–4.

Roos, C. I., and C. H. Guiterman. 2021. "Dating the Origins of Persistent Oak Shrubfields in Northern New Mexico Using Soil Charcoal and Dendrochronology." *The Holocene* 31: 1212–20.

Roos, C. I., T. W. Swetnam, T. J. Ferguson, M. J. Liebmann, R. A. Loehman, J. R. Welch, E. Q. Margolis, 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 of the United States of America* 118: e2018733118.

Rother, M. T., J. M. Huffman, C. H. Guiterman, K. M. Robertson, and N. Jones. 2020. "A History of Recurrent, Low-Severity Fire without Fire Exclusion in Southeastern Pine Savannas, USA." *Forest Ecology and Management* 475: 118406.

Rother, M. T., J. M. Huffman, G. L. Harley, W. J. Platt, N. Jones, K. M. Robertson, and S. L. Orzell. 2018. "Cambial Phenology Informs Tree-Ring Analysis of Fire Seasonality in Coastal Plain Pine Savannas." *Fire Ecology* 14: 164–85.

Rothermel, R. C. 1983. *How to Predict the Spread and Intensity of Forest and Range Fires*. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station.

Savage, M., and T. W. Swetnam. 1990. "Early 19th-Century Fire Decline Following Sheep Pasturing in a Navajo Ponderosa Pine Forest." *Ecology* 71: 2374–8.

Schoennagel, T., T. T. Veblen, D. Kulakowski, and A. Holz. 2007. "Multidecadal Climate Variability and Climate Interactions Affect Subalpine Fire Occurrence, Western Colorado (USA)." *Ecology* 88: 2891–902.

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: 362–80.

Schwilk, D. W., and A. C. Caprio. 2011. "Scaling from Leaf Traits to Fire Behaviour: Community Composition Predicts Fire Severity in a Temperate Forest." *Journal of Ecology* 99: 970–80.

Seklecki, M. T., H. D. Grissino-Mayer, and T. W. Swetnam. 1996. "Fire History and the Possible Role of Apache-Set Fires in the Chiricahua Mountains of Southeastern Arizona." In *Effects of Fire on Madrean Province Ecosystems: A Symposium Proceedings. General Technical Report RM 289* 238–46. Fort Collins, CO: USDA Forest Service.

Shumway, D. L., M. D. Abrams, and C. M. Ruffner. 2001. "A 400-Year History of Fire and Oak Recruitment in an Old-Growth Oak Forest in Western Maryland, U.S.A." *Canadian Journal of Forest Research* 31: 1437–43.

Skinner, C. N., J. H. Burk, M. G. Barbour, E. Franco-Vizcaino, and S. L. Stephens. 2008. "Influences of Climate on Fire Regimes in Montane Forests of North-Western Mexico." *Journal of Biogeography* 35: 1436–51.

Smith, K. T., E. Arbellay, D. A. Falk, and E. K. Sutherland. 2016. "Macroanatomy and Compartmentalization of Recent Fire Scars in Three North American Conifers." *Canadian Journal of Forest Research* 46: 535–42.

Smith, K. T., and E. K. Sutherland. 1999. "Fire-Scar Formation and Compartmentalization in Oak." *Canadian Journal of Forest Research* 29: 166–71.

Stahle, D. W., E. R. Cook, D. J. Burnette, M. C. A. Torbenson, I. M. Howard, D. Griffin, J. V. Diaz, et al. 2020. "Dynamics, Variability, and Change in Seasonal Precipitation Reconstructions for North America." *Journal of Climate* 33: 3173–95.

Stambaugh, M. C., and R. P. Guyette. 2008. "Predicting Spatio-Temporal Variability in Fire Return Intervals Using a Topographic Roughness Index." *Forest Ecology and Management* 254: 463–73.

Stambaugh, M. C., R. P. Guyette, R. Godfrey, E. R. McMurry, and J. M. Marschall. 2009. "Fire, Drought, and Human History near the Western Terminus of the Cross Timbers, Wichita Mountains, Oklahoma, USA." *Fire Ecology* 5: 51–65.

Stambaugh, M. C., R. P. Guyette, and J. Marschall. 2011. "Longleaf Pine (*Pinus palustris* Mill.) Fire Scars Reveal New Details of a Frequent Fire Regime." *Journal of Vegetation Science* 22: 1094–104.

Stambaugh, M. C., J. M. Marschall, E. R. Abadir, B. C. Jones, P. H. Brose, D. C. Dey, and R. P. Guyette. 2018. "Wave of Fire: An Anthropogenic Signal in Historical Fire Regimes across Central Pennsylvania, USA." *Ecosphere* 9: e02222.

Stambaugh, M. C., J. Sparks, R. P. Guyette, and G. Willson. 2011. "Fire History of a Relict Oak Woodland in Northeast Texas." *Rangeland Ecology & Management* 64: 419–23.

Stephens, S. L., C. N. Skinner, and S. J. Gill. 2003. "Dendrochronology-Based Fire History of Jeffrey Pine—Mixed Conifer Forests in the Sierra San Pedro Martir, Mexico." *Canadian Journal of Forest Research* 33: 1090–101.

Stephens, S. L., A. L. Westerling, M. D. Hurteau, M. Z. 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: 354–60.

Stewart, O. C. 2002. *Forgotten Fires: Native Americans and the Transient Wilderness*. Norman, OK: University of Oklahoma Press.

Stokes, M. A. 1980. "The Dendrochronology of Fire History." In *Proceedings of the Fire History Workshop: October 20–24, 1980, Tucson, Arizona. General Technical Report RM-GTR-81*, edited by M. A. Stokes and J. H. Dieterich, 1–3. Ft. Collins, CO: US

Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.

Strahan, R. T., A. J. Sánchez Meador, D. W. Huffman, D. C. Laughlin, and L. Flory. 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: 1755–65.

Sutherland, E. K., P. M. Brown, D. A. Falk, H. D. Grissino-Mayer, E. Velasquez, C. A. Woodhouse, and P. Brewer. 2014. "Fire History Analysis and Exploration System." 2.0. Fire Research and Management Exchange System, FHAES Working Group, USA. http://www.frames.gov/partner-sites/fhaes/fhaes-home/.

Swanson, F. J. 1981. "Fire and Geomorphic Processes." In *Fire Regimes and Ecosystem Processes*. General Technical Report WO-GTR-26 401–20. Washington, DC: US Department of Agriculture, Forest Service.

Swetnam, T. W. 1993. "Fire History and Climate Change in Giant Sequoia Groves." *Science* 262: 885–9.

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: 1189–206.

Swetnam, T. W., and C. H. Baisan. 1996. "Historical Fire Regime Patterns in the Southwestern United States since AD 1700." In *Fire Effects in Southwestern Forests: Proceedings of the Second La Mesa Fire Symposium. General Technical Report RM-GTR-286*, edited by C. D. Allen, 11–32. Los Alamos, NM: USDA Forest Service.

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: 120–50.

Swetnam, T. W., and J. L. Betancourt. 1990. "Fire-Southern Oscillation Relations in the Southwestern United States." *Science* 249: 1017–20.

Swetnam, T. W., and J. L. Betancourt. 1998. "Mesoscale Disturbance and Ecological Response to Decadal Climatic Variability in the American Southwest." *Journal of Climate* 11: 3128–47.

Swetnam, T. W., and P. M. Brown. 2011. In *Climatic Inferences from Dendroecological Reconstructions*, edited by M. K. Hughes, T. W. Swetnam, and H. F. Diaz, 263–96. New York: Springer.

Swetnam, T. L., D. A. Falk, A. Hessl, and C. Farris. 2011. "Reconstructing Landscape Patterns of Historic Fires and Fire Regimes." In *The Landscape Ecology of Fire*, edited by D. McKenzie, C. Miller, and D. A. Falk. Dordrecht: Springer.

Swetnam, T. W., D. A. Falk, E. K. Sutherland, P. M. Brown, and T. J. Brown. 2011. *Fire and Climate Synthesis (FACS) Project—Final Report to the Joint Fire Science Program*. JFSP Project No. 09-2-01-10. Tucson, AZ: University of Arizona.

Swetnam, T. W., J. Farella, C. I. Roos, M. J. Liebmann, D. A. Falk, and C. D. Allen. 2016. "Multi-Scale Perspectives of Fire, Climate and Humans in Western North America and the Jemez Mountains, USA." *Proceedings of the Royal Society of London Series B: Biological Sciences* 371: 20150168.

Syphard, A. D., J. E. Keeley, A. H. Pfaff, and K. Ferschweiler. 2017. "Human Presence Diminishes the Importance of Climate in Driving Fire Activity across the United States." *Proceedings of the National Academy of Sciences of the United States of America* 114: 13750–5.

Tande, G. F. 1979. "Fire History and Vegetation Pattern of Coniferous Forests of Jasper National Park, Alberta." *Canadian Journal of Botany* 57: 1912–31.

Taylor, A. H. 2004. "Identifying Forest Reference Conditions on Early Cut-over Lands, Lake Tahoe Basin, USA." *Ecological Applications* 14: 1903–20.

Taylor, A. H., and C. N. Skinner. 1998. "Fire History and Landscape Dynamics in a Late-Successional Reserve, Klamath Mountains, California, USA." *Forest Ecology and Management* 111: 285–301.

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: 704–19.

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 of the United States of America* 113: 13684–9.

Tepley, A. J., E. Thomann, T. T. Veblen, G. L. W. Perry, A. Holz, J. Paritsis, T. Kitzberger, K. J. Anderson-Teixeira, and E. Lines. 2018. "Influences of Fire-Vegetation Feedbacks and Post-Fire Recovery Rates on Forest Landscape Vulnerability to Altered Fire Regimes." *Journal of Ecology* 106: 1925–40.

Trouet, V., A. H. Taylor, E. R. Wahl, C. N. Skinner, and S. L. Stephens. 2010. "Fire-Climate Interactions in the American West since 1400 CE." *Geophysical Research Letters* 37: L04702.

Van de Water, K., and M. North. 2010. "Fire History of Coniferous Riparian Forests in the Sierra Nevada." *Forest Ecology and Management* 260: 384–95.

Van Horne, M. L., and P. Z. Fule. 2006. "Comparing Methods of Reconstructing Fire History Using Fire Scars in a Southwestern United States Ponderosa Pine Forest." *Canadian Journal of Forest Research* 36: 855–67.

Van Wagner, C. E. 1978. "Age-Class Distribution and the Forest Fire Cycle." *Canadian Journal of Forest Research* 8: 220–7.

Varner, J. M., J. M. Kane, J. K. Kreye, and E. Engber. 2015. "The Flammability of Forest and Woodland Litter: A Synthesis." *Current Forestry Reports* 1: 91–9.

Veraverbeke, S., B. M. Rogers, M. L. Goulden, R. R. Jandt, C. E. Miller, E. B. Wiggins, and J. T. Randerson. 2017. "Lightning as a Major Driver of Recent Large Fire Years in North American Boreal Forests." *Nature Climate Change* 7: 529–34.

Verrall, A. F. 1938. "The Probable Mechanism of the Protective Action of Resin in Fire Wounds on Red Pine." *Journal of Forestry* 36: 1231–3.

Villarreal, M. L., J. M. Iniguez, A. D. Flesch, J. S. Sanderlin, C. Cortés Montaño, C. R. Conrad, and S. L. Haire. 2020. "Contemporary Fire Regimes Provide a Critical Perspective on Restoration Needs in the Mexico-United States Borderlands." *Air, Soil and Water Research* 13: 1178622120969191.

Wahl, E. R., E. Zorita, V. Trouet, and A. H. Taylor. 2019. "Jet Stream Dynamics, Hydroclimate, and Fire in California from 1600 CE to Present." *Proceedings of the National Academy of Sciences of the United States of America* 116: 5393–8.

Waito, J., M. P. Girardin, J. C. Tardif, F. Conciatori, Y. Bergeron, and A. A. Ali. 2018. "Recent Fire Activity in the Boreal Eastern Interior of North America Is below that of the Past 2000 Yr." *Ecosphere* 9: e02287.

Wang, T., A. Hamann, D. Spittlehouse, and C. Carroll. 2016. "Locally Downscaled and Spatially Customizable Climate Data for Historical and Future Periods for North America." *PLoS One* 11: e0156720.

Wang, X., M.-A. Parisien, S. W. Taylor, J.-N. Candau, D. Stralberg, G. A. Marshall, J. M. Little, and M. D. Flannigan. 2017. "Projected Changes in Daily Fire Spread across Canada over the Next Century." *Environmental Research Letters* 12: 025005.

Weaver, H. 1951. "Fire as an Ecological Factor in the Southwestern Ponderosa Pine Forests." *Journal of Forestry* 49: 93–8.

Westerling, A. L. 2016. "Increasing Western US Forest Wildfire Activity: Sensitivity to Changes in the Timing of Spring." *Philosophical Transactions of the Royal Society of London. Series B* 371: 20150178.

Westerling, A. L., A. Gershunov, T. J. Brown, D. R. Cayan, and M. D. Dettinger. 2003. "Climate and Wildfire in the Western United States." *Bulletin of the American Meteorological Society* 84: 595–604.

Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. "Warming and Earlier Spring Increase Western US Forest Wildfire Activity." *Science* 313: 940–3.

Whitlock, C., P. E. Higuera, D. B. McWethy, and C. E. Briles. 2010. "Paleoecological Perspectives on Fire Ecology: Revisiting the Fire-Regime Concept." *The Open Ecology Journal* 3: 6–23.

Whitlock, C., and M. A. Knox. 2002. "Prehistoric Burning in the Pacific Northwest: Human Versus Climatic Influences." In *Fire, Native Peoples, and the Natural Landscape*, edited by T. R. Vale, 195–231. Washington, DC: Island Press.

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: 2110–21.

Whitman, E., E. Batllori, M.-A. Parisien, C. Miller, J. D. Coop, M. A. Krawchuk, G. W. Chong, and S. L. Haire. 2015. "The Climate Space of Fire Regimes in North-Western North America." *Journal of Biogeography* 42: 1736–49.

Whitman, E., M. A. Parisien, D. K. Thompson, and M. D. Flannigan. 2019. "Short-Interval Wildfire and Drought Overwhelm Boreal Forest Resilience." *Scientific Reports* 9: 18796.

Wolf, J. J. 2004. "A 200-Year Fire History in a Remnant Oak Savanna in Southeastern Wisconsin." *American Midland Naturalist* 152: 201–13.

Wright, C. S., and J. K. Agee. 2004. "Fire and Vegetation History in the Eastern Cascade Mountains, Washington." *Ecological Applications* 14: 443–59.

Yamazaki, D., D. Ikeshima, R. Tawatari, T. Yamaguchi, F. O'Loughlin, J. C. Neal, C. C. Sampson, S. Kanae, and P. D. Bates. 2017. "A High-Accuracy Map of Global Terrain Elevations." *Geophysical Research Letters* 44: 5844–53.

Yocom, L. L., P. Z. Fulé, P. M. Brown, J. Cerano, J. Villanueva-Diaz, D. A. Falk, and E. Cornejo-Oviedo. 2010. "El Nino-Southern Oscillation Effect on a Fire Regime in Northeastern Mexico Has Changed over Time." *Ecology* 91: 1660–71.

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., P. Z. Fulé, P. M. Brown, J. Cerano-Paredes, E. Cornejo-Oviedo, C. Cortés Montaño, S. A. Drury, et al. 2017. "Climate Drives Fire Synchrony but Local Factors Control Fire Regime Change in Northern Mexico." *Ecosphere* 8: e01709.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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