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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.

KEYWORDS
climate, dendrochronology, fire regime, fire scar, humans, pyrogeography, surface fires, synthesis, topography, tree ring, wildfire

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

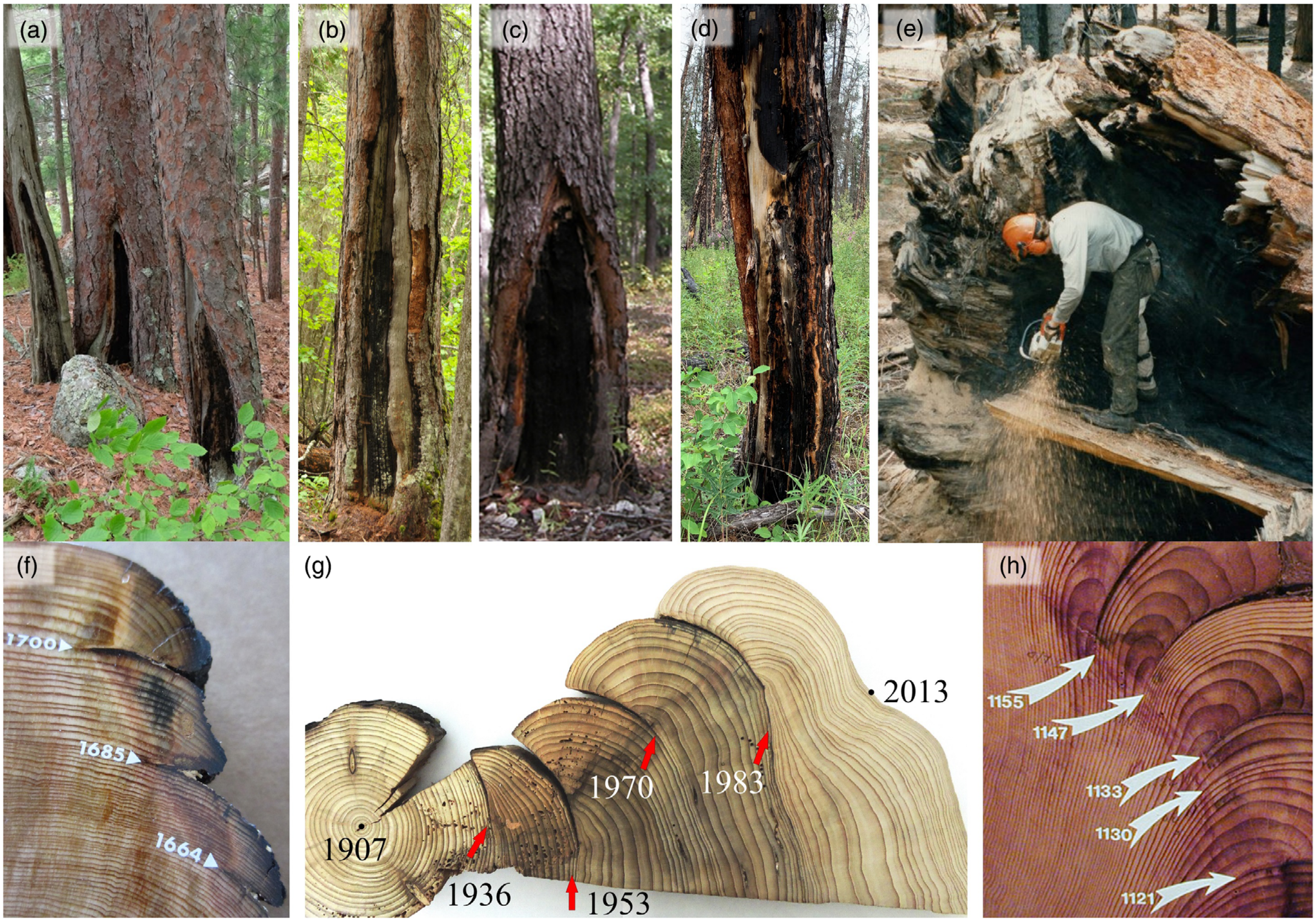

FIGURE 1 Tree-ring fire scars: (a) on multiple red pine (*Pinus resinosa*) in Minnesota, USA (image by L. B. Johnson), (b) on western larch (*Larix occidentalis*) in Montana, USA (image by C. E. Naficy), (c) on black oak (*Quercus velutina*) in Missouri, USA (image by M. Stambaugh), (d) on jack pine (*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 understudied 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

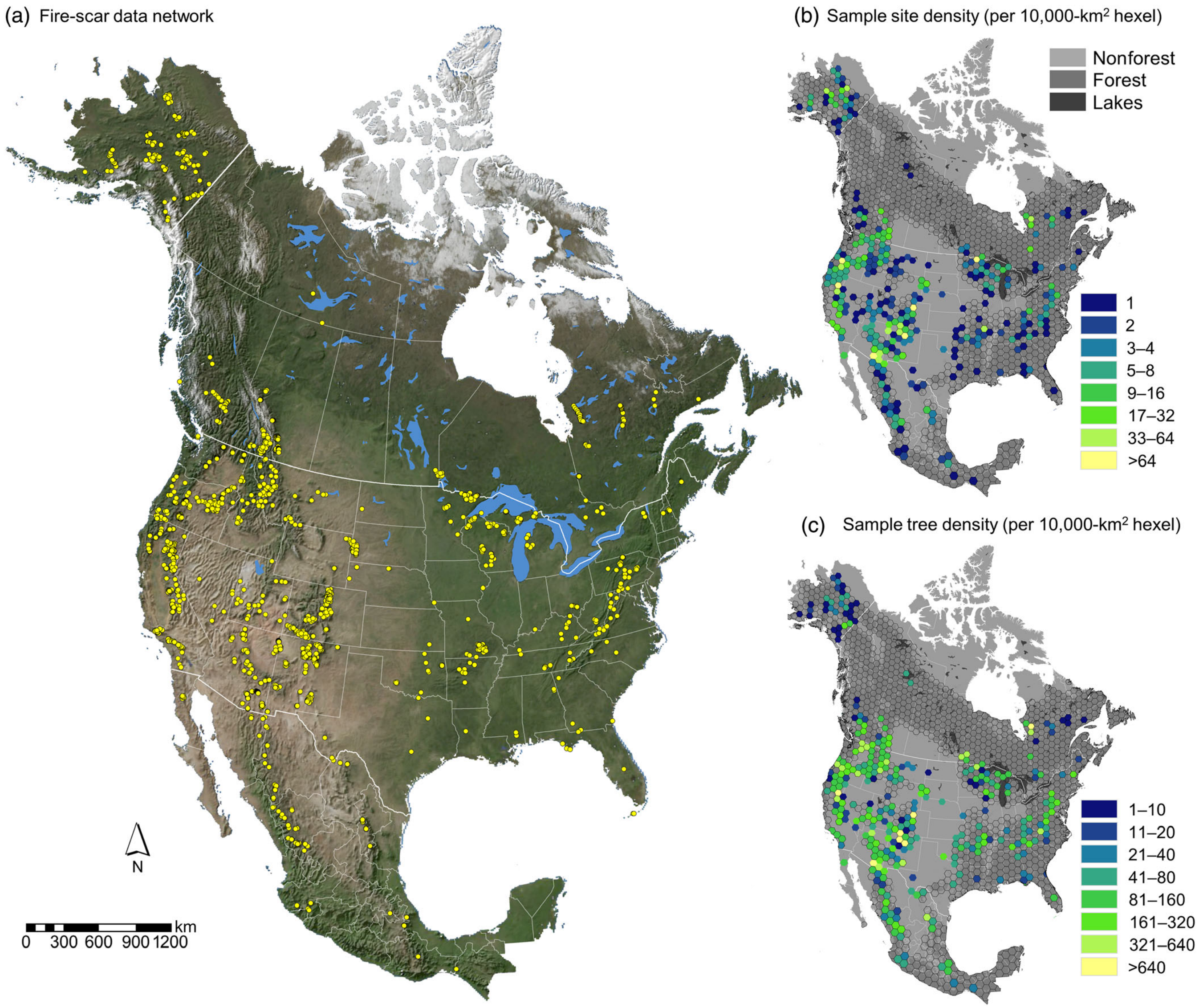

FIGURE 2 Distribution of fire-scar sample sites (a) across North America. The number of sample sites (b) and sampled trees (c) was calculated per 10,000-km^2 hexel. Gray shading in (b) and (c) represents current forest cover based on 1-km MODIS imagery. Hexel outlines are shown only if at least 10% of 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).

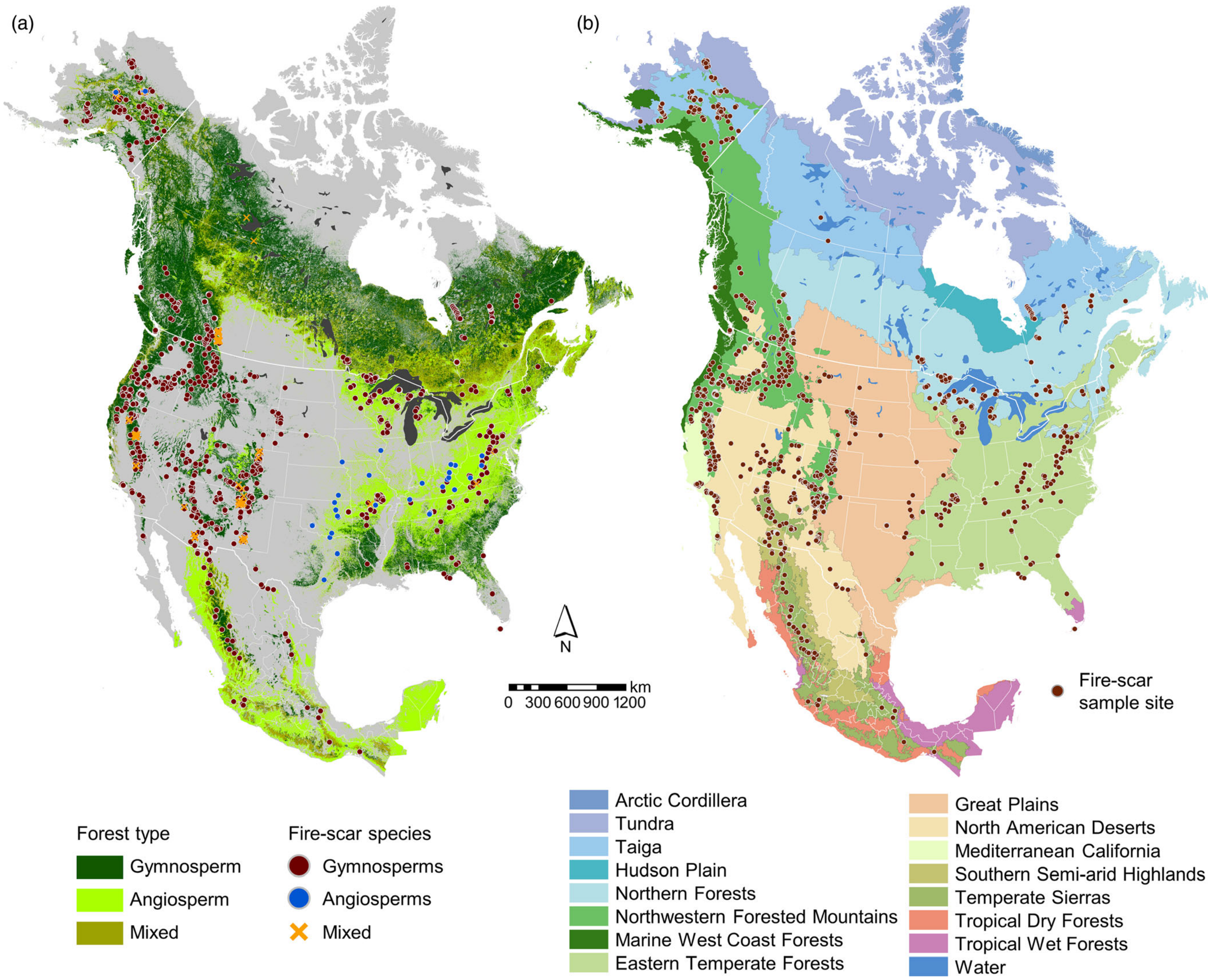

FIGURE 3 The North American tree-ring fire-scar network mapped with (a) gymnosperm and angiosperm forests and (b) level 1 ecoregions. The fire-scar sites in (a) are coded by the same forest classes, which highlights areas where the current mapped forest class differs from the species with fire scars (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 (km^2)	Site density (no./10,000 km^2)
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

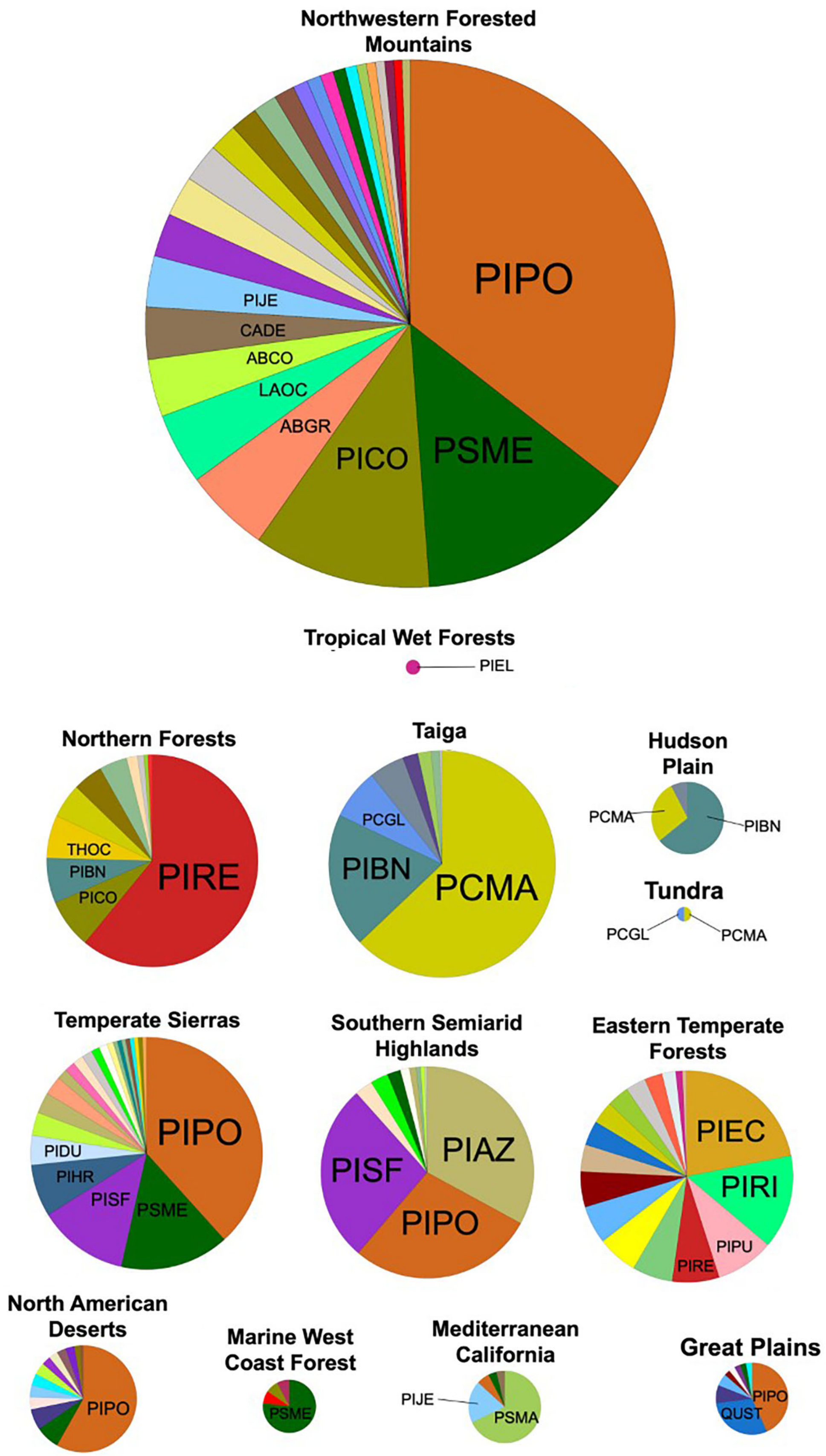

FIGURE 4 Proportion of fire-scarred tree species (four-letter species codes) sampled by site for North American ecoregions. The pie chart size is scaled by the relative number of sites in each ecoregion. See Appendix S1: Table S1 for the full species names and the count of all species.

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

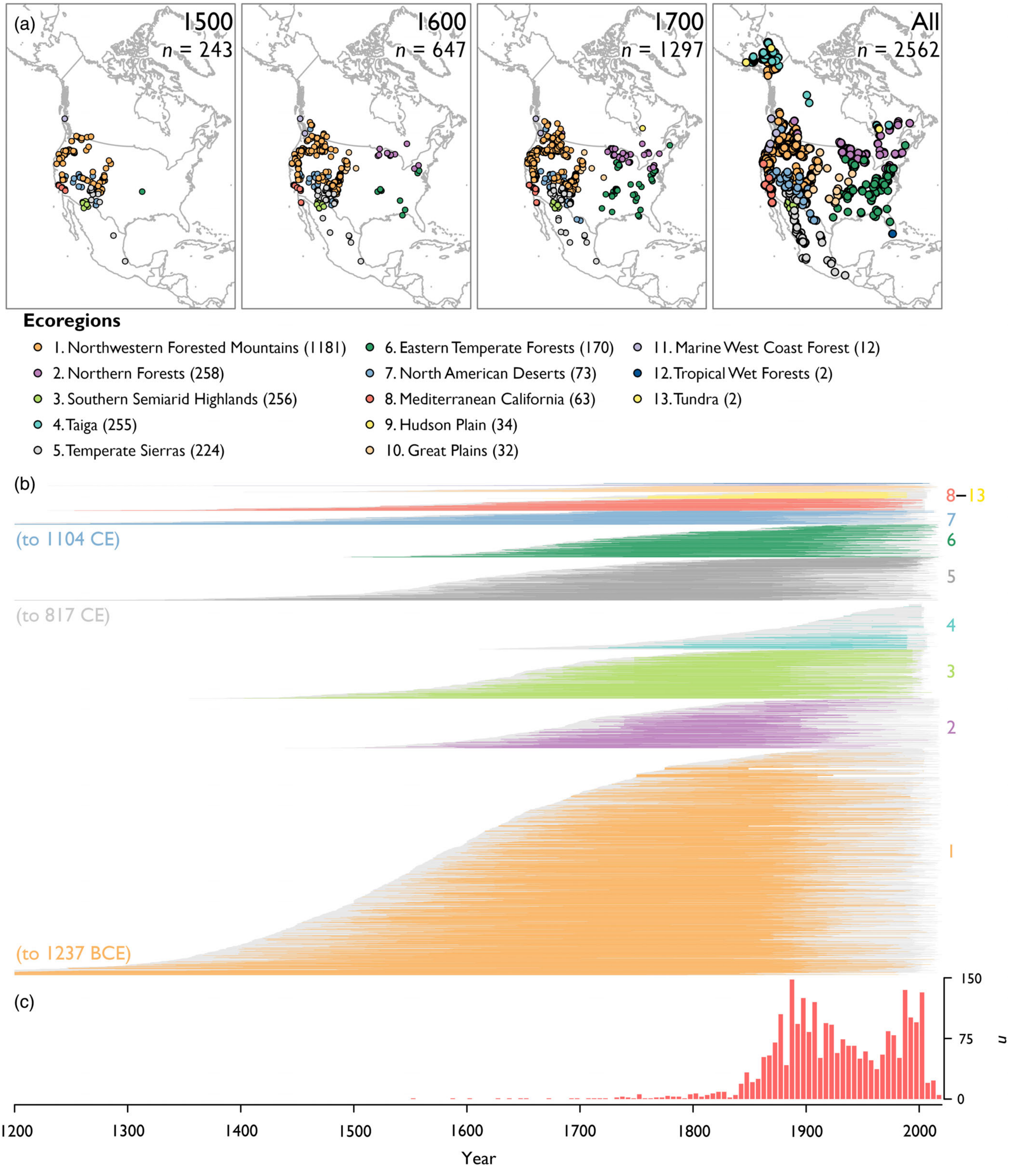

FIGURE 5 Sample depth of the North American tree-ring fire-scar network in time and space by ecoregion. (a) Maps of the spatial distribution of the network in time. Sites are color coded by ecoregion. (b) Sample depth through time of fire-scar sites by ecoregion back to 1200 Common Era (CE). The tree-ring 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.

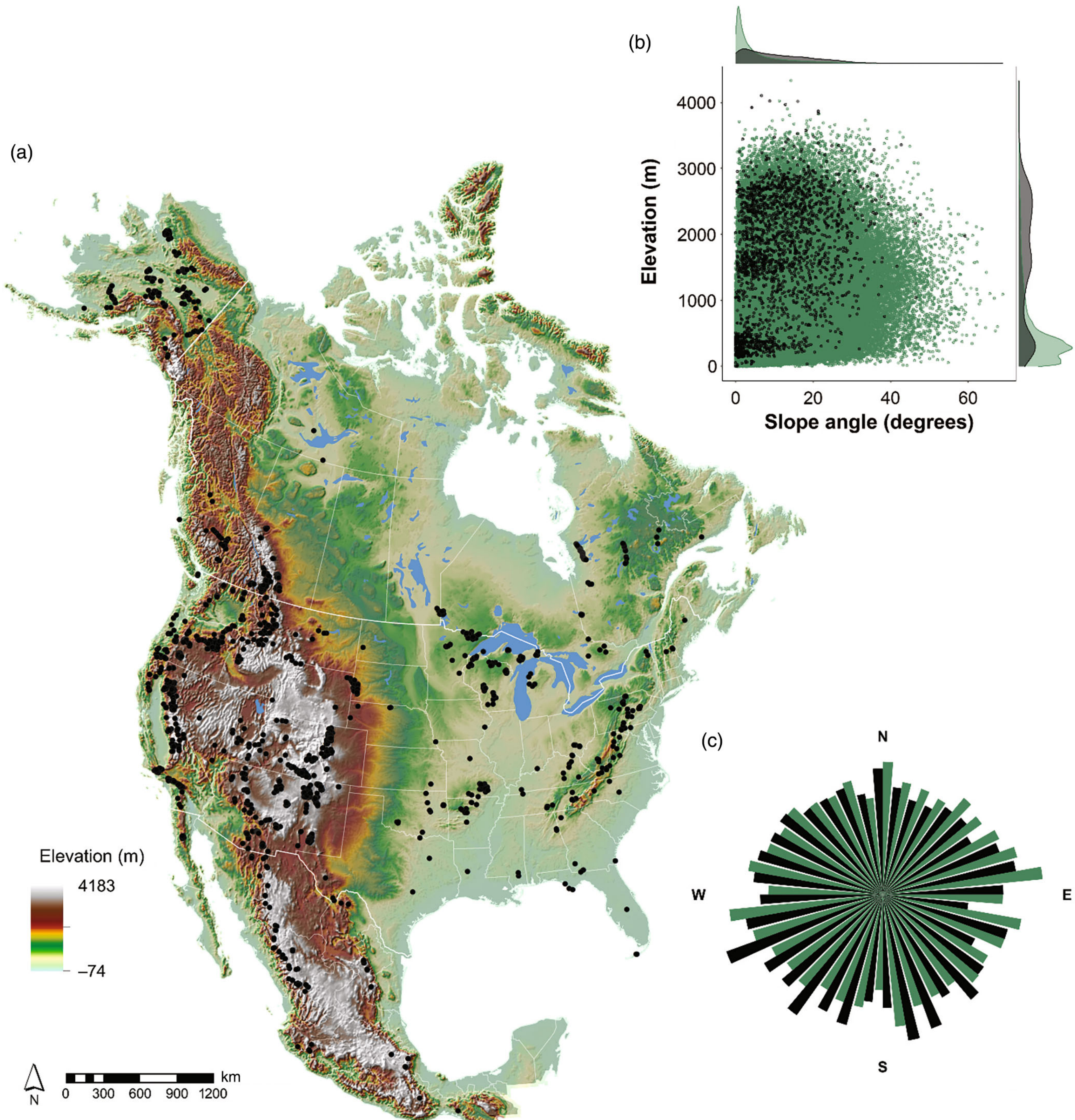

FIGURE 6 (a) Elevation and fire-scar sites (black points) in North America. (b) Slope angle versus elevation of random points (green) in North American forests and tree-ring fire-scar sites (black). (c) Slope aspect of random points in North American forests (green) and tree-ring fire-scar sites (black). 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

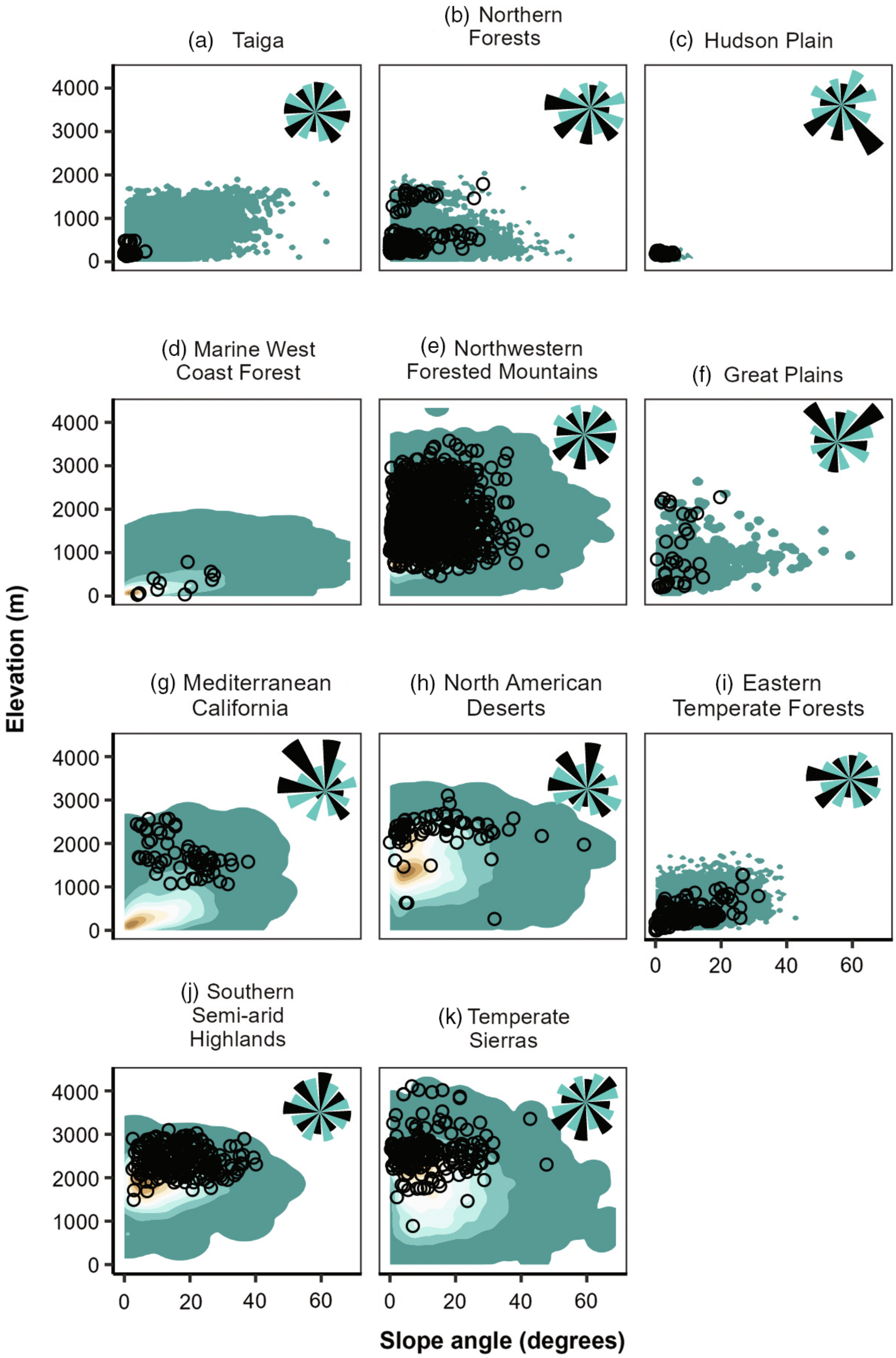

FIGURE 7 (a–k) Slope, elevation, and slope aspect (inset windroses) for random points in forests (colored) and tree-ring fire-scar sites (black) for North American ecoregions. For slope and elevation, the colored surface represents the possible topographic space derived from two-dimensional kernel density 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 ecoregional 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 > $\sim$18°C) and driest (MAP < $\sim$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 > $\sim$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

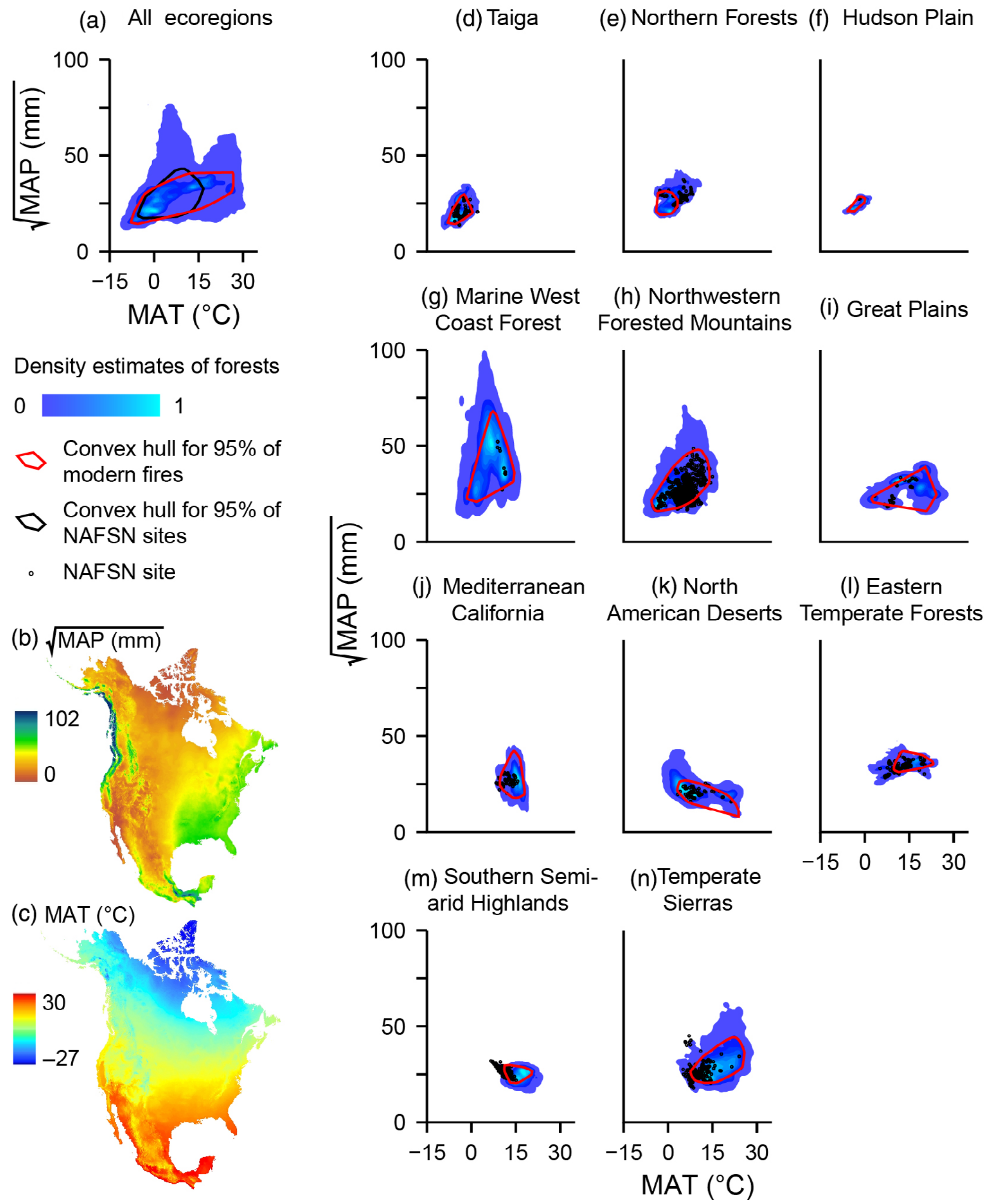

FIGURE 8 (a–n) Climate space of forests, the North American fire-scar network (NAFSN) sites, and modern fires in terms of mean annual precipitation (MAP; square root transformed) and mean annual temperature (MAT) by ecoregion. Forests: Density estimates of the forested climate space were derived using 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

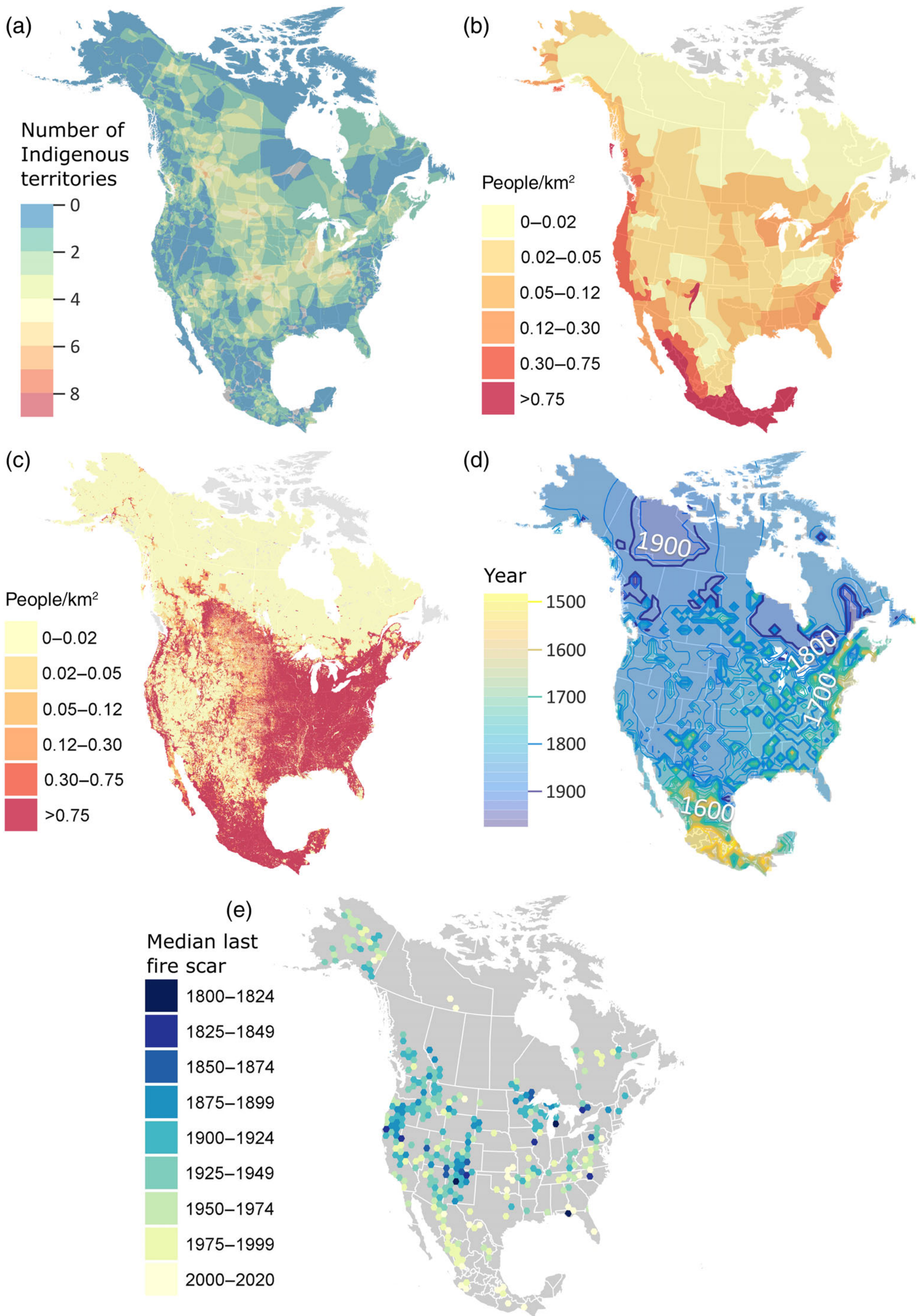

FIGURE 9 Maps of human factors linked to the North American tree-ring fire-scar network. (a) Territories of >600 North American Indigenous tribes (https://native-land.ca), (b) pre-European contact human population density estimates (Driver & Massey, 1957), (c) current (2020) human population density (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-km^2 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, oldwood 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.

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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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SUPPORTING INFORMATION

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

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