



Applying the usual rules to an unusual ecological situation: Fire rotation in Great Lakes Pine Forests

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ABSTRACT

Fire regimes in Eastern North America are often determined from historical data because land-use change and natural resource policy have confounded natural fire processes. It is good practice to combine multiple historical data sources, which can serve to both corroborate findings and fill knowledge gaps that might exist when trying to gain a full picture of historical ecological processes. In the Great Lakes Region (GLR) fire rotation, or the number of years it takes to burn an area equivalent to the area of interest, is an extensively used metric that has been calculated based on the Euro-American settlement era General Land Office Public Land Survey (GLO) records. However, fire rotation methods and GLO records are best suited for understanding high-severity fire, and low- to moderate-severity fires have received less attention in forested ecosystems in this region. We used dendrochronological (tree-ring) data to evaluate GLO data and fire rotation methods in relation to low-severity fires. Tree-ring and GLO data were well-aligned in some ways, with high concurrence of tree species, tree density, and common fire dates. However, GLO data did not identify fires for survey points closest to any of our sites ($n = 26$), though 71% of sites burned within one year and all sites burned within 8 years of surveys. Mean fire return intervals for our sites ranged from 2 to 9 years for all fires and 6–20 years for fires recorded on $\geq 25\%$ of samples within sites (1602–2018) with relatively minor effects of filtering on return intervals. Thus, fires were historically frequent and widespread within sites. We estimate that fires burned on average 858 km² to 2564 km² per year within five ecological landscapes with rotation intervals ranging between 11 (Northeast Sands) and 34 years (Northern Highlands; $\mu = 22$ years across all five landscapes). We found 25 regional fire years that were synchronous among multiple (2–5) ecological landscapes over a 218-yr period with evidence that drought plays a role in regionally widespread fire years. High-severity fire was likely limited in the GLR; however, low- to moderate-severity fires were abundant, large-scale, widespread, and an important forcing mechanism shaping forests of the GLR over millennia.

1. Introduction

In 1939, Aldo Leopold traveled to the southeast US as a consultant for the Soil Conservation Service to visit Herbert Stoddard, his friend and colleague who was studying declining bobwhite quail populations in the Red Hills region of South Georgia and north Florida. Stoddard was among the first to advocate for the importance of fire in longleaf pine management – directly challenging forestry dogma at the time that fire should be suppressed at all costs (Way, 2006). Upon returning from that trip Leopold wrote “the common assumption is that Stoddard sacrifices forestry and erosion control to game. It seems more likely that his opponents are sacrificing game, forest safety, and forest value to their desire to apply the usual rules to an unusual ecological set-up” (Leopold, 1939). In the subsequent 80 years Stoddard’s work has

become so engrained that fire and forestry are almost synonymous in the piney woods of the southeast, which now leads the country in its use of prescribed fire (Melvin, 2018).

Neither Stoddard’s understanding of fire as an ecological process nor Leopold’s early efforts to initiate landscape restoration have taken hold in the Great Lakes Region (GLR), where fire use is still in its infancy and fire dependent communities often in dire condition (Alstad et al., 2016; Melvin, 2018; Meunier et al., 2019a). Changes in land-use, climate, and invasive species have all affected fire dependent ecosystems; however, a lack of fire is a primary factor in their degradation and loss (Sauer, 1950; Axelrod, 1985; Alstad et al., 2016). While prescribed fire is used to maintain open ecosystems, particularly prairie and to a lesser extent savanna and barrens (Vogl, 1971; Melvin, 2018), direct knowledge of historical fire regimes and subsequent changes are more

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limited in northern forests despite the historic prevalence of fire-dependent pines and oaks (Fahey, 2014; Frelich et al., 2015).

Leopold's comment inherently requires an understanding of a usual and "unusual ecological set-up" in relation to fire ecology. Understanding a system's fire ecology typically entails reconstructing historical fire regime attributes such as fire frequency, severity, scale, predictability, seasonality and spatial patterns over extended periods and prior to fire exclusion (Heinselman, 1981; Pickett and White, 1985; Morgan et al., 2001; Daniels et al., 2017). Most commonly however, fire frequency (or its inverse, fire return interval) and severity are the attributes used to classify and map fire regimes (Heinselman, 1978; Hardy et al., 2001; Steel et al., 2015) and techniques for reconstructing fire history vary by these attributes due to the nature of evidence left behind (Agee, 2005). Frequency metrics, like mean fire return interval (MFRD), are most appropriate in frequent fire systems, whereas area-based estimates, like fire rotation intervals, are more common where higher severity fires with few surviving trees, and subsequent even-aged stands occur (Dickmann and Cleland, 2002; Kent, 2014).

It follows that all methods and associated metrics for reconstructing fire regimes have advantages and disadvantages. Dendrochronological (tree-ring based) reconstructions of fire return intervals are "point specific" evidence that a fire occurred exactly where fire scarred trees are located (Swetnam and Baisan, 1996) and usually have limited utility for reconstructing size or spatial complexity of fires (Daniels et al., 2017). Fire rotation, while area specific, can usually only reconstruct the last stand-replacing fire (older evidence is lost in subsequent fires), is temporally less precise as regeneration may not be immediate, and small-scale fires (< 1000 s ha) are more difficult to reconstruct (Kent, 2014; Daniels et al., 2017). Fire rotation, also called fire cycle (Van Wagner, 1978) or natural fire rotation (Heinselman, 1973), is the time required to burn an area equal to a defined area of the landscape (Romme, 1980). The entire area may not burn during this period; some sites may burn repeatedly and others not at all. Fire cycle is a problematic term (Reed, 2006), but is sometimes distinguished from fire rotation in that it is calculated based on the distribution of ages in a time-since-fire map (Johnson and Larson, 1991; Johnson and Gutsell, 1994; Morgan et al., 2001).

One of the most common data sources for determining fire regimes in the GLR has been Euro-settlement era General Land Office (GLO) survey notes (Cleland et al., 2004), which allows for broad scale mapping and interpretation. The original GLO Public Land Survey provides the earliest systematic record (1832–1866 in Wisconsin) of forest composition in the Lake States (Cleland et al., 2004). GLO surveyors noted tree species and their diameters along section lines in a grid of transects ca. one mile apart along with notes of recently burned areas, windthrows, and other features of interest (Stewart, 1935; Schulte and Mladenoff, 2005). Researchers have used these disturbance observations to calculate disturbance rotation intervals, typically by mapping disturbance patches from surveyor notes to determine disturbance area and dividing the area by a recognition window (time period disturbances would be observable to surveyors) to estimate disturbance area per annum (Maclean and Cleland, 2003). Most commonly, a 15-yr recognition window has been used for calculating fire rotation (Canham and Loucks, 1984; Whitney, 1986; Zhang et al., 1999; Cleland et al., 2004; Schulte and Mladenoff, 2005), although this is based on detection for high-severity fires only. A shorter recognition window would be necessary for low-severity maintenance fires and adjusting the recognition window can adjust fires rotation models to account for differences in fire severity (Almendinger, 2010), although this is rarely done and to our knowledge the effects of adjusting recognition window have not been systematically evaluated.

In addition to interpolating surveyor notes to delineate fire and wind disturbances directly, GLO data have been used to calculate disturbance probabilities via estimated stand-age and associated successional classes (Lorimer and White, 2003; LANDFIRE, 2013). GLO data have also been used to calculate tree density, which has been used for

determining disturbance severity (Schulte and Mladenoff, 2005) and to infer general descriptions of disturbance frequency (i.e., high frequency vs. low frequency; Radeloff et al., 1999; Williams and Baker, 2012; Baker, 2014; Shea et al., 2014). However, rotation intervals are the main quantitative measures of fire regimes derived from the GLO, which is congruent with even-age silviculture, the most common forest management practice in GLR conifers (Reed, 1984; Bergeron et al., 1999). Schulte and Mladenoff (2005) estimated fire rotation intervals for northern Wisconsin landscapes and found that rotation intervals ranged from 810-yr to 3029-yr for fire dependent red and white pine forests respectively, which, as they point out, is too infrequent to support either species.

Compared to the GLO records, there has been a lack of data from other sources spanning broad spatial scales, which has influenced how disturbance regimes are interpreted in the GLR (Meunier et al., 2019a). GLO data are inherently biased toward high-severity disturbance, which leaves more evidence, and for much longer, than low-severity disturbance; thus, surveyors could more readily observe intermediate and high-severity disturbances (Schulte and Mladenoff, 2005). Because of this reliance on GLO data for seeking to understand broad patterns, there is a tendency to view fire as of minor or secondary importance to wind disturbance and when considering fire disturbances, to focus on intermediate to high-severity events, and fire rotation (e.g., Van Wagner, 1978; Canham and Loucks, 1984; Frelich and Lorimer, 1991; Cleland et al., 2004; Schulte and Mladenoff, 2005; Rhemtulla et al., 2009), resulting in an incomplete understanding of disturbance regimes in the GLR (Schulte and Mladenoff, 2005; Meunier et al., 2019a).

Interpretation of GLO data rely on a number of assumptions that have not been adequately evaluated relative to historical data on low-severity disturbance, including their suitability for reconstructing basic components of rotation intervals such as fire areas, severity, and recognition window, as well as ability in describing landscape patterns used to derive fire regimes generally. Interpolations of modern data collected following the same approach as the GLO in Michigan, for example, were able to map relative forest composition and dominant vegetation types but were unable to estimate areas occupied by each type or recreate landscape patterns at small (< 10⁴ ha) scales (Manies and Mladenoff, 2000). Stevens et al. (2016), using Forest Inventory Analysis data, could not infer the rotation of high-severity patches across a landscape even with systematic sampling of even-aged stands. They concluded that such methods cannot quantify historical high-severity fire effects in mixed-severity fire regimes within unmanaged forests (Stevens et al., 2016). In West Virginia, comparisons among mapping methods using GLO data found errors over broad areas were common and little agreement among mapping techniques even when mapping fire regimes generally by fire regime groups (FRG, Thomas-Van Gundy, 2014). Notably, the lowest levels of agreement among GLO disturbance mapping techniques were for the more frequent fire regimes (FRG I and III, Thomas-Van Gundy, 2014).

Dendrochronological reconstructions of fire and stand history in the GLR have recently provided quantitative measures confirming that low-severity fire events were common and likely more important than once realized (Guyette et al., 2016; Johnson and Kipfmüller, 2016; Meunier et al., 2019a, Meunier et al., 2019b). When using historical data to infer knowledge about fundamental ecological processes, including fire regimes, it is prudent to use multiple historical data sources (Swetnam et al., 1999; Schulte and Mladenoff, 2001) which can be used to test assumptions and biases, provide confirmatory evidence, and fill temporal or contextual gaps (Swetnam et al., 1999). GLO data have been contextualized and sometimes tested against other historical data sources, including dendrochronological data, stand-origin maps, and varved lake sediment cores, although this has primarily focused on high-severity disturbance (Whitney, 1986; Zhang et al., 1999, Almendinger, 2010).

The overlying objective of this study was to use combined dendrochronological and GLO data to evaluate fire rotation methods for

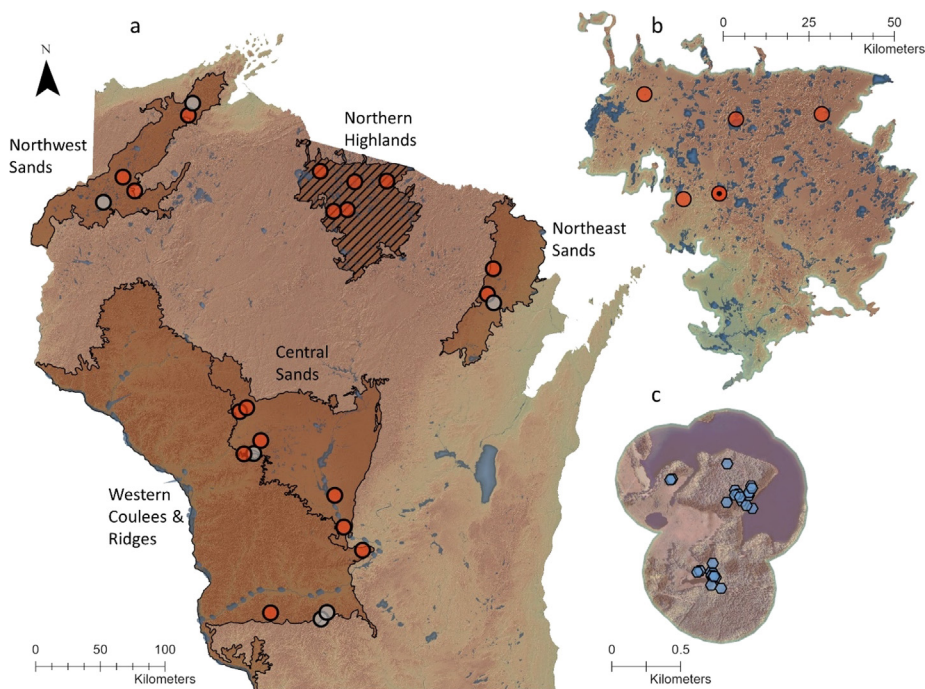


Fig. 1. Study area spanning much of Wisconsin, USA and (a) regional scale (100s km²), (b) example of study sites within the Northern Highlands Ecological Landscape scale (10s km²), and (c) samples within a single site (scale 1s km²). Red circles in regional scale map are sites with crossdated fire history; blue circles are sites with only partially dated or without crossdated tree-ring fire history, but with tree-ring and General Land Office survey density data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

describing fire regimes within fire dependent landscapes of the GLR. We made comparisons of (1) disturbance events directly (as noted by surveyor notes and tree-ring records), (2) fires detected within 15-yr recognition windows used to calculate rotation intervals, and (3) estimates of tree density which are used to determine disturbances and/or disturbance severity. Additionally, (4) we evaluated scale of low-severity fires and potential ramifications for estimates of fire rotation intervals. Our goal was not to compare exact metrics used to calculate rotation intervals between disparate data sources (dendrochronological and GLO), but rather to try and understand the utility and limitations of tree-ring and GLO data sources, of fire rotation generally, as well as the potential to use multi-proxy data to better describe fire processes across landscapes.

2. Methods

2.1. Study area

Our study spanned five ecological landscapes throughout Wisconsin, USA, (Fig. 1; Cleland et al., 1997; WI DNR, 2015). Ecological landscapes are broad ecoregions with diverse biophysical settings defined, in part, by successive glaciation events. Within these landscapes we collected dendrochronology-based stand structure and fire history data from red pine (*Pinus resinosa*) dominated stands that spanned relatively productive dry-mesic sites (e.g. Northern Highlands, NH) to deep, well-drained, glacial lakebed (Central Sands, CS), dry outwash sands (Northwest, NW, and Northeast, NE) and pine relicts on sandstone outcrops (Western Coulees and Ridges, WCR, Fig. 1). We also used Euro-American settlement era General Land Office (GLO) Public Land Survey record data within and/or adjacent to these same sites (Sickley et al., 2001). The GLO Public Land Survey documented historic land cover and collected data on location, species, and diameter of trees used to mark section lines and corners, as well as detailed notes of disturbances and other features such as lakes, wetlands, trails, and settlements (Schulte and Mladenoff, 2001). Ecological landscapes are geographically extensive units (e.g., 3995–24,972 km²) commonly used for analyses of GLO data (e.g., Manies et al., 2001; Schulte and Mladenoff, 2005; Rhemtulla et al., 2009).

2.2. Dendrochronological data collection and analysis

We established plots within red pine-dominated stands that were either single 0.5 ha plots ($n = 8$) in more extensive stands, or 200 m² circular plots (0.02 ha, $n = 46$) from multiple smaller stands comprising a single site ($n = 18$; 26 sites total). Stands were either relatively intact (e.g., unlogged) old growth or had been harvested in the cutover period (ca. 1860–1910) but had no subsequent logging disturbance and contained well preserved historical evidence (pre-Euro-settlement era stumps). Our goal for all plots was to characterize fire history and stand density ca. 1860 prior to intensive land-use impacts. Because we could not know a priori which trees were alive in 1860, we collected data from all trees in plots that were potentially pre-1860 trees (≥ 40 cm DBH or exhibited old-age characteristics) and collected sections from all remnant stumps, and partial sections from snags, and fire scarred living trees at 10 cm height within plots. We considered the pith date at cut height (10 cm) to be the year of tree establishment (Brown et al., 2008). We also collected fire-scar samples opportunistically by searching the vicinity of plots (within ca. 200 m) for additional samples to extend fire chronologies (Farris et al., 2012).

In the laboratory, we sanded samples until the cellular structure of xylem was clearly visible with magnification (Grissino-Mayer and Swetnam, 2000) and used dendrochronological methods to crossdate samples (Grissino-Mayer and Swetnam, 2000; Speer, 2010) and assign exact calendar years for tree recruitment and all fire scars. We assigned seasonal positions to fire scars based on locations within ring series (Grissino-Mayer, 2001) and assigned ring-boundary scars (dormant season position) to the year containing the earlywood immediately following fire scars. We compiled fire-scar dates into composite chronologies for each plot and analyzed them using Fire History Analysis and Exploration System software version 2.0. (FHAES, Brewer et al., 2019).

We evaluated the ability of 0.02 ha subplots embedded within 0.5 ha plots to accurately describe tree density and pooled 0.02 ha plots by site when describing stand density. Plot size is important in determining forest structure; many forest descriptors stabilize with 0.5 ha sample areas (Busing and White, 1993; Zenner and Peck, 2009; Fraver and Palik, 2012), but circular large-tree subplots in cluster plot designs average 0.06 ha (Paul et al., 2018). We compared GLO and tree-ring

based estimates of tree density at site and ecological landscape scales with ANOVA (SigmaPlot Systat Software, 2010).

We analyzed fire recurrence at site, ecological landscape, and regional (statewide) scales (Fig. 1). Sites were usually comprised of either single large or multiple smaller adjacent stands with areas ranging in size (2–48 ha). We carried out statistical analyses with three filters: (1) all fire years, with at least two samples; (2) fire years in which $\geq 10\%$ of samples were scarred; and (3) fire years in which $\geq 25\%$ of sample trees were scarred, representing sequentially more extensive fire years (Swetnam and Baisan, 1996; Tarancón et al., 2018). Fires are a contagious disturbance (Falk et al., 2007) and fire regimes are temporally and spatially autocorrelated - the probability of a fire regime at one point is dependent, in part, on fire regimes on adjacent points (Morgan et al., 2001). Filtering eliminates fire dates that appear on one or few samples and provides evidence of more spatially representative, widespread fire events. Filtered fire scar data at a site scale has been shown to provide complete inventories for fire years > 100 ha, whereas only 3.8% of fire years < 100 ha were detected (Fulé et al., 2003; Van Horne and Fulé, 2006; Farris et al., 2010).

In order to estimate landscape and regional spatial scales of fires, we analyzed synchrony of fire events within and among sites and ecological landscapes. Fires are spatially heterogeneous, and while fire-scars cannot capture the spatial complexity or continuity of burning, fire-scar synchrony, or the proportion of sample units (i.e., study sites) that record a fire in a given year, has been used as a relative index of total area burned (e.g., Morrison and Swanson, 1990; Swetnam, 1993; Taylor and Skinner, 1998). Spatially distributed fire-scar data tend to record fires in relative proportion to the area burned and synchronous scarring at more than two sites results exclusively from widespread fires burning between sites (Farris et al., 2010) and is a useful way to understand regional and even continental scale fire events (Morgan et al., 2001).

We also used a non-spatial ratio method to estimate areas burned for calculating fire rotation based on percentage of sites in which a particular fire year was recorded on sample trees within ecological landscapes (Baker, 2017; Taylor and Skinner, 2003; Guyette et al., 2006).

The fire rotation interval is calculated by the equation (Baker, 2009; 2017):

$$FR = (\text{Observation Period} / \text{Fraction Burned})$$

where FR is fire rotation, in years, *Observation Period* is the timespan in years for which there are reconstructed records of fire, and *Fraction Burned* is the fraction of the ecological landscape (Cleland et al., 1997; WI DNR, 2015) estimated to have burned during the observation period, obtained by summing the estimated fraction burned from ratio estimates or % of sites recording particular widespread fire years synchronously (Guyette et al., 2006; Baker, 2017). To estimate proportion of sites burned we first filtered for fires occurring on $\geq 25\%$ of samples within sites, which we composited into site chronologies and filtered again for fire years occurring among multiple sites, which represent the most widespread fires within ecological landscapes. *Observation Period* was the truncated time period when all sites within a landscape were recording fires. Both sites within a landscape and scarred trees within sites tend to be clustered (Baker and Dugan, 2013), which could result in ratio estimates that are biased and too short, and potentially underestimated unburned areas (Baker, 2017). However, in a large modern corroboration study, fire rotation intervals derived from fire-scars with non-spatial ratio methods were within 10% of rotation intervals derived from fire-atlas data, and large fires, which accounted for 97% of area burned, were accurately estimated (Farris et al., 2010; Dugan and Baker, 2014; Baker, 2017). Yet, to help address this concern we determined the proportion of ecological landscapes that were pine at the time of Euro-American settlement (pine representing > 25% of GLO section corner witness trees) and report areas burned/yr (based on rotation estimates) for both ecological landscapes, and reduced areas representing the portion of landscapes that were pine.

We evaluated synchronous fire years among ecological landscapes

to understand regionally significant fire years (100s km²). We also calculated the rate of fire scarring by year (1650–2000) for every site, then averaged scarring rates by ecological landscape, and across all landscapes. We used superposed epoch analysis (SEA) to understand climate drivers (average Palmer Drought Severity Index, PDSI, for WI, Cook et al., 2007) for fire years based on rate of scarring, this included: all fire years, fire years with > 10% and 25% scarring across all landscapes.

2.3. General Land Office data collection and analysis

In this study we use data from GLO Public Land Survey surveyor notes on fire occurrence, witness tree species, and vegetation types in Wisconsin (Sickley et al., 2001; Mladenoff, 2009). The survey, which was designed to form the basis of property boundaries and land records during the Euro-American settlement era, split the land into contiguous 1.6 km × 1.6 km (1 mi × 1 mi) grid; each grid cell is called a section (Stewart, 1935). Surveyors placed posts at section corners and halfway between section corners (i.e. quarter-corners) to mark the section boundaries. To aid in re-identifying corner posts, surveyors took notes on the species, diameter, and location relative to the corner of two to four “witness trees” (Stewart, 1935). While traversing section lines, surveyors also kept note of dominant overstory and understory species and observations of fire or wind disturbance (Schulte and Mladenoff, 2001). Disturbances were noted in two ways: surveyors noted occasions when they entered and exited large disturbed areas on section lines, and they also noted general observations of disturbances at corners (using words such as “burnt,” “burned,” and “fire” for fire disturbance; Schulte and Mladenoff, 2005).

For each tree-ring fire history site we determined (1) the closest GLO corner or quarter-corner point, extracting data on the date of the survey, the species of witness trees, and surveyor notes on overstory and understory species; (2) the nearest GLO survey point for which fires were noted, either as a fire disturbance area entry or exit point or where fires were mentioned in the surveyor’s notes and extracted data on date of the survey; and (3) the nearest GLO site with red pine as a witness tree. We used the “Generate Near Table” tool in ArcMap 10.3 (ESRI, 2014) to identify distances between tree-ring plots and GLO records. We also calculated the tree density (number trees/ha) in a 1.6 km (1 mile) radius from tree-ring plot locations using the Cottam and Curtis (1956) method with a correction factor applied if the number of trees at a GLO corner was less than four (Cottam and Curtis, 1956; Bolliger et al., 2004).

We used GLO records to calculate the area in each ecological landscape associated with pine ecosystems. To do this, we calculated for each section the proportion of associated section corner and quarter-corner witness trees that are pine trees [identified by surveyors as red pine (*P. resinosa*), white pine (*P. strobus*), jack pine (*P. banksiana*), or simply pine]. We selected each section that had $\geq 25\%$ pine. For each ecological landscape we calculated the area of all selected “pine” section. These analyses were conducted in R (R Core Team, 2019).

We evaluated the similarities and differences of GLO fire records and dendrochronological data by (1) examining distance from fire history site to nearest GLO fire record, (2) evaluating the congruence between dendrochronological fire dates and GLO fire dates, and (3) using the survey date at the GLO point nearest the fire history site to determine number of fire years occurring within the standard 15-yr recognition window. We also evaluated how well data from dendrochronological sites match non-fire data from the GLO records, including data on species composition and tree density. Finally, we compared dendrochronologically derived fire rotation intervals to those reported in Schulte and Mladenoff (2005).

3. Results

We dated 459 fire-scar samples among 20 sites (six sites did not

Table 1

Study sites with fire history information (n = 20) from the year of first fire event to 2018 organized by ecological landscape and latitude (north to south).

Site	EL	No. stands	No. plots	No. samples	No. yrs w fires	MFRI All	MFRI 10%	MFRI 25%	Years
Inch Lake	NWS	1	1*	34	53	5	16	19.5	1668–2018
Totagatic River	NWS	1	1*	27	65	4	6	9	1710–2018
Lampson Pines*	NWS	3	3	14	47	4	6	7	1747–2018
Frog Lake	NH	1	1*	14	24	5	8	8	1833–2018
Buckatabon	NH	3	3	15	27	8	8	13	1697–2018
Cathedral Point	NH	1	1*	24	24	7	31	8	1791–2018
Finnerud Pines	NH	1	3	39	32	8	11	13	1699–2018
Squirrel River*	NH	3	3	12	21	8	8	17	1744–2018
Wolf Lane	NES	1	1*	16	23	5	7	8	1818–2018
Camp Bird	NES	1	1*	17	34	5	6	9	1762–2018
Tar Dam Road*	NES	1	3	12	31	8	8	15	1718–2018
Levis Mound	CS	3	3	18	101	2	3	9	1608–2018
Bruce Mound	CS	1	1*	59	39	7	10	15	1681–2018
Wildcat	CS	1	1*	49	30	4	7	9	1712–2018
Stony Bluff	CS	2	1	20	39	5	10	9	1704–2018
Quincy Bluff	CS	2	2	23	86	4	5	8	1642–2018
WI Dells	CS	3	3	28	87	3	4	7	1681–2018
Fort McCoy	CS	2	2	3	22	9	6	6	1786–2018
Pine Bluff	WCR	1	3	17	64	4	5	6	1684–2018
Snow Bottom*	WCR	2	2	18	46	6	6	7	1661–2018

Sites with partially dated samples, No. plots – 0.5 ha plots, all others comprised of 0.02 ha plots, MFRI is mean fire return interval (years) for ≥ 2 recording trees, – too few samples to estimate MFRI statistic, EL – ecological landscape (NWS-Northwest Sands, NH-Northern Highlands, NES-Northeast Sands, CS-Central Sands, WCR-Western Coulees & Ridges).

Table 2

Comparisons between General Land Office survey and tree-ring reconstructed fires for study sites among five ecological landscapes of Wisconsin.

Site	Dist (km)	Window	Fires (n)	Fire Yrs [< 2 trees]	Near Disturb (km)	Near Disturb	Tree ring
<i>Northwest Sands</i>							
IL	0.02	1841–56	5	1841, 1847, 1853 [1845, 1856]	6.89	1858	1856
TR	0.11	1840–55	7	1840, 1855 [1845, 1846, 1847, 1848, 1854]	23.27	1848	1848
LP*	0.16	1841–56	5	1841, 1851, 1855 [1845, 1846]	12.49	1848	1846
SL	0.37	1840–55	–	–	11.55	1856	–
WM	0.15	1837–52	–	–	7	1858	–
<i>Northern Highlands</i>							
FL	0.26	1850–65	2	[1855, 1864]	0.73	1860	1855
BN	0.12	1846–61	2	[1854, 1861]	11.93	1863	1861
CAP	0.65	1845–60	4	1846 [1851, 1856, 1860]	14.37	1860	1860
FP	0.48	1848–63	3	1850 [1855, 1856]	3.5	1860	1856
SQR*	0.29	1848–63	1	1855	3.02	1860	1855
<i>Northeast Sands</i>							
WL	0.15	1841–56	3	1850, 1855 [1843]	4.22	1856	1855
CB	0.49	1841–56	2	1852 [1844]	0.49	1856	1852
TDR*	0.02	1838–53	3	1840 [1839, 1851]	2.91	1853	1851
WBR	0.06	1824–39	–	–	4.94	1853	–
TL	0.05	1841–56	–	–	0.62	1856	–
<i>Central Sands</i>							
BM	0.27	1832–47	2	1833, 1847	4.24	1848	1847
WR	0.14	1838–53	3	1841 [1851, 1853]	3.36	1853	1853
STB	0.16	1831–46	3	1833 [1840, 1845]	7.31	1847/53	1847/52
QB	0.10	1836–51	5	1842 [1840, 1843, 1847, 1848]	7.72	1851	1848
WD	0.18	1830–45	8	1833, 1836, 1838, 1842, 1845 [1832, 1835, 1843]	21.78	1851	1850
FM*	0.36	1831–46	4	n/a, [1832, 1833, 1841, 1844]	1.56	1853	1848
LM	0.35	1833–48	–	–	2.39	1848	–
<i>Western Coulees & Ridges</i>							
PB	0.18	1830–45	7	1831, 1833, 1835, 1838, 1839, 1841 [1844]	7.08	1845	1844
SB*	0.30	1818–33	2	[1831, 1833]	25.95	1833	1833
RP	0.22	1817–32	–	–	44.82	1833	–
TC	0.04	1818–32	–	–	53.16	1833	–

*Sites with partially dated samples, – sites without overlapping tree-ring based fire history information. Data are organized by ecological landscape and latitude and includes distance from nearest General Land Office survey location (Dist), 15-yr fire recognition window (outer date is year of survey), number of fires reconstructed from tree-ring methods during the 15-yr period for recorded on multiple samples (fires recorded on single samples are in brackets, bolded years are years closest to survey year). Additional information on distance to, and date of, the nearest noted fires by surveyors with associated tree-ring reconstructed fire dates are also included.

have dated samples), 19 with overlapping GLO survey fire history records. Our samples contained 2514 fire scars with 295 unique fire years from 1602 to 2018. Fires historically were frequent across all sites and landscapes with MFRI's ranging from 2 to 9 years for all fires and 6–20 years for fires recorded on ≥25% of samples within sites

(Table 1). Fire disturbances were not noted in GLO survey records closest in proximity to any of our sites (0.02–0.65 km, μ = 0.22 km); however, most sites (71%) had burned within one year prior to surveys, and every site had at least one fire within 8 years prior to surveys (Table 2). The nearest fire disturbances that were recorded in survey

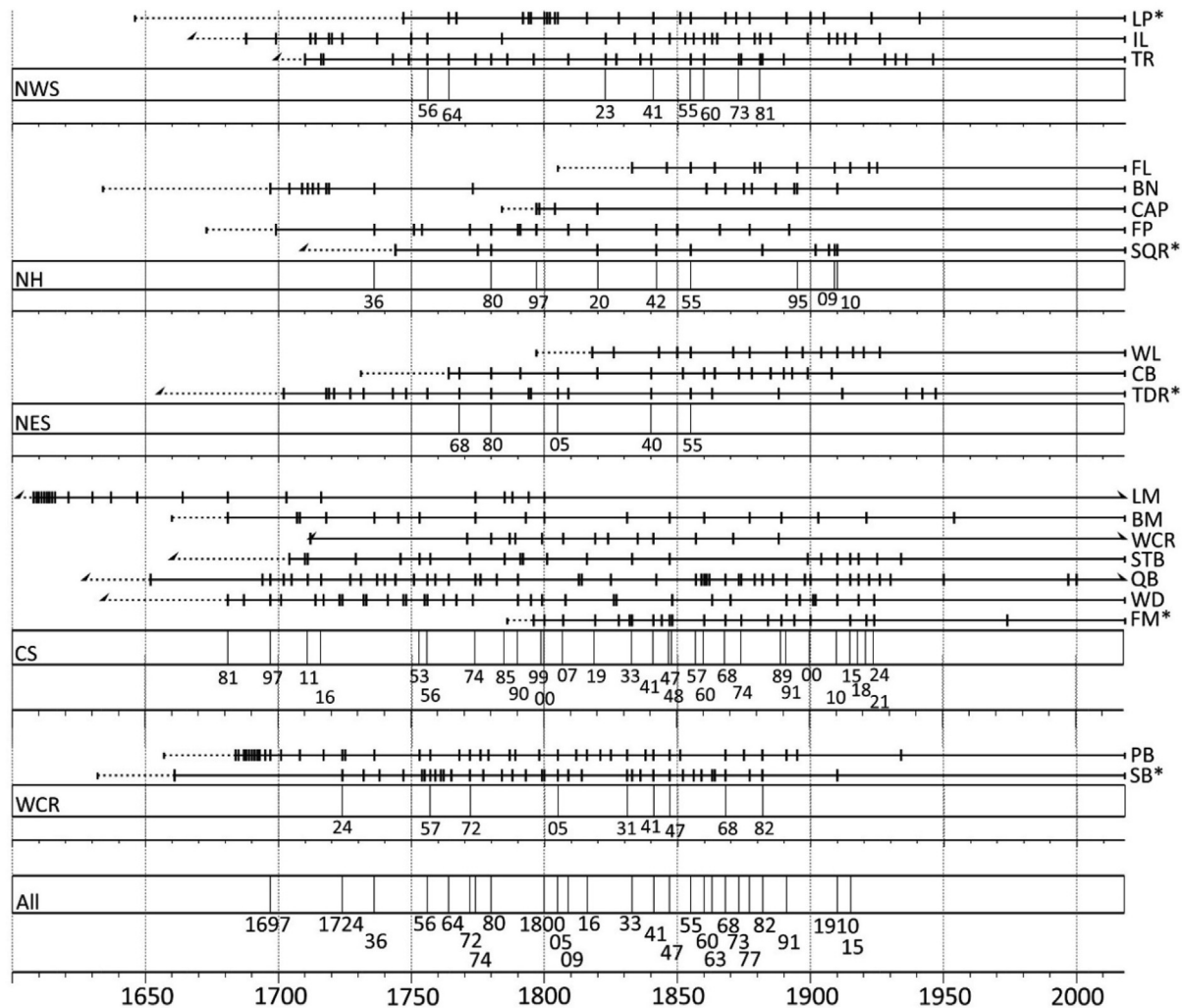


Fig. 2. Fire history across 20 sites in Wisconsin. Site codes with asterisks are partially dated sites. Horizontal lines represent composited fire histories for each site with fires (vertical ticks) filtered for fires found on $\geq 25\%$ of recorder trees scarred (≥ 2 recorder trees) illustrating widespread fire years within sites. Composited fires dates below each landscape are for fires recorded on multiple sites within an ecological landscape and were used for calculation of fire rotation intervals. Composited fires dates at bottom (All) are for fire years found within multiple ecological landscapes based on site data (fires $\geq 25\%$ of recorder trees) and represent regionally important, widespread fire events across ecological landscapes. All but one fire year (1774) were found in three or more ecological landscapes.

records ranged from 0.49 km (Camp Bird in NE Sands) to more than 53 km (Trout Creek in the Western Coulee and Ridges, WCR) from our sites (Table 2). Distances between plots and surveyor records of nearest fires were similar among ecological landscapes ($\bar{x} = 12.25$ km) except for longer distances in WCR ($\bar{x} = 32.75$ km, $P = 0.026$). WCR was also the only landscape where pine was not recorded as either a witness or overstory tree for surveyor records closest to our sites. Notably, only 6% of the WCR landscape was pine, whereas the other landscapes ranged from 56% (Northern Highlands) to 93% (Northwest Sands) pine.

While fires were not recorded in surveyor records for survey points closest to our sites, we almost always shared common fire years for nearest GLO survey points where fires were noted (Table 2). There was only one fire year (1858) recorded by surveyors for which we did not have a tree-ring based record. In the 30 years of surveys (1833–1863), surveyors noted 10 unique fire years among the landscapes for fires nearest our sites, four of which (1833, 1847, 1860, and 1863) appear to have been regionally significant fire years according to tree-ring records (Table 2, Fig. 2). In the same 30-year time period, we have tree-ring records of fires burning in every year except two.

We evaluated the ability of 8 m radius subplots embedded within four quadrats comprising our 0.05 ha plots ($n = 8$) to estimate tree density with dendrochronological methods. We found no significant

differences among density estimates based on plot size (0.02 ha subplots, 0.125 ha quadrats, 0.5 ha plots) indicating that tree density could be adequately described with 8 m radius (0.02 ha) plots. We also averaged tree density at the site level, which contained two to three 8 m radius plots for all but two sites (Trout Creek in WCR, and Stoney Bluff in CS) further mitigating potential effects of small plot sizes. While GLO surveys spanned the time period between 1832 (south) and 1866 (north), we reconstructed all tree-ring based estimates of density to ca. 1860 (at ca. 10 cm height without pith correction factor) so comparisons are approximate. In general, density estimates between dendrochronology and GLO survey methods were remarkably similar (Fig. 3) with no significant differences at the ecological landscape scale ($F = 2.069$, $P = 0.083$). We did find differences among sites and tree-ring based densities were higher overall ($P < 0.001$) and with high variance. Historically southern Wisconsin (i.e., WCR), for example, was predominately oak savanna (Curtis, 1959) thus tree-ring based site selection would be biased toward denser forest relative to the surrounding landscape here (Fig. 3). Sites in the WCR landscape were also further from red pine stands noted by surveys ($\mu = 25$ km, versus 0.2–1.3 km). Even among WCR sites, Trout Creek was an outlier consisting of only one plot within a single small pine relict, but with the highest historical tree density of any of our plots as well as some of the

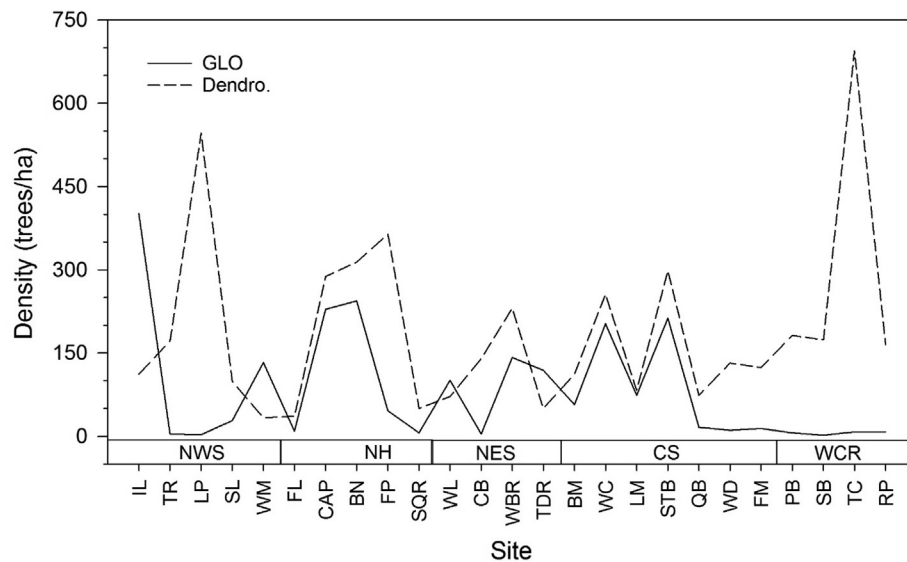


Fig. 3. Comparison of historical tree density estimates between dendrochronology and General Land Office (GLO) methods. X-axis contains site abbreviations ($n = 25$) organized by ecological landscapes (Northwest Sands – NWS, Northern Highlands – NH, Northeast Sands – NES, Central Sands – CS, and Western Coulees & Ridges – WCR).

oldest living trees (> 261 years) for any of our sites.

Our data suggests that widespread fire years were common (Fig. 2). At the site scale, we found relatively minor effects of filtering on mean fire return intervals with difference between all fires and those recorded on $\geq 10\%$, or $\geq 25\%$ of samples were 6, 9, and 10 respectively (average across sites, Table 1). We analyzed fire history information from a variety of sites with different fire exclusion dates, innermost dates, and quality of samples (e.g., deterioration with gaps in the wood where evidence of fire was missing), so determining an analysis period for which to calculate MFRI was challenging and the effects of filtering sometimes variable (Table 1). In some instances, a higher level of filtering, for example, resulted in shorter MFRI (Table 1) due to a minimum recorder trees needed for analysis, which could have changed the period of analysis eliminating long tails, or periods without fires.

We evaluated landscape-scale fires by finding widespread fire years within ecological landscapes. These were synchronous fires among sites within a landscape first filtered for fires on 25% or more of recorder trees at the site scale (Fig. 2). We calculated fire rotation intervals using truncated chronologies for each ecological landscape when all sites within a landscape were recording fires (full representation of sites between first and last widespread fire years). Rotation intervals ranged from 11 (Northeast Sands) to 34 years (Northern Highlands) and averaged 22 years across all five landscapes (Table 3). The Northern Highlands ecological landscape likely had the least area burned per annum (ca. 88–159 km²) and the Western Coulees & Ridges the most (ca. 1,419 km²) when not restricting area to pine. We estimate that anywhere from 858 km² (212,115 acres, pine only) to approximately 2564 km² (0.63 million acres) burned on average per year across all five ecological landscapes over a 15–213-year time period

($\bar{x} = 116$ years, Table 3).

We also found evidence for regionally significant fire years which we defined as the most widespread fires years at the site scale (filtered for fires recorded on $\geq 25\%$ of samples) that were synchronous among multiple ecological landscapes (Fig. 2). This composite resulted in 25 regional fire years over a 218-yr period (Fig. 2). Two of these widespread fire years (1877, 1910) were found among all five ecological landscapes and nine (1780, 1809, 1816, 1860, 1863, 1868, 1873, 1882, 1891) were found among four different landscapes. All but one regional fire year, 1774, was found in at least three landscapes. Between 1697 and 1915 the MFRI was nine years for regionally significant fire years alone. We also see an increasing role of climate effects on more widespread fires (Fig. 4). We found no significant relationship between fire occurrence and Palmer Drought Severity Index (PDSI, Cook et al., 2007) prior to, or following, fire events, nor did we see a relationship between fire and PDSI when considering all fire years. However, fire years were significantly related to dry conditions when considering fires with $\geq 10\%$ rate of scarring and related to moderate drought with $\geq 25\%$ rate of scarring (Fig. 4).

4. Discussion

In this era of global change, historic conditions have an increasingly important role in informing the future by understanding the past (Swetnam et al., 1999; Safford et al., 2012), but effective intervention depends on our understanding forest dynamics and the processes involved (Stephens et al., 2010; Levine et al., 2017). In the eastern US, fire’s role in science, management, and society generally is not yet well founded (Pyne, 2007) and often poorly understood (Stambaugh et al.,

Table 3

Fire rotation interval estimates by ecological landscape for periods of overlapping tree-ring fire history data within a landscape. Large fire years used to calculate rotation were derived from fire years first filtered for fires occurring on $\geq 25\%$ of samples by site, then filtered for fires that were synchronous across multiple sites within an ecological landscape.

Ecological Landscape	Area (km ²)	*Area Pine (km ²)	No. Sites (stands)	Time Period	No. Yrs	All Fire Yrs (n)	Large Fire Yrs (n)	EL Area Burned/yr (km ²)	Pine Area Burned/yr (km ²)	Rotation Interval (yrs)
NWS	5066	4715	3 (5)	1756–1881	125	74	8	217	202	23.3
NH	5390	2989	5 (9)	1842–1910	68	43	5	159	88	34
NES	3995	2489	3 (3)	1840–1855	15	6	2	357	222	11.2
CS	8858	5504	6* (14)	1711–1924	213	121	27	412	256	21.5
WCR	24,972	1582	2 (3)	1724–1882	158	75	9	1419	90	17.6

*Area pine was calculated as proportion of the landscape where $\geq 25\%$ of GLO witness trees were pine.

*Levis Mound (1602–1800) and Fort McCoy (1786–2018) in the Central Sands were treated as one site (Six rather than seven sites total) due to the distinct, non-overlapping time periods covered.

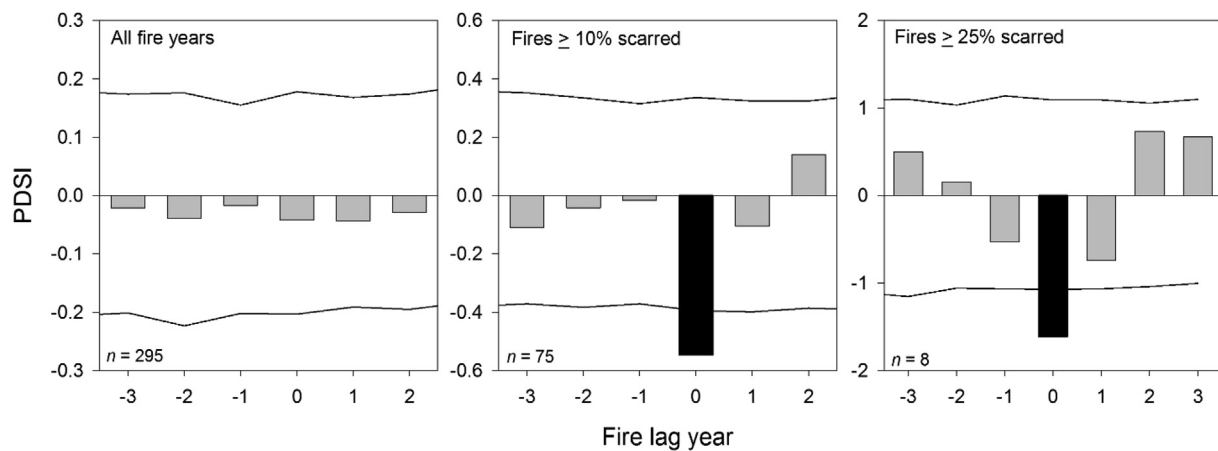


Fig. 4. Results of superposed epoch analysis (SEA) of the average Palmer Drought Severity Index (PDSI) across Wisconsin (Cook et al., 2007) for years prior and subsequent to fire event years (year 0) for all fires and those with $\geq 10\%$, and $\geq 25\%$ average rate of scarring across all ecological landscapes. Positive PDSI values indicate wet conditions, negative values represent dry conditions; note changing scale of y-axes. Solid bars indicate PDSI values outside of a 99% confidence interval (95% CI depicted by lines). All CI's are based on 1000 Monte Carlo simulations of random distributions of annual PDSI (1650–2000).

2016). The southeastern US is somewhat of an anomaly, attributable in part to Stoddard's work, where an understanding of the role of fire in shaping forests was a starting place for informing silviculture systems (Way, 2006). In the GLR, understanding forest disturbance processes has so far largely been an afterthought and, when tied to silviculture, primarily through the lens of succession and simple seral stages (Franklin and Johnson, 2012; Meunier et al., 2019a). Fire rotation, one of the most common fire regime metrics in the GLR (Heinselman, 1973; Van Wagner, 1978; Whitney, 1987; Schulte and Mladenoff, 2005), illustrates this well. Fire rotation is dependent on close coupling of mortality and recruitment (Flannigan and Bergeron, 1998; Miller and Safford, 2017), the same high-severity disturbances discernable with GLO data – in turn the most common data source used to characterize broad scale fire regimes in the GLR (e.g., Stearns, 1949; Van Wagner, 1978, Bormann and Likens, 1979; Lorimer, 1980; Grimm, 1984; Whitney, 1986; Zhang et al., 1999; Manies and Mladenoff, 2000; Lorimer and White, 2003; Cleland et al., 2004; Schulte and Mladenoff, 2005; Schulte et al., 2005, 2007). However, recent research has begun to highlight that tree mortality and establishment in red pine dominated forests in the GLR was not punctuated or episodic but rather continual in the presence of frequent, low-intensity surface fires (Fraver and Palik, 2012; Meunier et al., 2019a).

Our data, collected within 34 forested stands comprising 20 sites among 5 ecological landscapes, indicates that fires (predominately low- to moderate-severity) were more numerous and widespread than previously recognized. The scale of historical fires in Great Lakes conifer forests is thought to have averaged 4000 ha (40 km²) with a maximum of 160,000 ha (1600 km², Heinselman, 1973; LANDFIRE, 2018). Frelich (2002) estimated that the top 3% of fires burned 97% of the landscape and were 40 times the area of the average fire estimates based on fire rotation. Heinselman (1973) also determined that major fire years (> 260 km²) accounted for the majority (ca. 80%) of total area burned. We estimate that in Wisconsin, low- to moderate-severity fires burned at least three times more often than noted by GLO surveyors (based on GLO survey period fire years alone) and burned on average between 858 km² per year based on the areas of pine alone, which is likely an underestimate in the WCR for example for which only 6% was pine, to 2564 km² per year across the five ecological landscapes or > 60 times the assumed historical average of 40 km² (Table 3). In northern Wisconsin alone (NWS, NH, NES) an average of 513 to 733 km² burned per year. From 1833 to 1863 when GLO surveys took place among our study sites (Table 2), we reconstructed seven regionally significant fire years that burned across at least three ecological landscapes, each of which likely accounted for burned areas similar or, more likely,

exceeding the assumed maximum fire extent (i.e., 1600 km²) in the GLR (LANDFIRE, 2018, Fig. 2). It is difficult to attribute exact areas or scale to any of these fire years and we did not attempt to calculate regional rotation intervals across multiple landscapes, but historically fires were both common and widespread with regionally significant (i.e., 1000 s km²) fire years occurring ca. every 10 years (Table 1, Fig. 2).

Our fire rotation estimates ranged from 11 years in the Northeast Sands (3995 km²) to 34 years in the Northern Highlands (5390 km²). Notably, Schulte and Mladenoff (2005) calculated 712 and 3314 year high-severity fire rotation intervals in these same ecological landscapes; 65 and 98 times the rotation interval for low- to moderate-severity fires. Other calculations of fire rotation intervals in the GLR have incorporated low-severity fires. Heinselman's (1973) work in the BWCAW is a rare example in that he collected fire-scar and stand structure data to determine fire regimes. He determined that low-severity fires burned every 40–50 years and high-severity fires every 150–300 years. Rotation for all fires in the BWCA were estimated to be ca. 100 years, though Heinselman (1973) cautioned against using a single, overly simplistic fire rotation metric to describe fire regimes there. Rotation intervals estimated with GLO data that incorporated all fires in northern Michigan ranged from 107 years (Cleland et al., 2004), to ca. 200 years (Whitney, 1987), and 480 years in the Upper Peninsula (Zhang et al., 1999). These estimates are not only disparate for the same or similar methods used and landscapes evaluated, but also 4–21 times our average rotation interval estimates in northern WI (23 years, NWS, NH, NES). Our fire rotation estimates are approximate and likely over-estimates in cases, particularly in landscapes with fewer and/or more spatially aggregated study sites. However, we used only large fire years in calculations, essentially discarding 67% (NES) to 89% (NWS) of all fires within the analysis period ($\mu = 82\%$, Table 2). Notably, fire scars have been found to provide a complete inventory only for larger fire years (Fulé et al., 2003; Farris et al., 2010).

High-severity fire regimes are typically found in cold, wet environments where ignition and conditions conducive to burning (e.g., extreme drought) occur infrequently (Gedalof et al., 2005; Krawchuk and Moritz, 2011) and large patches of high-severity fire, which comprise most of the area burned, drive landscape dynamics (Reilly et al., 2017). Alternatively, moderately wet climates are most fire prone due to greater fuel production but also periodic dry spells for burning, promoting frequent low- to moderate-severity fires (Sauer, 1952; Meyn et al., 2007; Krawchuk and Moritz, 2011). Our data suggest an increasing role of drought with larger fire years (Fig. 4). Some regionally significant fire years were also pronounced droughts (e.g., 1697, 1736, 1800 etc.), including 1736 one of the most extreme droughts in >

400 years (Cook et al., 2007). More commonly however, fires occurred under moderately dry conditions which in turn occurred more regularly than extreme drought (Fig. 4) and could have helped moderate severe fire effects. Notably, PDSI is most effective in determining long-term drought (several months) at low and middle latitudes and has less utility in capturing shorter term drought conditions, which may have been more common in the GLR (Alley, 1984). Similarly, fire probability is often thought to increase with stand age due to general increases of fuel (Clark, 1990; Heinzelman, 1973). Van Wagner (1970) suggested that red pine produces the most flammable pure stand of any north-eastern tree species when growing at high density with a clean floor, though he admitted that his rationale was based mainly on silvical knowledge of red pine. Historically in the GLR there were likely few dense, even-age stands of red pine, and typically they burned frequently, with low-severity where hazardous fuels build up would have been limited (Meunier et al., 2019a).

General Land Office survey data was in many ways well aligned with dendrochronological data; pines were almost always noted in survey points closest our plots (WCR an obvious outlier), density estimates were remarkably similar in most cases (Fig. 3), and many of the fire years recorded by surveyors were also years for which we reconstructed fires with dendrochronology methods, some of the most common years were large fire years by either account (e.g., 1833, 1847, 1860, Table 2, Fig. 2). However, we also confirmed that GLO fire records do not provide good data on low-severity fire. Within assumed 15-yr recognition windows, multiple fires were detected at all the fire history sites within the 15-yr period preceding the year the surveyor passed by the site, while none of the GLO sites nearest the fire history sites noted fire. Reconstructing minimum size of detectable fires is challenging with any historical data, including GLO 1.6 × 1.6 km survey grids. Size of historical high-severity fires estimated from GLO data in this region averaged 144 to 507 ha, though highly variable with most fires smaller (down to 4.5 ha; Schulte and Mladenoff, 2005). In this study all tree-ring based fire history sites were within 650 m of a GLO survey corner, with over half of sites within 200 m and likely even closer to section lines. Thus, it is likely that low-severity fires were large enough to be encountered by surveyors for the majority of sites.

By coupling GLO and dendrochronological data, we were able to gain a more complete picture of fire regimes in the GLR. We show here that while catastrophic fire was likely infrequent, low- to moderate-severity fires were abundant, large-scale, and widespread. Unfortunately, the relative lack of broad scale data on low-severity fires has likely inflated the importance of high-severity events while also unintentionally devaluing low-severity fires. Given the high frequency and widespread nature of low-severity fire among multiple landscapes, it is likely that it was one of the primary forcing mechanisms shaping coniferous forests across the entire region (Meunier et al., 2019a). Our inherent desire to apply the usual rules has, it seems, retarded our understanding of an “unusual ecological set-up.” Our results suggest we need to revisit the usual rules that have been applied to pine forests in the GLR, but also to re-evaluate the very concept of usual and unusual ecological situations.

Declaration of Competing Interest

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

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References

- Agee, J.K., 2005. The complex nature of mixed severity fire regimes. In: Lagene, L., Zelnik, J., Cadwallader, S., Hughes, B. (Eds.), *Mixed severity fire regimes: ecology and management*. Vol. AFE MISCO3, Washington State University Cooperative Extension Service/The Association for Fire Ecology, Spokane, Washington.
- Alley, W., 1984. The Palmer drought severity index: limitations and assumptions. *J. Clim. Appl. Meteorol.* 23, 1100–1109.
- Almendinger, J.C., 2010. Using Public Land Survey (PLS) records for silvicultural interpretation. Minnesota Department of Natural Resources, Ecological Land Classification Program. https://files.dnr.state.mn.us/forestry/ecssilviculture/communityTables_Figures/methods/PLSData_%20Methods.pdf.
- Alstad, A.O., Damschen, E.I., Givnish, T.J., Harrington, J.A., Leach, M.K., Rogers, D.A., Waller, D.M., 2016. The pace of plant community change is accelerating in remnant prairies. *Sci. Adv.* 2, e1500975.
- Axelrod, D.I., 1985. Rise of the grassland biome, central North America. *Bot. Rev.* 51, 163–201.
- Baker, W.L., 2009. *Fire Ecology in the Rocky Mountain Landscapes*. Island Press, Washington, D.C.
- Baker, W.L., 2014. Historical forest structure and fire in Sierran mixed-conifer forests reconstructed from General Land Office survey data. *Ecosphere* 5, 79.
- Baker, W.L., 2017. Restoring and managing low-severity fire in dry-forest landscapes of the western USA. *PlosOne*. <https://doi.org/10.1371/journal.pone.0172288>.
- Baker, W.L., Dugan, A.J., 2013. Fire-history implications of fire scarring. *Can. J. Forest Res.* 43, 951–962.
- Bergeron, Y., Harvey, B., Leduc, A., Gauthier, S., 1999. Forest management guidelines based on natural disturbance dynamics: stand- and forest level considerations. *For. Chron.* 75, 49–54.
- Bolliger, J., Schulte, L.A., Burrows, S.N., Sickley, T.A., Mladenoff, D.J., 2004. Assessing ecological restoration potentials of Wisconsin (USA) using historical landscape reconstructions. *Rest. Ecol.* 12, 124–142.
- Bormann, F.H., Likens, G.E., 1979. Catastrophic disturbance and the steady state in northern hardwood forests. *Amer. Sci.* 67, 660–669.
- Brewer, P.W., Velásquez, M.E., Sutherland, E.K., Falk, D.A., 2019. Fire History Analysis Exploration System (FHAES) version 2.0 [software]. <http://www.fhaes.org>. DOI:10.5281/zenodo.
- Brown, P.M., Wienk, C.L., Symstad, A.J., 2008. Fire and forest fire history at Mt Rushmore. *Ecol. Appl.* 18, 1984–1999.
- Busing, R.T., White, P.S., 1993. Effects of area on old-growth forest attributes: implications for the equilibrium landscape concept. *Lands. Ecol.* 8, 119–126.
- Canham, C.D., Loucks, O.L., 1984. Catastrophic windthrow in the presettlement forest of Wisconsin. *Ecology* 65, 803–809.
- Clark, J.S., 1990. Patterns, causes, and theory of fire occurrence during the last 750 yr in northwestern Minnesota. *Ecol. Mono.* 60, 135–169.
- Cleland, D.T., Avers, P.E., McNab, W.H., Jensen, M.E., Bailey, R.G., King, T., Russell, W.E., 1997. National hierarchical framework of ecological units. In: Boyce, M.S., Haney, A. (Eds.), *Ecosystem Management: Applications for Sustainable Forest and Wildlife Resources*. Yale University Press, New Haven, Connecticut, pp. 181–200.
- Cleland, D.T., Crow, T.R., Saunders, S.C., Dickmann, D.I., Maclean, A.L., Jordan, K.K., Watson, R.L., Sloan, A.M., Brososke, K.D., 2004. Characterizing historical and modern fire regimes in Michigan (USA): a landscape ecosystem approach. *Lands. Ecol.* 19, 311–325.
- Cook, E.R., Seager, R., Cane, M.A., Stahl, D.W., 2007. North American drought: reconstructions, causes and consequences. *Earth-Sci. Rev.* 81, 93–134.
- Cottam, G., Curtis, J.T., 1956. The use of distance measures in phytosociological sampling. *Ecology* 37, 451–460.
- Curtis, J.T., 1959. *The Vegetation of Wisconsin: An Ordination of Plant Communities*. University Press, Madison, Wisconsin.
- Daniels, L.D., Yocum Kent, L.L., Sherriff, R.L., Heyerdahl, E.K., 2017. Deciphering the complexity of historical fire regimes: diversity among forests of western North America [Chapter 8]. In: Amoroso, M.M., Daniels, L.D., Baker, P.J., Camarero, J.J. (Eds.), *Dendroecology: Tree-Ring Analysis Applied to Ecological Studies*. Springer, Cham: Ecological Studies 231, pp. 185–210.
- Dickmann, D.I., Cleland, D.T., 2002. Fire return intervals and fire cycles for historic fire regimes in the Great Lakes Region: a synthesis of the literature. Research Report, Great Lakes Ecological Assessment, U.S. Forest Service.
- Dugan, A.J., Baker, W.L., 2014. Modern calibration and historical testing of small-area, fire interval reconstruction methods. *Int. J. Wildland Fire* 37, 265–272.
- Environmental Systems Research Institute (ESRI), 2014. *ArcGIS Desktop 10.3*. Redlands, CA.
- Fahey, R.T., 2014. Composition, structure, and trajectories of Great Lakes coastal pine forests in relation to historical baselines and disturbance history. *Am. Midl. Nat.* 172, 285–302.
- Falk, D.A., Miller, C., McKenzie, D., Black, A.E., 2007. Cross-scale analysis of fire regimes. *Ecosystems* 10, 809–823.
- Farris, C.A., Baisan, C.H., Falk, D.A., Yool, S.R., Swetnam, T.W., 2010. Spatial and

- temporal corroboration of a fire-scar-based fire history in a frequently burned ponderosa pine forest. *Ecol. Appl.* 20, 1598–1614.
- Farris, C.A., Baisan, C.H., Falk, D.A., Van Horne, M.L., Fulé, P.Z., Swetnam, T.W., 2012. A comparison of targeted and systematic fire-scar sampling for estimating historical fire frequency in south-western ponderosa pine forests. *Int. J. Wildland Fire* 22, 1021–1033.
- Flannigan, M.D., Bergeron, Y., 1998. Possible role of disturbance in shaping the northern distribution of *Pinus resinosa*. *J. Veg. Sci.* 9, 477–482.
- Franklin, J.F., Johnson, K.N., 2012. A restoration framework for federal forests in the Pacific Northwest. *J. Forest.* 110, 429–439.
- Fraver, S., Palik, J.P., 2012. Stand and cohort structures of old-growth *Pinus resinosa*-dominated forests of northern Minnesota, USA. *J. Veg. Sci.* 23, 249–259.
- Frelich, L.E., Lorimer, C.G., 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes Region. *Ecol. Mono.* 61, 145–164.
- Frelich, L.E., 2002. *Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-Deciduous Forests*. Cambridge University Press, New York.
- Frelich, L.E., Reich, P.B., Peterson, D.W., 2015. Fire in the upper midwestern oak forest ecosystems: an oak forest restoration and management handbook. Gen. Tech. Rep. PNW-GTR-914. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 64 p.
- Fulé, P.Z., Henlein, T.A., Covington, W.W., Moore, M.M., 2003. Assessing fire regimes on Grand Canyon landscapes with fire scar and fire record data. *Int. J. Wildland Fire* 12, 129–145.
- Gedalof, Z., Peterson, D.L., Mantua, N.J., 2005. Atmospheric, climatic, and ecological controls on extreme wildfire years in the northwestern United States. *Ecol. Appl.* 15, 154–174.
- Grimm, E.C., 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. *Ecol. Mono.* 54, 291–311.
- Grisino-Mayer, H.D., Swetnam, T.W., 2000. Century-scale climate forcing of fire regimes in the American Southwest. *Holocene* 10, 213–220.
- Grisino-Mayer, H.D., 2001. FHX2 Software for analyzing temporal and spatial patterns in fire regimes from tree-rings. *Tree-Ring Res.* 57, 115–124.
- Guyette, R.P., Spetich, M.A., Stambaugh, M.C., 2006. Historic fire regime dynamics and forcing factors in the Boston Mountains, Arkansas, USA. *For. Ecol. Manage.* 234, 293–304.
- Guyette, R.P., Stambaugh, M.C., Dey, D.C., Marschall, J.M., Saunders, J., Lampereur, J., 2016. 350 years of fire-climate-human interactions in a Great Lakes sandy outwash plain. *Forests* 7, 189. <https://doi.org/10.3390/f7090189>.
- Hardy, C.C., Schmidt, K.M., Menakis, J.P., Sampson, R.N., 2001. Spatial data for national fire planning and management. *Int. J. Wildland Fire* 10, 353–372.
- Heinselman, M.L., 1973. Fire in the virgin forests of the Boundary Waters Canoe Area Minnesota. *Quat. Res.* 3, 329–382.
- Heinselman, M.L., 1978. Fire in wilderness ecosystems. In: Hendee, J.C., Stanley, G.H., Lucas, R.C. (Eds.), *Wilderness management*. USDA Forest Service Publication No. 1365, Washington, DC, pp. 249–278.
- Heinselman, M.L., 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. In: Mooney, H.A., Bonnicksen, J.M., Christensen, N. L., Lotan, J.E., Reiners, W.A. (Eds.), *Fire regimes and ecosystem properties*. USDA Forest Service Gen. Tech. Report WO-26, Washington, D.C., pp. 7–57.
- Johnson, E.A., Gutsell, S.L., 1994. Fire frequency models, methods, and interpretations. *Adv. Ecol. Res.* 35, 239–287.
- Johnson, E.A., Larson, C.S., 1991. Climatically induced change in fire frequency in the southern Canadian Rockies. *Ecology* 72, 194–201.
- Johnson, L.B., Kipfmüller, K.F., 2016. A fire history derived from *Pinus resinosa* Ait. for the islands of eastern Lac La Croix, Minnesota, USA. *Ecol. Appl.* 26, 1030–1040.
- Kent, L.Y., 2014. An evaluation of fire regime reconstruction methods. ERI Working Paper No. 32. Ecological Restoration Institute and Southwest Fire Science Consortium, Northern Arizona University: Flagstaff, AZ. 15 p.
- Krawchuk, M.A., Moritz, M.A., 2011. Constraints on global fire activity vary across a resource gradient. *Ecology* 92, 121–132.
- LANDFIRE: LANDFIRE Vegetation Dynamics Models. 2013. LANDFIRE Project, U.S. Department of Agriculture, Forest Service; U.S. Department of Interior, Available: <http://www.landfire.gov/index.php> [2019 [2019, November 12].
- LANDFIRE, 2018. LANDFIRE Biophysical Settings (BpS) models and descriptions. U.S. Department of Agriculture Forest Service, U.S. Department of the Interior, U.S. Geologic Survey, The Nature Conservancy (Producers), Arlington, Virginia, USA.
- Leopold, A., 1939. Unpublished letter from Aldo Leopold to E. Holt, 2 October Aldo Leopold Papers 10-2, 8.
- Levine, C.R., Cogbill, C.V., Collins, B.M., Larson, A.J., Lutz, J.A., North, M.P., Restaino, C.M., Safford, H.D., Stephens, S.L., Battles, J.J., 2017. Evaluating a new method for reconstructing forest conditions from General Land Office survey records. *Ecol. Appl.* 27, 1498–1513.
- Lorimer, C.G., 1980. The use of land survey records in estimating presettlement fire frequency. In: Stokes, M.A., Dieterich, J.H. (Eds.) *Proceedings of the fire history workshop, 20-24 October 1980, Tucson, Arizona*. U.S. Forest Service Gen. Tech. Report RM-81, pp. 57–62.
- Lorimer, C.G., White, A.S., 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. *For. Ecol. Manage.* 185, 41–64.
- Maclean, A.L., Cleland, D.T., 2003. Determining the spatial extent of historical fires with geostatistics in Northern Lower Michigan. In: *Fire, fuel treatments, and ecological restoration: Conference Proceedings, 16-18 April 2002, Fort Collins, CO*. USDA Forest Service Proceedings RMRS-P-29, pp. 16–18.
- Manies, K.L., Mladenoff, D.J., 2000. Testing methods to produce landscape-scale presettlement vegetation maps from the U.S. public land survey records. *Lands. Ecol.* 15, 741–754.
- Manies, K.L., Mladenoff, D.J., Nordheim, E.V., 2001. Assessing large-scale surveyor variability in the historic forest data of the original U.S. Public Land Survey. *Can. J. For. Res.* 31, 1719–1730.
- Melvin, M.A., 2018. National prescribed fire use survey report. National Association of State Foresters and the Coalition of Prescribed Fire Councils, Tech. Rep. 03-18.
- Meunier, J., Holoušek, N., Brown, P., Sebasky, M., 2019a. Re-evaluating pattern and process to understand resilience in transitional mixed conifer forests. *Ecology* 100, e02839.
- Meunier, J., Holoušek, N.S., Sebasky, M., 2019b. Fire regime characteristics in relation to physiography at local and landscape scales in Lake States pine forests. *For. Ecol. Manage.* 454, 117651.
- Meyn, A., White, A.P., Buhk, C., Jentsch, A., 2007. Environmental drivers of large, infrequent wildfires: the emerging conceptual model. *Prog. Phys. Geogr.* 31, 287–312.
- Miller, J.D., Safford, H.D., 2017. Corroborating evidence of a pre-Euro-American low-to moderate-severity fire regime in yellow pine-mixed conifer forests of the Sierra Nevada, California, USA. *Fire Ecol.* 13, 58–90.
- Mladenoff, D.J., 2009. See Wisconsin through the eyes of 19th century surveyors. University of Wisconsin, Madison, WI, USA. PUB-CE-4018.
- Morgan, P., Hardy, C.C., Swetnam, T.W., Rollins, M.G., Long, D.G., 2001. Mapping fire regimes across time and space: understanding coarse and fine-scale fire patterns. *Int. J. Wildland Fire* 10, 329–342.
- Morrison, P., Swanson, F.J., 1990. Fire history and pattern in a Cascade Range landscape. U.S. Forest Service General Technical Report PNW-GTR-254. Pacific Northwest Research Station. Portland, Oregon, USA.
- Paul, T.S., Kimberley, M.O., Beets, P.N., 2018. Thinking outside the square: evidence that plot shape and layout in forest inventories can bias estimates of stand metrics. *Methods Ecol. Evol.* 10, 381–388.
- Pickett, S.T., White, P.S., 1985. *Patch Dynamics and Natural Disturbance Regimes*. Academic Press, New York, pp. 472.
- Pyne, S.J., 2007. Problems, paradoxes, paradigms: triangulating fire research. *Int. J. Wildland Fire* 16, 271–276.
- R Core Team, 2019. R: A language and environment for statistical computing. R foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- Radeloff, V.C., Mladenoff, D.J., He, H.S., Boyce, M.S., 1999. Forest landscape change in northwestern Wisconsin pine barrens from pre-European settlement to the present. *Can. J. For. Res.* 29, 1649–1659.
- Reed, W.J., 1984. The effects of the risk of fire on the optimal rotation of a forest. *J. Environ. Econ. Manag.* 11, 180–190.
- Reed, W.J., 2006. A note on fire frequency concepts and definitions. *Can. J. For. Res.* 36, 1884–1888.
- Reilly, M.J., Dunn, C.J., Meigs, G.W., Spies, T.A., Kennedy, R.E., Bailey, J.D., Briggs, K., 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). *Ecosphere* e01695.
- Rhemtulla, J.M., Mladenoff, D.J., Clayton, M.K., 2009. Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s-1930s-2000s). *Ecol. Appl.* 19, 1961–11078.
- Romme, W.H., 1980. Fire history terminology: report the ad hoc committee. In: Stokes, M.A., Dieterich, J.H. (Eds.), *Proceedings of the fire history workshop*. USDA Forest Service General Technical Report RM-GTR-81. Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Safford, H.D., Wiens, J.A., Hayward, G., 2012. The growing importance of the past in managing ecosystems of the future. In: Wiens, J.S., Hayward, G., Safford, H.D., Giffen, C.M. (Eds.), *Historical Environmental Variation in Conservation and Natural Resource Management*. John Wiley and Sons, New York, New York, USA, pp. 319–327.
- Sauer, C.O., 1950. Grassland, climax, fire and man. *J. Range Manage.* 3, 16–22.
- Sauer, C.O., 1952. *Agriculture Origins and Dispersals*. Bowman Memorial Lectures, American Geographical Society, 110 pp.
- Schulte, L.A., Mladenoff, D.J., 2001. The original US public land survey records: their use and limitations in reconstructing presettlement vegetation. *J. For.* 99, 5–10.
- Schulte, L.A., Mladenoff, D.J., 2005. Severe wind and fire regimes in northern forests: historical variability at the regional scale. *Ecology* 86, 431–445.
- Schulte, L.A., Mladenoff, D.J., Burrows, S.N., Sickley, T.A., Nordheim, E.V., 2005. Spatial controls of pre-Euro-American wind and fire disturbance in northern Wisconsin (USA) forest landscapes. *Ecosystems* 8, 73–94.
- Schulte, L.A., Mladenoff, D.J., Crow, T.R., Merrick, L.C., Cleland, D.T., 2007. Homogenization of northern U.S. Great Lakes forest due to land use. *Lands. Ecol.* 22, 1089–1103.
- Shea, M.E., Schulte, L.A., Palik, B., 2014. Reconstructing vegetation past: pre-Euro-American vegetation for the Midwest (Recreating Area, USA). *Ecol. Rest.* 32, 417–433.
- Sickley, T.A., Mladenoff, D.J., Radeloff, V.C., Maines, K.L., 2001. A pre-European settlement vegetation database for Wisconsin. Forest Landscape Ecology Lab. University of Wisconsin. https://www.sco.wisc.edu/glo/dist/docs/GLOUserGuide_v3.pdf (accessed 19 February 2020).
- SigmaPlot Version 12.0, 2010. Systat Software, San Jose, CA.
- Speer, J.H., 2010. *Fundamentals of Tree-Ring Research*. University of Arizona Press, Tucson.
- Stambaugh, M.C., Guyette, R.P., Marschall, J.M., Dey, D.C., 2016. Scale dependence of oak woodland historical fire intervals: contrasting The Barrens of Tennessee and Cross Timbers of Oklahoma, USA. *Fire Ecol.* 12, 65–84.
- Stearns, F.W., 1949. Ninety years of change in a northern hardwood forest in Wisconsin. *Ecology* 30, 350–358.
- Steel, Z.L., Safford, H.D., Viers, J.H., 2015. The fire frequency-severity relationship and the legacy of fire suppression in California forests. *Ecosphere* 6. <https://doi.org/10.1890/ES14-00224.1>.
- Stephens, S.L., Fry, D.L., Collins, B.M., Skinner, C.N., Franco-Vizcaino, E., Freed, T.J.,

2010. Fire-scar formation in Jeffrey pine-mixed conifer forests in the Sierra San Pedro Mártir, Mexico. *Can. J. For. Res.* 40, 1497–1505.
- Stevens, J.T., Safford, H.D., North, M.P., Fried, J.S., Gray, A.N., Brown, P.M., Dolanc, C.R., Dobrowski, S.Z., Falk, D.A., Farriss, C.A., Franklin, J.F., Fulé, P.Z., Haggmann, R.K., 2016. Average stand age from forest inventory plots does not describe historical fire regimes in ponderosa pine and mixed-conifer forests of western North America. *PlosOne*. <https://doi.org/10.1371/journal.pone.0147688>.
- Stewart, L.O., 1935. *Public Land Surveys—History, Instructions, Methods*. Collegiate Press, Ames, Iowa, USA.
- Swetnam, T.W., 1993. Fire history and climate change in giant sequoia groves. *Science* 262, 885–889.
- Swetnam, T., Baisan, C., 1996. Historical fire regime patterns in the southwestern United States since AD 1700. In: Allen, C.D. (Ed.), *Fire effects in southwestern forest: proceedings of the 2nd La Mesa fire symposium*. USDA Forest Service, Rocky Mountain Research Station, General Technical Report RM-GTR-286, pp. 11–32.
- Swetnam, T.W., Allen, C.D., Betancourt, J.L., 1999. Applied historical ecology: using the past to manage for the future. *Ecol. Appl.* 9, 1189–1206.
- Tarancón, A.A., Fulé, P.Z., Sanchez Meador, A., Kim, Y., Padilla, T., 2018. Spatiotemporal variability of fire regimes in adjacent Native American and public forests, New Mexico, USA. *Ecosphere* 9, e02492.
- Taylor, A.H., Skinner, C.N., 1998. Fire history and landscape dynamics in a late-successional reserve, Klamath Mountains, California, USA. *For. Ecol. Manage.* 111, 285–301.
- Taylor, A.H., Skinner, C.N., 2003. Spatial patterns and controls on historical fire regimes and forest structure in the Klamath Mountains. *Ecol. Apps.* 13, 704–719.
- Thomas-Van Gundy, M.A., 2014. Mapping fire regimes from data you may already have: assessing LANDFIRE fire regime maps using local products. In: Waldrop, T.A. (Ed.), *Proceedings, wildland fire in the Appalachians: discussions among managers and scientists*. General Technical Report SRS-199. U.S. Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC, 208 p.
- Van Horne, M.L., Fulé, P.Z., 2006. Comparing methods of reconstructing fire history using fire scars in a southwestern United States ponderosa pine forest. *Can. J. For. Res.* 36, 855–867.
- Van Wagner, C.E., 1970. Fire and red pine. In: *Proceedings: 10th Tall Timbers Fire Ecology Conference*, August 20–21, Fredericton, New Brunswick. Tallahassee, FL, Tall Timbers Research Station.
- Van Wagner, C.E., 1978. Age-class distribution and the forest fire cycle. *Can. J. For. Res.* 8, 220–226.
- Vogl, R.J., 1971. Fire and the northern Wisconsin pine barrens. In: *Proceedings of the tall timbers fire ecology conference*, August 20–21, 1970, New Brunswick, Canada. Tall Timbers Research Station, Florida State University, Tallahassee, Florida, USA, pp. 175–209.
- Way, A.G., 2006. Burned to be wild: Herbert Stoddard and the roots of ecological conservation in the southern longleaf pine forest. *Environ. Hist.* 11, 500–526.
- Whitney, G.G., 1986. Relation of Michigan's presettlement pine forest to substrate and disturbance history. *Ecology* 67, 1548–1559.
- Whitney, G.G., 1987. An ecological history of the Great Lakes forest of Michigan. *Ecology* 75, 667–684.
- Williams, M.A., Baker, W.L., 2012. Spatially extensive reconstructions show variable-severity fire and heterogeneous structure in historical western United States dry forests. *Global Ecol. Biogeogr.* 21, 1042–1052.
- Wisconsin Department of Natural Resources (WI DNR), 2015. *Ecological landscapes of Wisconsin: an assessment of ecological resources and a guide to planning sustainable management*. Wisconsin Department of Natural Resources, PUB-SS-1131 2015, Madison.
- Zenner, E.K., Peck, J.E., 2009. Characterizing structural conditions in mature managed red pine: spatial dependency of metrics and adequacy of plot size. *For. Ecol. Manage.* 257, 311–320.
- Zhang, Q., Pregitzer, K.S., Reed, D.D., 1999. Catastrophic disturbance in the presettlement forest of the Upper Peninsula of Michigan. *Can. J. For. Res.* 29, 106–114.