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Re-evaluating pattern and process to understand resilience in transitional mixed conifer forests

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Abstract. A key challenge to maintaining resilient landscapes is adapting to and maintaining dynamic ecological processes. In fire-dependent ecosystems, this includes identifying and defining mechanisms through which fire influences forest structure and functionality. Interpretations of tree patterns via land survey records in the Lake States have often highlighted the importance of infrequent moderate to extreme disturbance events. However, historical survey methods are limited to observing higher severity disturbances and over large landscapes, thus it is not clear if the origin, structure, and forcing factors for either patterns or processes are adequately quantified by these methods. We used dendrochronological methods to determine how fire history and stand structure, including cohort structure, tree density, and spatial patterning, are linked within Lake States mixed conifer forests in Wisconsin. We found relatively short mean fire return intervals (MFRIs) ranging from 6 to 13 yr with little variation in fire frequency among sites. Current densities of red-pine-dominated forests are 4–37 times historical (ca. 1860) densities (mean 12×) and almost entirely spatially random, whereas historically forests were spatially aggregated at stand scales. Stands also contained multiple and/or loosely defined cohort structures suggesting very different controls operating historically than currently. Heterogeneity that helped maintain ecosystem resilience in these ecosystems historically came from frequent fire disturbance processes that affected stand-scale forest resistance. This was likely the historical dynamic across fire-adapted transitional pine forests of the Lake States.

Key words: fire history; forest structure; General Land Office; Lake States; Pinus resinosa; *red pine; spatial pattern; Wisconsin.*

Introduction

Ecological resilience has become a central objective in forest management in the face of greater climate variability and altered disturbance regimes (Churchill et al. 2013). Increasingly, building forest resilience has relied on emulating patterns associated with natural disturbance processes (Perera et al. 2004). Spatial heterogeneity and stand structure at multiple scales are critical components of ecosystem resilience (Levin 1998, North et al. 2009, Moritz et al. 2011). In many dry forest types, landscape-scale forest resilience, the capacity to persist through and reorganize after disturbance to maintain ecosystem structure, often depends on stand-scale forest resistance, the capacity to absorb disturbance and remain largely unchanged (Holling 1973, DeRose and Long 2014). In these same dry forests, there is often reliable historical evidence of frequent, low-severity fire regimes and a mosaic of multi-aged stands (White 1985, Brown and Wu 2005). It follows that departure of current forests from historical conditions is relatively well understood in these ecosystems (Covington and Moore 1994, Swetnam and Baisan 1996, Allen et al. 2002, Fulé et al. 2004). Evidence and subsequent understanding of historical forest dynamics outside of these dry, usually montane, forest types are often more limited and, in many cases, land managers are faced with sustaining highly altered systems with incomplete knowledge of historical structure and the processes that shaped them.

In the northern Lakes States, once expansive pine forests have been nearly eliminated following a widespread and intensive cutover period ca. 1860–1910, with an estimated <0.6% of "relatively intact" pine forests remaining (Frelich 1995, Buckman et al. 2006). Quantitative data from reference stands are largely lacking and extant stands are rare, thus likely representing a narrow range of variability.

Similarly, these stands have been without fire disturbance, arguably the most important driver in these systems, since effective fire exclusion. These factors together limit the utility of these extant remnant stands for understanding long-term forest patterns and the

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processes that shaped them (Fraver and Palik 2012). Information on historical disturbance regimes in the Lake States most commonly come from interpretations of tree patterns (size, density, and species composition) during early settlement era (ca 1832–1866 in Wisconsin) Public Land Survey System General Land Office records (GLO; e.g., Stearns 1949, Bourdo 1956, Cottam and Curtis 1956, Curtis 1959, Lorimer 1980, Loucks 1983, Whitney 1986, Manies and Mladenoff 2000, Schulte and Mladenoff 2001, Lorimer and White 2003, Cleland et al. 2004, Schulte and Mladenoff 2005). These records are a consistent and valuable resource for understanding historical systems, but their interpretations rely on a number of assumptions that have not been adequately tested (Fulé et al. 2013, Levine et al. 2017), including assumptions based on patterns themselves (e.g., tree configuration).

Two common ways GLO data are used to understand historical disturbance processes are with density-dependent disturbance probabilities (Van Wagner 1978, Dickmann and Cleland 2002) and recognition of abrupt changes in tree density to calculate fire rotation intervals (Schulte and Mladenoff 2005, Baker 2014). However, errors in GLO density estimates, attributed to limitations of the data itself and not methodological processes, are common (Hagmann et al. 2013, Levine et al. 2017). GLO-based reconstructions of density, for example, (Baker 2012, 2014) were 2.5 times higher than historical timber inventories in the Klamath Indian Reservation, Oregon (Hagmann et al. 2013) and 2–5 times higher in the Sierra Nevada mixed-conifer forests (Stephens et al. 2015). Similarly, while limitations of GLO data have tended to focus primarily on surveyor bias and statistical bases for estimating point-to-tree distances (Schulte and Mladenoff 2001, Zenner and Peck 2009, Hanberry et al. 2012), these methods are only unbiased when the spatial pattern of trees follows a random pattern and remains constant (Kleinn and Vilčko 2006). Accuracy and precision of GLO data decrease as trees diverge from random spacing and/or tree density varies across the landscape (Cottam and Curtis 1956, Engemann et al. 1994, Kronenfeld 2009). However, there is a paucity of detailed stand-level forest structure or spatial data in the Lake States to evaluate how these underlying issues may impact interpretations of GLO tree patterns or processes that shaped them (Fraver and Palik 2012).

Frequent low-intensity fires in pine forests are often associated with lower tree densities, higher proportions of multi-cohort stands, and greater within-stand spatial variability including aggregated tree patterns as compared to fire-excluded forests (Drobyshev et al. 2008, Larson and Churchill 2012, Knapp et al. 2017). One of the most important roles of heterogeneity in forest structure is in moderating and regulating disturbances such as fire (Parsons et al. 2017). Aggregated spatial patterns modify fire spread and intensity of subsequent fires, fostering variability in fire effects (Knapp and Keeley 2006, Sánchez Meador et al. 2009, Parsons et al. 2017). Analyses of GLO data have generally determined that mixed conifer forests in the Lake States were historically lower density, more open forests (Bolliger et al. 2004, Stoltman et al. 2007), but these data are only suitable at very large spatial scales (Manies and Mladenoff 2000, Schulte and Mladenoff 2001) and cannot capture fine-scaled patterns typical of frequent fire forests (Larson and Churchill 2012) nor reliably detect low-severity fires (Lorimer 1980). These issues are assumed to be minor due to disturbances characterized by infrequent windstorms, occasionally followed by stand-replacing fire, and subsequent broad-scale regeneration events dominating stand dynamics (Frelich 2002, Cleland et al. 2004, Schulte and Mladenoff 2005). Mortality and recruitment in Lake State pine stands are believed to be closely coupled with cohorts of similarly aged trees recruiting following single disturbance events (Fraver and Palik 2012).

It follows that departure of forest structure from historical conditions is generally most pronounced in more frequent fire landscapes due to a comparatively greater deviation from natural disturbance regimes (Mast and Wolf 2006, Romme et al. 2009, Evans et al. 2011). Fire suppression, for example, has had little effect on high elevation forests where fire is infrequent and dependent on severe drought (Sherriff et al. 2001). However, without reliable historical forest structure and disturbance data, we cannot understand departure from historical conditions nor project resilience of forests under climate change in Lake States transitional forest, particularly when resilience is viewed, at least in part, as the influence of a disturbance on subsequent structure and function (DeRose and Long 2014). The identification of stand structure and spatial pattern targets that are empirically linked to resilience, climate adaptation, and desired ecological function is a major remaining task for Lake States transitional mixed conifer forests (Puettmann et al. 2009, Churchill et al. 2013). Thus, the objective of this study was to examine spatial patterns of tree-recruitment and structural components of historical forests, coupled with reconstructed historical disturbance processes to provide insights into mechanisms influencing forest stand structure and to evaluate interpretations of ecological function (Boyden et al. 2005, Sánchez Meador et al. 2010, Meunier et al. 2014). Specifically, we evaluated how stand structure, including cohort structure, tree density, and spatial patterning, is linked to fire history within Lake States mixed conifer forests.

Methods

Study area

Our study area spanned four ecological landscapes, three within the Laurentian Mixed Conifer Forest, and the fourth within the tension zone of the Southern Broadleaf Forest of Wisconsin, USA (Fig. 1; Cleland et al. 1997, WI DNR 2015). The tension zone represents a region of overlap between northern and southern climate and northern

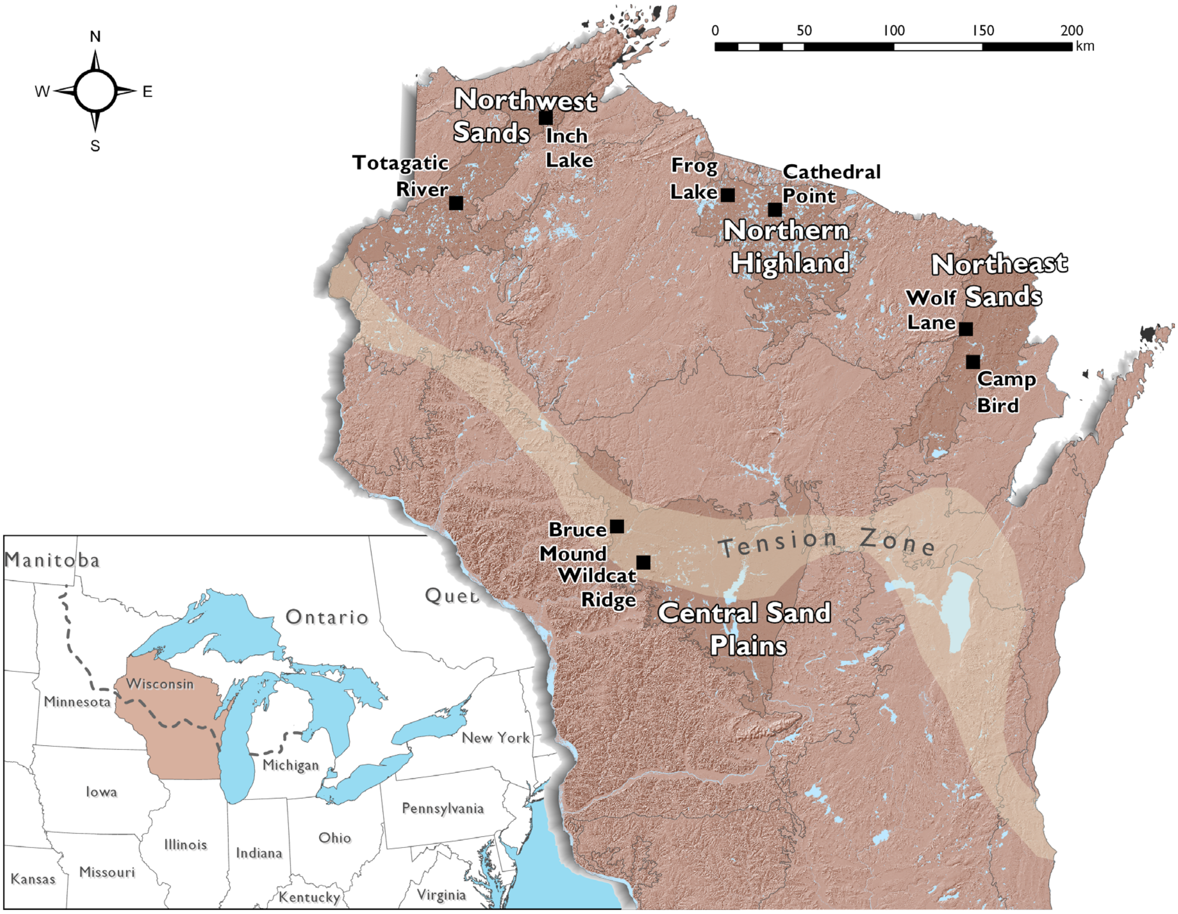

FIG. 1. Study sites (n = 8) among four ecological landscapes; three of which are within the Laurentian Mixed Conifer province (Northwest and Northeast Sands, Northern Highland), and the fourth ecological landscape is within the tension zone of the Southern Broadleaf Forest province (Curtis 1959; Central Sands) of Wisconsin, USA.

hardwood and prairie–forest floristic provinces (Curtis 1959). The Laurentian mixed forest (LMF) is itself a transitional ecoregion between boreal and broadleaf deciduous forest zones (Bailey 1995) and traverses the northern Lake States (Minnesota, Wisconsin, Michigan; hereafter Lake States) as well as southern Ontario and portions of New England. These broad ecoregions, and the ecological landscapes within them, are a result of successive glaciation events. Our eight study sites were all within natural origin red pine (*Pinus resinosa*) dominated stands that spanned relatively productive dry-mesic sites (e.g., Northern Highlands) to deep, well-drained, glacial lakebed (Central), or dry outwash sands (Northwest and Northeast, Fig. 1). 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). By sampling Euro-settlement era cutover stands via remnant wood we could utilize a wider range of sites, with a longer period of fire activity, than would have been possible with using only extant old-growth stands.

Data collection and analysis

We established 0.5-ha plots within two red pine-dominated stands in each ecological landscape (n = 8 plots, Fig. 1) to reconstruct timing, frequency, and severity of fire as related to spatial and temporal patterns of forest demography, tree patterning, and spatial arrangement. Many forest descriptors, including spatial patterns of mature red pine forests (Zenner and Peck 2009), stabilize with 0.5-ha sample areas (Busing and White 1993, Fraver and Palik 2012). Our goal in each 0.5-ha plot was to characterize stand structure in 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 entire 0.5-ha plots. Plots were comprised of four quadrats that were adjacent but sometimes irregularly configured to fit within forest stands without major changes in slope, aspect or other stand characteristics. We defined historical or "pre-Euro-settlement" as 1860 and earlier for comparisons between current and historical conditions. 1860 marks the end of the period just prior to intensive harvest and Euro-settlement impacts in this region and prior to 1860 stands had longer-term intact fire regimes. We mapped all pre-fire-exclusion living and remnant trees (snags, logs, and stumps) within the entire 0.5-ha plot and subsampled all living trees, regardless of age or size, within 200-m^2 circular subplots centered in each of four quadrats comprising the main 0.5-ha plot. Subplots were centered in each quadrat and served as reference points to measure distance and azimuth for stem mapping. Subplots, with more abundant post fire exclusion trees, were also used as the post-fire-exclusion spatial reference (800-m^2 area/plot) to compare to pre-exclusion spatial patterns determined over entire 0.5-ha plots. While plot areas were small, changes in spatial pattern at tree-neighborhood and within-stand patch scales typically are most apparent within 20 m (Frelich et al. 1998). Within each subplot, we cored all living trees > 4 cm diameter at breast height (DBH, 1.4 m) at approximately 10 cm above ground level. All seedlings (<1.4 m high) and saplings (>1.4 m and ≤ 4 cm DBH) were counted by species within the subplot. We sampled all fire-scarred remnant trees in each plot, as well as opportunistically by searching nearby vicinity of each plot (within ~200 m) for additional fire-scarred remnants to include in the fire history for each site.

In the laboratory, we stabilized cores by gluing into wooden core mounts and cross sections as needed to wooden backing boards. All samples were surfaced until cellular structure of xylem was clearly visible with magnification. We used dendrochronological methods to cross date all cores and cross sections (Grissino-Mayer and Swetnam 2000, Speer 2010) to determine tree establishment dates and exact calendar years for all fire scars. We considered pith dates at approximately 10 cm height to be the year of tree establishment, or origin (Brown et al. 2008). We estimated pith dates for samples that did not include pith with concentric circles of varying widths for samples within ~10 yr of pith (Brown et al. 2008). We complied fire-scar dates into composite chronologies for each plot and analyzed using program FHX2 (Grissino-Mayer 2001). We also assigned seasonal positions to fire scars based on locations within ring series (Grissino-Mayer 2001). We assigned ring-boundary scars (dormant season position) to the year containing the earlywood immediately following fire scars.

We calculated mean fire return intervals (MFRI) within sites for all years with at least two recording samples and fire injuries replicated twice (Grissino-Mayer 2001) using Fire History Analysis and Exploration System software version 2.0. (FHAES; Sutherland et al. 2014). We also generated median, minimum, maximum, and Weibull median probability intervals (WMPI). Filtering based on fire-scarring percentages (e.g., evaluating only fire years recorded on ≥10% of samples) eliminates small fires and provides a meaningful index of major fire years that burn large areas (Farris et al. 2010). Scale dependence is strong for small fires but decreases with increasing fire size, large fires are on average disproportionately more common at fine scales where scar formation occurs (Falk et al. 2007, Farris et al. 2010). We wanted to capture ecologically meaningful fires (e.g., beyond a single lightning struck tree) but also fires that shaped stand dynamics at relatively fine spatial scales.

Spatial analysis

Processes influencing change in forest structure and pattern operate through both time and space. We examined stand-level spatial patterns of trees (n = 8 plots, 1,324 trees) to gain insight into historical and environmental mechanisms influencing forest structure and pattern. More uniform tree spatial patterns, for example, are expected with competition as a primary control following punctuated mortality events vs. greater aggregation with more frequent low-severity fires and lower, patchy seedling survival (Larson and Churchill 2012). We used Ripley's $K(t)$ function to assess spatial patterns of trees, including whether trees were randomly distributed (i.e., complete spatial randomness or CSR), or had uniform or aggregated distributions. The $K(t)$ function estimates spatial dependence between points, producing a cumulative distribution function that represents the expected number of trees within a given distance of individual trees (Ripley 1981, Boyden et al. 2005). The model tests point data for departure from a spatially random pattern, and we used an $L(t)$ square-root transformation to stabilize variance. We also used an edge effect local correcting factor for complex shapes (Goreaud and Pélissier 1999) and computed 95% confidence intervals using a Monte Carlo simulated Poisson process with 1,000 simulations for an indication of statistical significance. Edge effects arise because a point (tree) close to the edge of the window may have its true nearest neighbor lie outside the window resulting in artificially large nearest neighbor distances. Significant differences ($P \leq 0.05$) between observed and random patterns occur where the $L(t)$ plot falls outside the simulated confidence envelope. We used a Clark and Evans (1954) aggregation index with a Cumulative Distribution Function (cdf) edge correction to evaluate degree of clustering or ordering of tree point patterns. The nearest neighbor distribution function $G(r)$ is estimated by using a Kaplan-Meier type edge correction with the mean of the distribution calculated from the cdf. All spatial statistics were computed in the spatstat library in R 3.3.1 (Baddeley and Turner 2005).

Results

Fire history

We cross dated a total of 240 fire-scarred sections (n = 14–59 samples/site) with 292 unique fire years among our eight sites (Table 1). Mean fire return intervals (MFRI) for fires recorded on at least two samples ranged from 6 to 13 yr. Of these fires, there were 29 fires that occurred within at least two sites (Fig. 2) with a MFRI of 7 yr for those widespread fire years alone. We did not limit analyses of MFRI to pre-settlement or pre-fire exclusion period but rather across all years with at least two recording trees with the period of analysis spanning 1660–2017.

Stand structure (density, cohort structure, spatial patterning)

We mapped and collected data from a total of 1,324 living and remnant trees within the eight plots. The majority of all trees were red (56%) and white (15%) pines. Living red pine (n = 336) were usually older than similarly sized white pine (n = 152, Fig. 3) and all trees that established prior to 1860 were red pines except for one remnant white pine (pith date 1791). Within subplots, only 1.4% of seedlings (48/3,337), and 4.8% of saplings (30/626) were red pine. White pine comprised 41% of saplings and 27% of seedlings with the remainder of young trees dominated by *Acer rubr*um seedlings (27%) and saplings (32%) as well as *Quercus rubra* seedlings (20%). Current stand densities were 4–37 times greater (mean 12×) than estimated historical density in 1860 (Table 2). In 1860, all but two stands had estimated densities >99 trees/ha, the density at which a stand is classified as forest as opposed to savanna (0.5–47 trees/ha) or woodland (47–99 trees/ha; Curtis 1959, Anderson and Anderson 1975).

None of our stands showed evidence of trees being spatially random historically, rather stands all had some level of spatial aggregation across spatial scales (Table 3, Fig. 4). In contrast, trees in current forests were completely spatially random in 29 of 32 subplots (Table 3, Fig. 4). While plots sometimes had complex shapes (Fig. 4), Ripley's $K(t)$ function test results were similar with and without edge corrections with no changes in

Table 1. Fire frequency (yr) for study sites among four ecological landscapes of Wisconsin.

Site	No. samples	No. years with fires	MFRI (SD)	WMPI	Range	Time span
Inch Lake (IL)	34	53	11 (11)	9	3–47	1668–2017
Totagatic River (TR)	27	65	8 (6)	7	1–25	1699–2017
Frog Lake (FL)	14	24	9 (6)	9	3–16	1805–2017
Cathedral Point (CP)	24	24	10 (8)	8	2–21	1784–2017
Wolf Lane (WL)	16	23	6 (3)	6	3–16	1797–2017
Camp Bird (CB)	17	34	7 (3)	7	3–14	1731–2017
Bruce Mound (BM)	59	39	13 (11)	10	2–33	1660–2017
Wildcat Ridge (WR)	49	30	6 (4)	5	2–16	1712–2017

Notes: Fire frequencies include mean fire return interval (MFRI) plus standard deviation, MFRI (SD); Weibull distribution median probability interval (WMPI; Grissino-Mayer 2001).

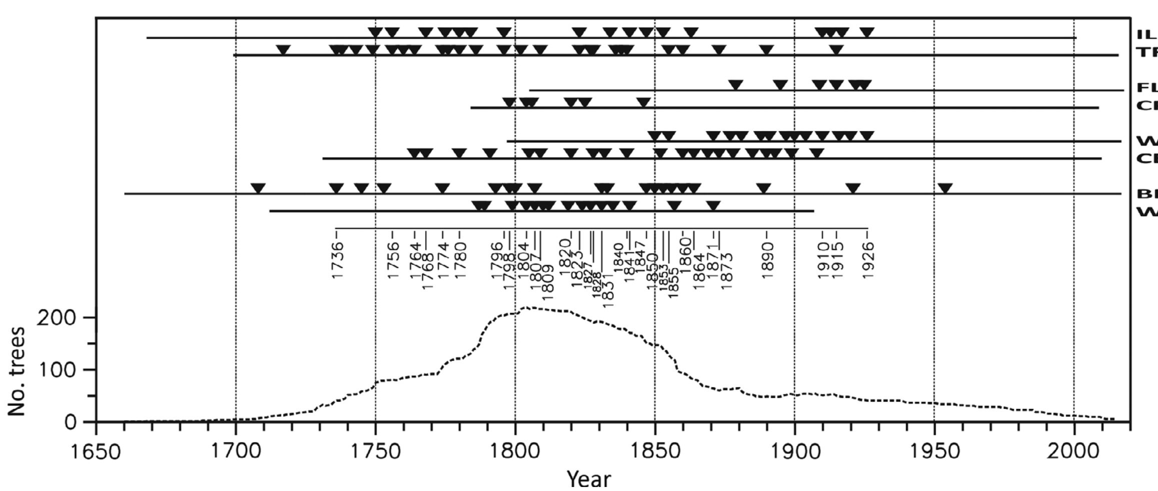

Fig. 2. Fire history across eight sites in Wisconsin. Horizontal lines represent composited fire histories for each site with fires filtered for those found on ≥2 trees within a site shown (mean fire return interval, MFRI 6–13). Composite fires (middle dates) are fires recorded in at least two sites and indicate more widespread fire events. Short composite MFRI's for the 29 most abundant fire years (MFRI = 7 yr) are in part a result of a shorter period of analysis (1736–1926) that excluded early and late periods with lower sample depth and subsequent longer fire return intervals. Site names are abbreviated (see Table 1 for full names) but ordered by ecological landscape and latitude (e.g., IL and TR are in the Northwest Sands).

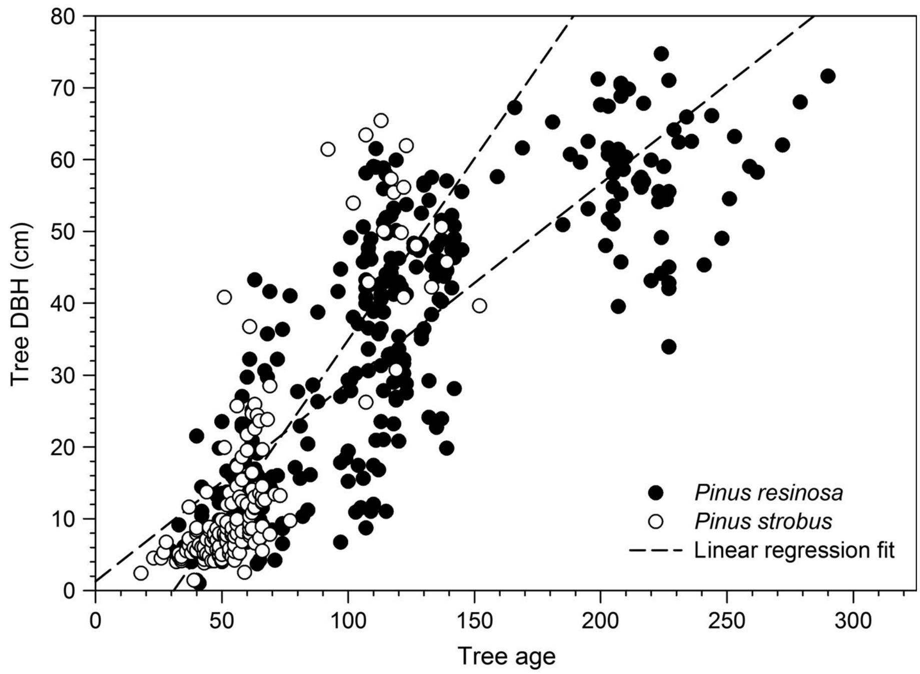

FIG. 3. Age and size relationship for all living red (*Pinus resinosa*, n = 336) and white pine (*P. strobus*, n = 152). Red pine were usually older than similarly sized white pine as is indicated by the steeper slope lines after approximately 70 yr of age. White pine post-dated our 1860 cut-off for pre-settlement trees (>157 yr old). Constraining comparisons to red pine <157 yr old changed regression line slopes, but relationships were similar with red pine older than similarly sized white pine after ~50 yr.

TABLE 2. Density estimates of historical (1860) and current (2017) red-pine-dominated forest in Wisconsin.

		Tree density (trees/ha)		
Site	Ecological landscape	Historical	Current	Current basal area (m^2)
Inch Lake	Northwest Sands	112	982	34
Totagatic River	Northwest Sands	172	1,828	39
Frog Lake	Northern Highlands	36	1,318	51
Cathedral Point	Northern Highlands	288	995	38
Wolf Lane	Northeast Sands	72	1,294	42
Camp Bird	Northeast Sands	140	833	40
Bruce Mound	Central Sands	112	1,032	51
Wildcat Ridge	Central Sands	256	995	31

significance. In all stands, aggregation indices (cdf) were significant for historical tree structure and in agreement with Ripley's $K(t)$ function though we did not detect clear patterns with levels of spatial aggregation. Frog Lake in the Northern Highlands Ecological Landscape, for example, had the highest degree of aggregation (lowest cdf value), while Cathedral Point, also in the Northern Highlands and most similar to Frog Lake, had the lowest degree of aggregation (Table 3).

DISCUSSION

Across the Lake States region, species diversity and structural complexity of forest systems have declined since pre-Euro-settlement with a trend toward forest homogenization (Olden and Poff 2003, Schulte et al. 2007). Our results support these trends with changes in species composition (Fig. 5), increases in stand densities (Table 2), and disparate spatial patterns (Table 3) in current forests relative to historical forests. Despite differences in forest density, stand and site characteristics, and geography across sites spanning >3° latitude, historical fire frequency was remarkably similar among sites with relatively short mean fire return intervals (MFRIs) ranging from 6 to 13 yr (Table 1, Fig. 6). Both our shortest (Wildcat Ridge) and longest (Bruce Mound) MFRIs were in the same Central Sands ecological landscape with similar physiology and site characteristics. Even among just our most widespread fire years that burned across multiple sites MFRI's were only 7 yr (Fig. 3).

TABLE 3. Spatial metrics for trees present in 1860 (0.5-ha plot) and for current forests in 2017 via four 200-m^2 subplots.

	Historical forest pattern (1860)					Current forest pattern (2017)		
Site	No. trees (0.5 ha)	$L(d) - d$ trends (0.5 ha)	DCLF GoF P	Aggregation index (cdf)	P	No. trees (subplots)	$L(d) - d$ trends (subplots)	DCLF GoF P
IL	58	A	0.001	0.545	0.001	79	R	0.075–0.950
TR	85	A	0.001	0.717	0.001	144	R	0.442–0.628
FL	18	A	0.001	0.444	0.005	106	1 A, 3 R	0.023–0.633
CP	144	A	0.001	0.950	0.190	78	R	0.278–0.837
WL	36	A	0.001	0.649	0.005	104	1 A, 3 R	0.005–0.731
CB	66	A	0.001	0.552	0.001	67	1 A, 3 R	0.009–0.436
BM	55	A	0.001	0.696	0.001	83	R	0.2537–0.803
WR	121	A	0.001	0.726	0.001	80	R	0.264–0.875

Notes: $L(d)$ is a linear transformation of Ripley's K-function where the expected K value is equal to Distance (d). $L(d) - d$ was interpreted as aggregated when exceeding the upper bounds of the 95% confidence envelope over some distance and also by the Diggle-Cressie-Loosmore-Ford (DCLF) goodness-of-fit test (GoF; Loosmore and Ford 2006). A is aggregated and R is random spatial tree patterns. Site names are abbreviated (see Table 1) but ordered by ecological landscape and latitude (e.g., IL and TR are in the Northwest Sands) consistent with all tables and figures.

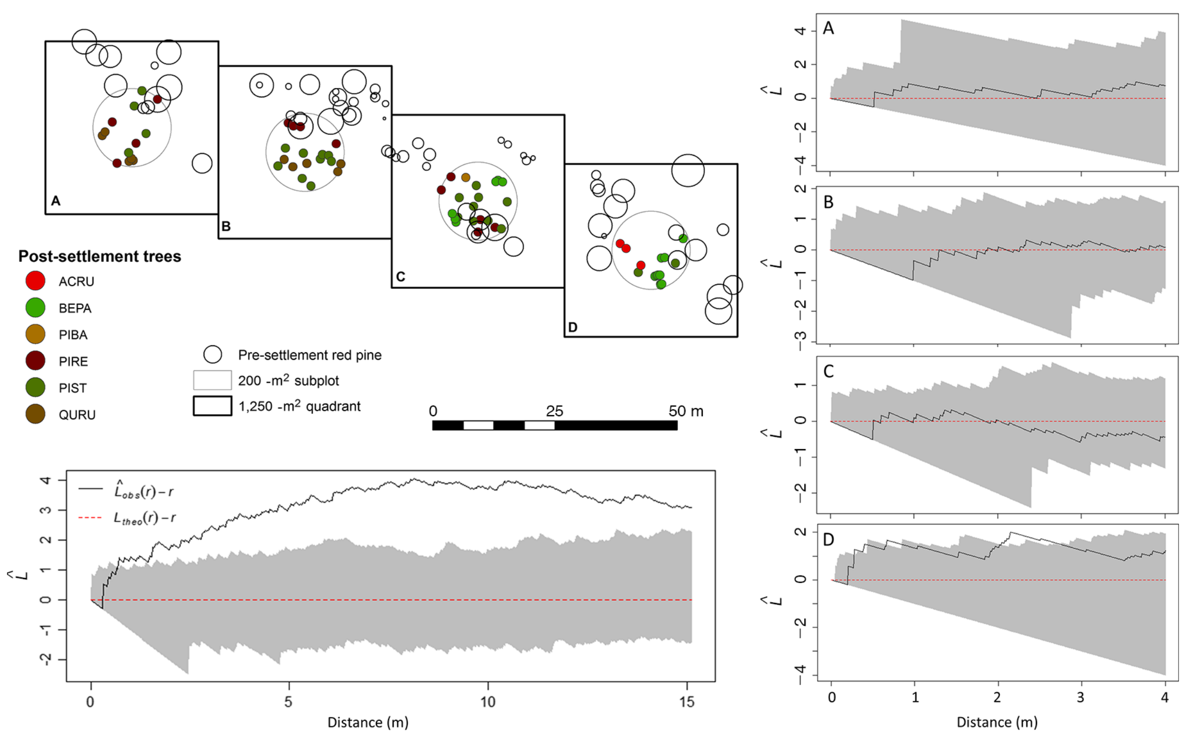

FIG. 4. Spatial arrangement of pre-Euro-settlement era (pre-1860) trees within the 0.5-ha Camp Bird plot and post-settlement trees within four 200-m^2 subplots (A–D) along with associated $L(d) - d$ graphs. $L(d) - d$ is plotted (solid black line) against the theoretical mean for complete spatial randomness (dashed red line) and 95% confidence interval envelope (shaded gray). $\hat{L}$ is an estimate of the square root transformed Ripley's K-function, $L(d)$, which linearizes and stabilizes its variance and is plotted against distance d. Tree point sizes are scaled by DBH. In all sites, pre-settlement trees were spatially aggregated, with all but one showing aggregation within 4 m. Three out of 32 subplots showed aggregated spatial arrangement of trees including subplot D in Camp Bird ($P = 0.009$). Post-settlement tree codes are Latin binomial symbols, the first two letters of the genus plus the first two letters of the specific epithet in accordance with USDA, NRCS (2018) PLANTS Database.

The short fire intervals we found cast doubt on widespread assumptions that fuels accumulate over time and result in higher disturbance probability with increasing forest age, which appears to be at best overly simplistic (Zylstra 2018) or more likely not applicable in the red-pine-dominated stands we evaluated. Similarly, there may be a tendency to view frequent fire (every 10–50 yr) as the driving force in creating savanna, as opposed to forest structural conditions (Heinselman 1996, Radeloff et al. 1999). Fire frequency is likely one of many interacting factors in stand development but alone cannot form the basis for classification of forest structural type.

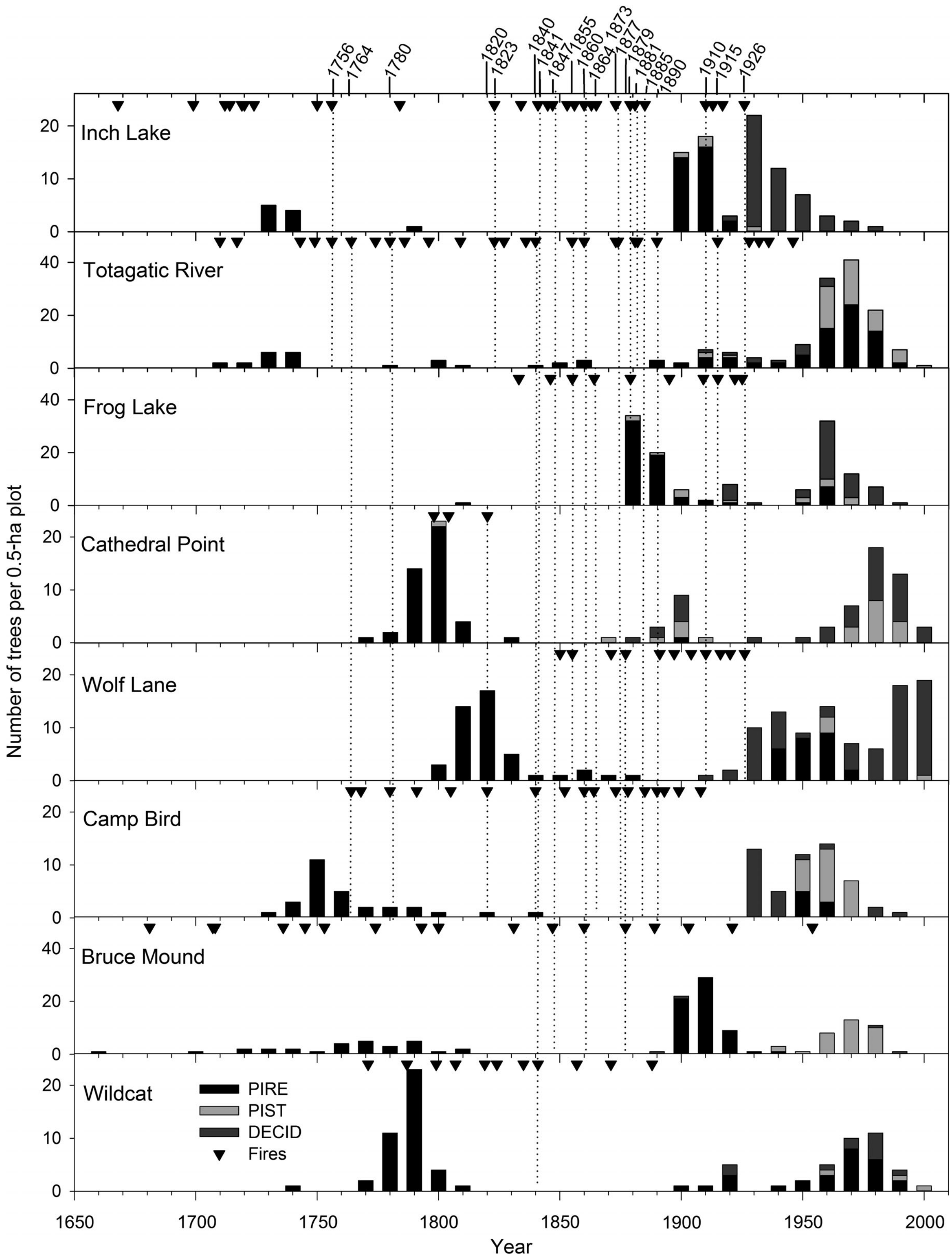

FIG. 5. Fire and 10-cm height pith dates for crossdated living and remnant (stumps, logs, snags) trees within plots arranged by latitude and ecological landscape. Pith dates illustrate recruitment for *P. resinosa* (PIRE), *P. strobus* (PIST), and lumped deciduous tree species (DECID). Fire dates by plot are for fires recorded on ≥25% of samples and dates and hashed lines are for synchronous fires across two or more sites.

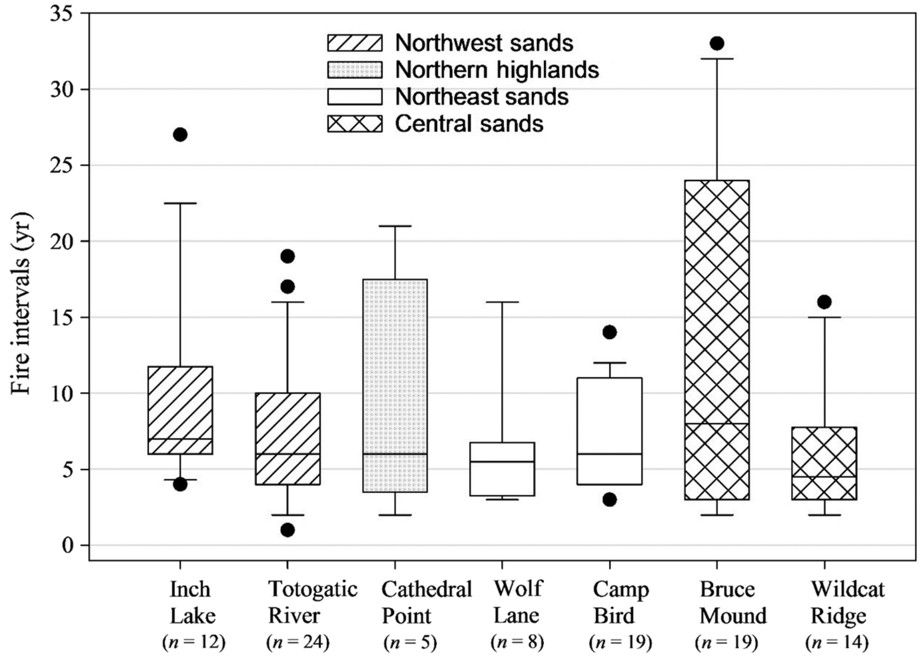

Fig. 6. Box and whisker plots of fire return intervals (1650–1900) for fires found on ≥2 trees (43% of all return intervals) within seven sites among four ecological landscapes. Lines of boxes represent median (middle) and the lower (25th) and upper (75th) quartiles, whiskers are the 10th and 90th quartiles, and circles are outliers. Longer upper quartiles (maximum values) likely represent longer fire intervals with the beginning of Euro-settlement fire exclusion. Sample sizes in parentheses (*x*-axis) are the number of pre-1900 fire intervals for each site. Note: We did not include Frog Lake (northern highlands) in this analysis as there were only two fires pre-1900.

Only two of our sites had low enough stem densities in 1860 to be considered savanna (Frog Lake, 36 trees/ha) or woodland (Wolf Lane, 72 trees/ha) and all sites had frequent fire regardless of density (Tables 1, 2). Stem densities we found were similar to dendrochronology reconstructions of historical overstory densities (51–246 trees/ha) in late 1800s western United States frequent fire landscapes (Fulé et al. 2002, Matonis et al. 2013). The Lake States region illustrates what Whittaker (1975) termed "ecosystems uncertain" in his ordination of global biomes based on precipitation and temperature (also Bond et al. 2005). This region is not at equilibrium with, nor limited by, climate and most areas could either be temperate grassland, savanna, woodland, or forest. It follows that conversion to dense woody vegetation occurs more rapidly in the absence of frequent fire in these systems than similar western frequent fire forests (Bond 2005) and is more difficult to reverse (Nowacki and Abrams 2008).

Our sites had a variety of red pine age structures, but not single cohort structure, which is how red pine forests are managed today (Gilmore and Palik 2006). Where cohorts were identifiable, they usually spanned ~30 yr of recruitment and multiple fire events (Fig. 5). Recruitment of red pine was limited by frequent, low-severity fires, but in no case eliminated by fire even with known large fire events like 1780 (Fig. 5, McMurry et al. 2007, Guyette et al. 2016). We acknowledge that our methods may have had size bias due to smaller stumps and other remnant wood deteriorating more quickly than larger remnant wood. Similar bias exists in the GLO data where survey instructions recommended that trees <5 inches diameter (12.7 cm) not be used (Bourdo 1956, Manies and Mladenoff 2000). However, we dated 18 remnant pieces of wood all ≤12.7 cm diameter (5.7–12.7 cm, $\mu = 9.3$ cm) at sample height that were established prior to 1860 suggesting that the legacy of even small diameter remnant wood can be persistent. Half of our sites were also unharvested stands where decomposition of stumps at least would not be a factor and stems <4 cm diameter within subplots were not included in current density estimates. Similarly, all sites were red pine-dominated stands where we did not encounter remnant white pine stumps; which, where they occur are usually evident though undatable.

Shifts in structure of an ecosystem are likely to cause substantial changes to its ecological function and resilience (Rodman 2015). Resilience of fire adapted communities is tenuous in the absence of fire and hysteresis, the failure of an ecosystem to return to its original state when fire is eventually restored as a process, is more likely in forests of the eastern United States (Beisner et al. 2003, Nowacki and Abrams 2008). The problem of how to manage for resilience in Lake States conifer forests is exacerbated by widely divergent views regarding natural disturbance regimes and resulting age structures in red pine-dominated stands in the region (Fraver and Palik 2012). Fire return intervals for red pine forests have been reported from 5 yr (Bergeron and Gagnon 1987) to more than 300 yr (Heinselman 1973). Similarly, views range from little role of wildfire at all in red pine (Bergman 1924), or fire regimes dominated by infrequent large stand-replacing events (Flannigan and Bergeron 1998, Frelich 2002), to red pine as one of the most fire-dependent species on Earth (Buckman et al. 2006).

Lacking detailed information on historic fire regimes in the Lake States transitional forests, we have relied on extrapolations from limited and widely scattered reference studies and/or interpretations of tree patterns with little understanding of biases and assumptions that follow (Hessburg et al. 2007). Transitional pine forest types in the Lake States are most commonly described as mixed-severity ecosystems where a combination of surface fires burned periodically (~40–50 yr) followed by stand-replacing fire (~150–300 yr). In practice, we tend to focus on replacement fires (and fire rotation intervals; Van Wagner 1978, Cleland et al. 2004) and the importance of intermediate or high severity wind events (Canham and Loucks 1984, Frelich and Lorimer 1991, Schulte and Mladenoff 2005, Rhemtulla et al. 2009). Surface fire is of secondary importance and thought to be limited to sandy outwash plains (e.g., Northwest and Northeast Sands in Wisconsin; Schulte and Mladenoff 2005). However, neither our fire history reconstructions nor the stand and spatial structure characteristics we measured supports this view.

In our sites, recruitment of red pine was limited, but not eliminated, by frequent fire (Fig. 5). In contrast, recruitment of all other tree species was primarily limited until after effective fire exclusion following the last widespread fire year in 1926, which helps explain the average 12-fold increase in current density in red pine forests and a nearly complete absence of natural regeneration of red pine (only 48 out of >3,300 seedlings recorded). Red pine trees generally showed a mix of age-classes and cohorts were often not well defined (Fig. 5). Where we found evidence approximating single cohort structure (e.g., Frog Lake and Cathedral Point) often stands were unharvested “old growth.” Individual stand histories certainly varied, but some of these stands (e.g., Frog Lake) were likely young at the time of cutover and therefore left standing. Currently, these same stands had relatively high basal areas made up primarily of large diameter trees and comprise much of the old growth in the region.

Quantitative description of tree spatial patterns offers insight into historical and environmental mechanisms influencing forest structure (Boyden et al. 2005, Sánchez Meador et al. 2010, Meunier et al. 2014). Recruitment in pines is often episodic (Millar et al. 2004, Brown and Wu 2005, Bunn et al. 2005). While climate must be favorable for seedling establishment and growth, conditions of stability and competition within stands often dictate recruitment success (Brenton 2012). White (1985) suggested that successful tree establishment in a frequent fire *P. ponderosa* system depended on “safe sites” where seedlings were missed by fires and could grow above lethal flame heights (Meunier et al. 2014). Spatially limited recruitment with frequent fire could lead to greater clumping of trees vs. spatially random or segregated patterns expected with coupled, episodic mortality and recruitment events associated with high intensity fires (Larson and Churchill 2012). Following high-severity fires, stand structure would likely be shaped primarily by climate and competition controls resulting in more uniform recruitment patterns. Historically, in the presence of frequent fires, trees were spatially aggregated and the opposite is true today, stands are almost entirely spatially random (Table 3, Fig. 4). Similarly, stands that had a longer frequent fire history usually had more complex age structures (Fig. 5).

The lack of variability in MFRI, ubiquitous and frequent low-severity fires, low density and spatially aggregated patterning, and variable cohort structure of historical transitional pine forests was remarkable and leads us to very different conclusions of historical disturbance processes than interpretations of historical tree patterns via the GLO notes that are so pervasive in this region. Our findings suggest density-independent regulation of tree populations was important, with establishment limited not by overstory density or mortality, but rather mortality of seedling and saplings with frequent fires as a primary forcing agent in these stands (Bond et al. 2005, Brown and Wu 2005). While the future may be very different from the past and historical disturbance regimes may not be appropriate targets for future management (Millar et al. 2007), understanding historical disturbance regimes is vital for building resilient ecosystems that can accommodate an uncertain future (Landres et al. 1999).

Reduction of compositional and structural diversity of forests is a global issue and evidence that fire created heterogeneity is critical for maintaining species diversity and ecosystem resilience (Binkley et al. 2007). This study indicates that much of the forest heterogeneity that helps maintain ecosystem resilience historically came from stand scale forest resistance in fire adapted pine forest of the Lake States. This should be the starting place for learning how to maintain ecosystem resilience in transitional pine forests, rather than an afterthought tied to 50 years of interpretations of tree patterns.

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