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REVIEW

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Using witness trees as pyro-indicators to depict past fire environments across the eastern United States

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Abstract

Understanding past fire environments is vitally important for applying silvicultural treatments, which often include prescribed burning to restore fire-dependent ecosystems. We have developed a novel method by which witness trees can be used as pyro-indicators to map past fire environments. The stepwise process first involves partitioning witness trees into two classes, pyrophobic and pyrophilic, based on their known ecophysiological traits. Pyrophilic percentages are then calculated at survey corners by dividing the number of pyrophilic trees by the total number of trees. Next, statistical spatial interpolation is applied to this point-based data set to produce a continuous response surface of pyrophilic percentages. The resultant maps capture gradients of fire importance across the pre-European-settlement landscape, which can be coupled with historic fire regime maps, thus providing additional information for better understanding and explaining past fire environments. We have applied this technique to various available witness-tree databases across the eastern United States. This paper serves as a compendium of our collective work to date.

Keywords Historic fire regimes, Ecophysiological traits, Tension zone line, Ecological mapping and classification

Resumen

El entender los ambientes de fuego pasados es de vital importancia para aplicar tratamientos silviculturales, los que frecuentemente incluyen quemas prescriptas para restaurar ecosistemas fuego-dependientes. Desarrollamos un método novedoso por el cual árboles testigo pueden ser usados como piro-indicadores para mapear ambientes de fuegos pasados. El proceso paso a paso implica primeramente el particionar árboles testigo en dos clases, pirófobos y pirófilos, basados en sus características ecofisiológicas conocidas. Los porcentajes de pirófilos son entonces calculados mediante relevamientos en rincones, dividiendo el número de árboles pirófilos por el número total de árboles. Luego, una interpolación estadística espacial es aplicada a este conjunto de puntos de bases de datos para producir una respuesta superficial continua de los porcentajes de pirófilos. Los mapas resultantes capturan gradientes de importancia del fuego a través de paisajes previos a la colonización europea, lo cual puede ser acoplado con mapas de fuego históricos, proveyendo de esta manera de información adicional para entender y explicar mejor ambientes de fuego pasados. Hemos aplicado esta técnica a varias bases de datos disponibles de árboles testigo a lo largo del este de los EEUU. Este trabajo sirve como un compendio de nuestro trabajo colectivo hasta el presente.

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Introduction

Many types of information and analytical techniques exist to reconstruct past ecological conditions (Whitney 1994). One of the most extensively used and informative data sets comes from witness or bearing trees——trees marked and scribed to identify survey corners (Bourdo 1956; Manies and Mladenoff 2000). In areas where the metes-and-bounds system of land measurement was used (e.g., original 13 colonies), witness trees were often comprised of single trees at corners of irregularly configured properties. As the United States expanded, the Land Ordinance of 1785 was initiated by the US Public Land Survey for lands west of Pennsylvania, known at the time as the Northwest Territory (Whitney and DeCant 2001). Based on the Rectangular Survey System, this systematic survey gathered a more robust set of data, including tree-to-corner distance and direction and tree diameter. Moreover, qualitative field notes were taken along survey lines, including vegetation types encountered with prominent tree species, surface features (upland vs. wetland, hilly vs. flat, etc.), and recent disturbances from windstorms or fire also recorded.

Given the enormity of work needed to transcribe and interpret hardcopy data, early studies of witness trees understandably focused on reconstructing tree composition (Sears 1921; Lutz 1930). By connecting quantitative witness-tree data to qualitative field notes taken along transects, investigators were able to derive forest stand maps (Sears 1925; Kenoyer 1929, 1933, 1939, 1942) or prairie locations (Sears 1926; Wackerman 1929). In some cases, pre-Euro-settlement vegetation maps were produced for entire states (Marschner 1930; Finley 1951; Potzger et al. 1956). By overlaying these products on existing soil and geologic maps, the relationships between vegetation and edaphic factors could be readily discerned (Crankshaw et al. 1965; Lindsey et al. 1965; Whitney 1986). Furthermore, the confounding and sometimes overriding impacts of Native American land use were also identified through witness-tree analysis (Dorney 1981; Dorney and Dorney 1989).

The advent of Geographic Information Systems (GIS) and associated geospatial analytics greatly streamlined and accelerated the processing of witness-tree data. By applying these new technologies, more nuanced characteristics such as forest stand structure and disturbance regimes could be projected over large areas using US Public Land Survey data. For instance, for the first time, pre-Euro-settlement forests, savannas, and prairies could be empirically classified and mapped by averaging tree-to-corner distances to calculate local tree densities (Leitner et al. 1991, Bolliger et al. 2004). By coupling quantitative witness-tree data with qualitative surveyor line notes, reductions in tree density and estimates of disturbance severity due to past wind and fire events could be established (Schulte and Mladenoff 2005).

In this review, we summarize the results of our novel method by which witness trees can be used as pyro-indicators to map past fire environments. Our work reflects a continuance of these new and inventive ways to extract the most out of witness-tree data——in this case, their use for documenting pre-Euro-settlement fire settings or importance across landscapes. The objective of this review is to display, describe, and discuss the results of these analyses that share a common methodology to amplify their possible impact at a regional scale.

Methods

From witness trees to pyrophilic percentages

Because this review article includes published analyses of individual datasets that varied in scale, extent, and survey methods, a generalized methods description is difficult to convey briefly. For detailed information please consult the original published works. Table 1 includes summary descriptive data for each study including (1) study area size, (2) survey type, (3) number of witness trees, (4) number of tree species/genera by fire-adaptation class, and (5) the original citation for the work. This review paper is organized by study areas and centered on the original analysis of witness trees used as pyro-indictors.

The first area where witness trees were used to infer fire history was the Monongahela National Forest in east-central West Virginia (Thomas-Van Gundy and Nowacki 2013). This work is based on deeds and land grants under the metes-and-bounds survey system common in the thirteen original colonies. The simple, stepwise procedure was applied as follows: (1) develop a geospatial database of witness-tree locations, (2) categorize witness trees as either pyrophiles or pyrophobes based on their ecophysiological traits (e.g., sprouting ability, bark thickness, fallen-leaf characteristics, successional status as related to disturbance, etc.), (3) calculate a pyrophilic percentage at each survey corner by dividing the number of pyrophilic trees by the total number of trees, and (4) run ordinary kriging on this point data to create a continuous response surface of pyrophilic percentages.

In West Virginia, a geospatial database of approximately 22,000 witness trees of 49 species, from the earliest deeds (1752–1899) was used for this analysis (Thomas-Van Gundy and Strager 2012). Much of the fire ecology information by species came from the Fire

Table 1 Summary information for the six studies included in this review

Study area	Area (ha)	Survey type	Number of witness trees/towns	Number of species/genera		Citation
				Pyrophilic	Pryophobic	
Monongahela National Forest	710,000	Meets-and-bounds	~22,000	19	30	Thomas-Van Gundy and Nowacki. 2013
Allegheny National Forest	671,843[a]	Rectangular	3003	16	29	Thomas-Van Gundy, Nowacki and Cogbill. 2015
Finger Lakes National Forest	112,146[a]	Rectangular	585	16	29	Thomas-Van Gundy, Nowacki and Cogbill. 2015
Green Mountain National Forest	734,003[a]	Proprietary towns	1007	16	29	Thomas-Van Gundy, Nowacki and Cogbill. 2015
White Mountain National Forest	1,181,553[a]	Proprietary towns	748	16	29	Thomas-Van Gundy, Nowacki and Cogbill. 2015
Northeastern United States	41,485,135[a]	Public land surveys, rectangular surveys, and deeds	701	16	29	Thomas-Van Gundy, Nowacki and Cogbill. 2015
Minnesota, two forested ecological domains	~15,309,058	Public land survey	354,836	16	36	Thomas-Van Gundy and Nowacki 2016
Wayne National Forest	34,622	Public land survey	5534	12	19	Nowacki et al. 2020
Southern Lake Michigan	2,254,616	Public land survey	28,082[b]	26	41	Thomas-Van Gundy et al. 2020
Southwestern Illinois	504,110	Public land survey	9807[b]	26	41	Thomas-Van Gundy et al. 2020
Southern Illinois	537,063	Public land survey	4976[b]	26	41	Thomas-Van Gundy et al. 2020
Minnesota and Wisconsin	34,648,861	Public land surveys	7376[c]	7	21	Nowacki and Thomas-Van Gundy 2022

[a] Area of interpolated surfaces, the square extent of the witness tree points used as input to kriging, minus larger lakes

[b] Number of points with up to four trees listed at a point

[c] Number of 8 × 8-km grids summarized and standardized by Goring et al. (2015)

Effects Information System (https://www.feis-crs.org/feis/). Most corners were represented by 1 or 2 trees, ranging up to 6 trees. For the interpolation, a minimum of two and a maximum of five neighboring points was used in the moving window to estimate pyrophilic percentages. Pyrophilic percentages were classed into 10-percentage bins to create the final color-coded map (Fig. 1). The techniques used here formed the basis for the methods used in subsequent study areas. To investigate possible environmental drivers of the distribution of pyrophilic and pyrophobic witness trees, a 500-m point grid was used to sample pyrophilic percentage from the interpolated surface and extract climate and topographic variables. Linear regression was used to investigate trends with pyrophilic percentage as the response variable and nine climate and topographic variables as predictor variables. Climate variables included mean annual temperature, growing degree days, number of frost days, mean annual precipitation, and growing season precipitation minus evapotranspiration all from PRISM climate normals. Topographic variables were derived from a digital elevation model and included elevation, slope, aspect, and topographic roughness.

To describe the importance of historic fire on national forests of the northeastern United States, we analyzed witness tree datasets based on grid surveys (pre-Public Land Survey) for the Allegheny and Finger Lakes National Forests, and the proprietary towns system for the Green Mountain and White Mountain National Forests (Thomas-Van Gundy et al. 2015). For a regional-scale view of trends in species composition, we used a dataset of 701 proprietary towns covering parts of many states in New England and Pennsylvania. As described in the methods for the Monongahela National Forest work, species and genera were grouped by their tolerance to a long-term regime of recurring surface fire. For the datasets specific to national forests, only one tree was recorded at each point resulting in designations of either 0 or 100% pyrophilic. For the region-wide dataset, the relative abundances for each genus or species were calculated and the fire-adapted categorization applied. Ordinary kriging was used to interpolate this percentage between points. In all interpolations, a maximum of five and a minimum of two neighboring points were used for calculations. In this analysis, we estimated the user resolution for the interpolated products by calculating

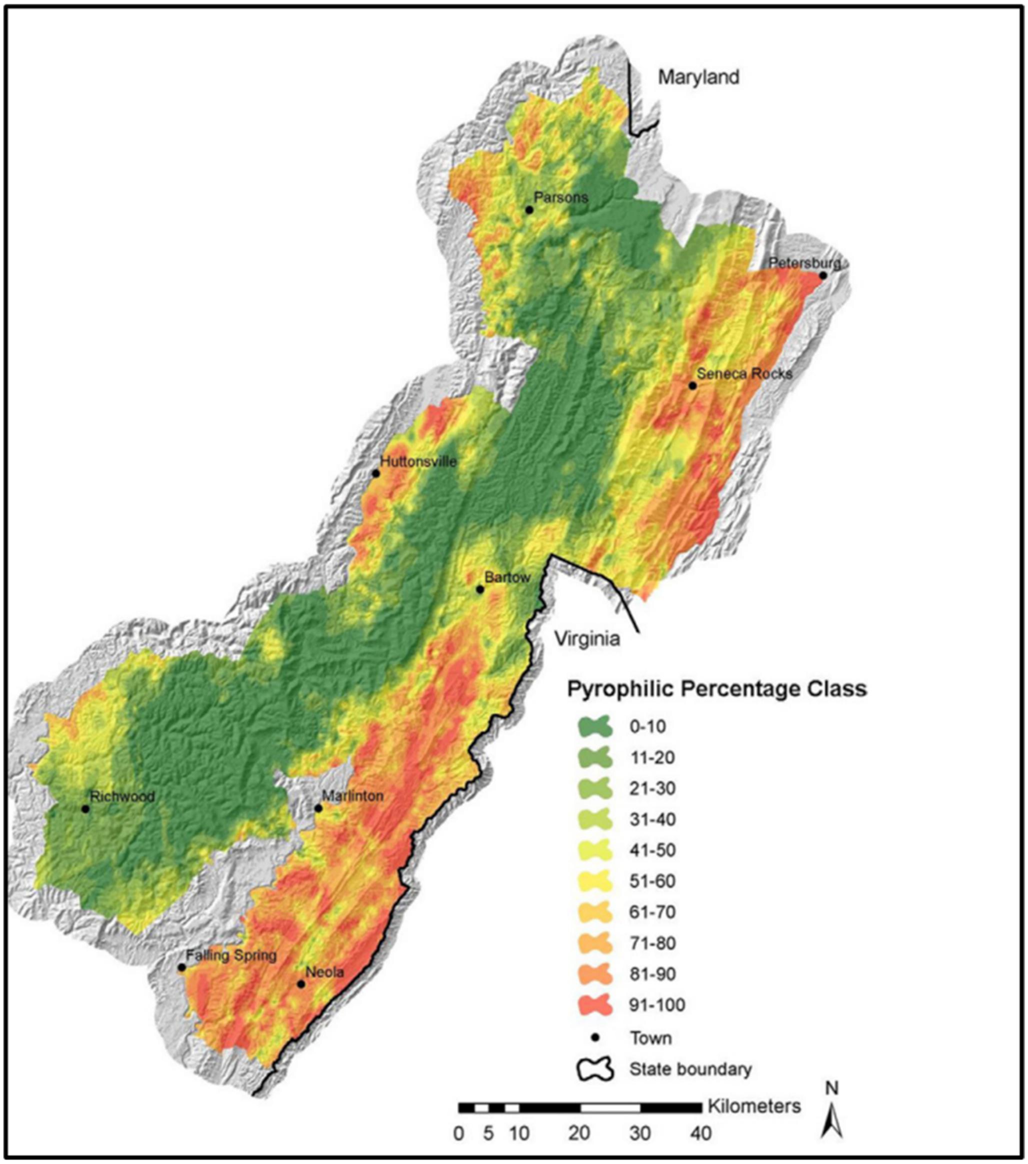

Fig. 1 A spatial depiction of the witness-tree-based pyrophilic percentage across east-central West Virginia based on ordinary kriging (Fig. 3 in Thomas-Van Gundy and Nowacki 2013). Categories have been color coded to reflect a gradient from low pyrophilic percentages (witness trees predominately pyrophobic; green) to high pyrophilic percentages (trees predominately pyrophilic; red)

nearest neighbor distances between pairs of observations and squaring the average distance. Known Native American settlements were mapped and buffered by simple 5 and 10 km circles to assess any relationships between Native American settlements and pyrophilic percentage. Mean pyrophilic percentages were calculated for the area within and outside the distance ranges using the interpolated data for individual national forests. The area in lakes was removed from these totals and a generalized linear model (beta distribution, logit link function, and least significant means for comparisons) was used to compare pyrophilic percentages within and beyond the set distances.

We used the Minnesota Bearing Tree Database (Almendinger 1996), assigning tree species or genus noted in the survey to either the pyrophilic or pyrophobic class based on published information of fire-adapted traits, to explore fire importance in ecological subsections in Minnesota (Thomas-Van Gundy and Nowacki 2016). In this dataset, coincident points were used to track trees at corners rather than listing multiple trees per point, creating an initial dataset of points as either

0 or 100% pyrophilic. To calculate a pyrophilic percentage from the coincident points, we used an 805-m grid to sample and summarize the points and tree species. From that grid, we used ordinary kriging to interpolate and smooth the data. The semivariogram model was optimized through the Geostatistical Analyst extension in Arc Map 10 and a minimum of five and a maximum of 50 neighboring grid cells were used to create the final interpolation. In this analysis, simple summary tables and frequency distributions were developed for ecological units at four spatial scales. The proportion of area in the pyrophilic percentage class (10-percent classes) was plotted and the median pyrophilic percentage calculated for each ecological unit to describe the general fire setting for the ecological unit. For example, landscapes with a median pyrophilic percentage of 33% or less and a positively skewed distribution were considered landscapes with a pyrophobic fire setting. Only the landtype associations encompassing the Chippewa and Superior National Forests were included in this part of the analysis.

For input to the forest plan revision efforts on the Wayne National Forest in southeastern Ohio we used a published dataset of witness trees from Public Land Surveys (Dyer and Hutchinson 2019) to depict fire importance (Nowacki et al. 2020). The methods used were very similar to those for the West Virginia study area with ordinary kriging used on pyrophilic percentage calculated at corner at point locations.

For three areas in Illinois and Indiana, existing georeferenced bearing tree data sets were used to describe fire importance within and on the edge of the historic prairie peninsula (Thomas-Van Gundy et al. 2020). Species and genera listed in these datasets were again characterized as either pyrophilic or pyrophobic and the pyrophilic percentage at each point calculated. If prairie was listed in the tree name column or as a vegetation type, that point was coded as 100% pyrophilic; all other points with no trees listed were coded as 100% pyrophobic. Ordinary kriging was used to interpolate pyrophilic percentage between points. We used the optimized model setting which attempts to minimize the root mean square error and chose a stable model with no anisotropy. A maximum of five neighboring points and a minimum of two points were used for averaging. The interpolated areas were then used to create new point data for statistical analysis. These new points were used as sample locations for obtaining topographic, climate, and soil data. Regression analysis was used to explore relationships between pyrophilic percentage and heat load index, percent slope, aspect (transformed), distance to water, drainage class, available water storage, summer potential evapotranspiration, mean growing season temperature, mean growing season precipitation, soil particle size, and elevation in separate regression models for the three study areas.

The Midwestern Tension Zone is a well-known ecological feature used to describe the ecology of midwestern forests. To explore the possible role of historic fire on the depiction of the tension zone (Nowacki and Thomas-Van Gundy 2022), we used an aggregated witness-tree dataset for Wisconsin and Minnesota (Goring et al. 2015). In this dataset, trees were identified only to genus to reduce error between common names and the large number of surveyors involved. As before, genera were categorized as either pyrophilic or pyrophobic. Three genera were difficult to classify, possessing species with both pyrophobic and pyrophilic tendencies: birch (*Betula*), spruce (*Picea*), and tamarack (*Larix*). Since pyrophilic paper birch (*Betula papyrifera*) was distributed across a greater portion of the study area compared to yellow birch (*Betula alleghaniensis*), we designated birch as pyrophilic. Since spruce is often set back by fire, it was designated pyrophobic. Since tamarack is often relegated to wetlands, it was designated pyrophobic. A pyrophilic percentage was calculated for each 8 × 8-km grid cell. No interpolation was made on the grid data and contour lines for the mean pyrophilic percentages were created through Spatial Analyst in ArcMap. The pyro-based tension zone was defined as the 50% pyrophilic percentage contour line. Tree genera were also classified by their adaptations to temperature regimes (Nowacki and Abrams 2015). The percentage of stems classed as cold or cool was calculated and the 50% cold-cool percentage contour used as a temperature-based tension zone.

Results and discussion

The West Virginian origins of pyrophilic percentage

The pyrophilic percentage method was conceived and first administered to a metes-and-bounds database in eastern West Virginia, centered on the Monongahela National Forest (Thomas-Van Gundy and Nowacki 2013). In this study area, very few direct measures of fire history, such as fire scared trees and charcoal preserved in lake sediments, are available necessitating inferred methods like this analysis of witness trees. The resultant map spatially depicts the pre-Euro-settlement fire environment as derived from and reflected in witness-tree ecophysiology and fire relations that have developed over a long-term regime of recurrent surface or periodic canopy fire.

Through this analysis, we found that gradients of pyrophilic percentage corresponded closely with elevation and vegetation zonation. Our output map (Fig. 1) showed fire grading from high importance at low elevations to low importance at high elevations. An orographic effect is clearly embedded in the dataset and landscape, with increased fire within a prominent rain shadow (i.e., Ridge and Valley Province) east of the rain-soaked Appalachian Highlands. The spatial arrangement of pyrophilic percentages essentially matches that of climate, increasing with temperature, growing season length, and water deficit and decreasing with precipitation and frost days. Since climate is inherently correlated with elevation (Nowacki and Wendt 2010), a complex gradient of fire-vegetation-elevation-climate exists, a feature common to mountainous regions (Whittaker 1967). Subsequent analyses have found positive associations of pyrophilic percentage to bison trail occurrence (a species which preferred open woodland habitats for grazing; Thomas-Van Gundy et al. 2021) and legacy seed banks of fire-adapted ground flora (Huebner et al. 2023).

The pyrophilic percentage maps do not connote past fire frequencies or severities per se, but the importance of fire as a driving force affecting past forest compositions. In this way, it differs from conventional fire regime maps based on vegetation such as the fire regime map product available through LANDFIRE (https://landfire.gov) or one based on chemistry and climate (Guyette et al. 2012). To help bridge this gap, Thomas-Van Gundy (2014) converted our pyrophilic percentage map to a fire regime map for comparison with a LANDFIRE-based product. Although it is impossible to know which map depicts pre-European settlement fire regimes better, there was a great deal of similarity between the two with a 61% spatial match. The high degree of correspondence between these two independently developed maps does help validate our method. It is important to point out that pyrophilic percentage maps represent a unique, tree-based way of capturing past fire influences on landscapes, displaying gradients of fire importance to be coupled with other, more conventional methods (e.g., fire regime maps) to help direct prescribed burning for ecosystems requiring fire for timber management and restoration purposes.

This approach, converting witness trees into spatial displays of pyrogenic percentages, has been recognized as an emerging way to assess how disturbance, specifically fire, impacts the ecological and evolutionary dynamics of plant communities (Napier and Chipman 2021). Moreover, its relevance to land management has been recognized, helping direct prescribed burning efforts to restore oak (*Quercus*) and oak-pine (*Quercus-Pinus*) ecosystems or regenerate these genera for timber management purposes on appropriate sites (Arthur et al. 2021). To date, this manuscript serves as a common reference to classify trees into functional groups based on their fire-adapted traits (pyrophilic or pyrophobic) to assess past Native American impacts (Fulton and Yansa 2020; Tulowiecki et al. 2022) and vegetation changes overtime (Hale and Peterson 2024, Keyser et al. 2017, 2019; Thomas-Van Gundy and Morin 2021; Waters and Weand 2023).

Concept expansion to the northeastern United States

We extended pyrophilic percentage mapping to the northeastern United States to further test and broaden its applicability over a large, biologically diverse area (Thomas-Van Gundy et al. 2015; spatial data available Thomas-Van Gundy et al. 2022). Witness-tree point data were specifically used to create pyrophilic percentage maps for four National Forests: White Mountain (New Hampshire, Maine), Green Mountain (Vermont), Finger Lakes (New York), and Allegheny (Pennsylvania) (Fig. 2). Since these National Forests are located within the conifer-northern hardwood biome (AKA Warm Continental Division; Bailey 2014), historical fire occurrence was limited by the overriding cool, moist, and snowy climate. However, localized areas of higher pyrophilic percentage did occur, often near large lakes and rivers, which parallels Native American preferences for settlement, transportation, and fishing. By superimposing known Native American villages on the National Forest set of maps (represented by stars in Fig. 2), we were able to show increased fire around locales where Native American activities were most prevalent in this otherwise cool and moist forest colloquially known as an "asbestos" forest. It is not surprising, given the prevailing cool and wet climate with short growing seasons and burn windows, that Native Americans were the primary ignition source (Abrams and Nowacki 2008, 2021) and that their land-use over millennia had a major impact of vegetation communities (Tulowiecki and Larsen 2015). Moreover, the effect of the prevailing westerlies on indigenous ignitions, thus promoting landscape-scale burns, is clearly seen on our maps, particularly on the lee (east) sides of Seneca Lake (cf. the west side of neighboring Cayuga Lake; Fig. 2a) and the Allegheny River (Fig. 2c).

An overarching regional pyrophilic percentage map was also produced using town-level summarizations of witness-tree data (Fig. 3) (Thompson et al. 2013). Here across New England states lies a tension zone where conifer-northern hardwoods interface with warmer oak-pine systems to the south (Cogbill 2000; Cogbill et al. 2002). Using a breakpoint at 50% of our interpolated pyrophilic percentage, this tension zone is clearly captured by pyrophilic percentage, further emphasizing how important fire was as a driver of southern oak-pine ecosystems vs. its limited and localized effect on northern hardwood ecosystems. Considered together, the production of maps at multiple scales will help land managers, conservationists, and researchers understand local pre-Euro-settlement fire regimes and their context within

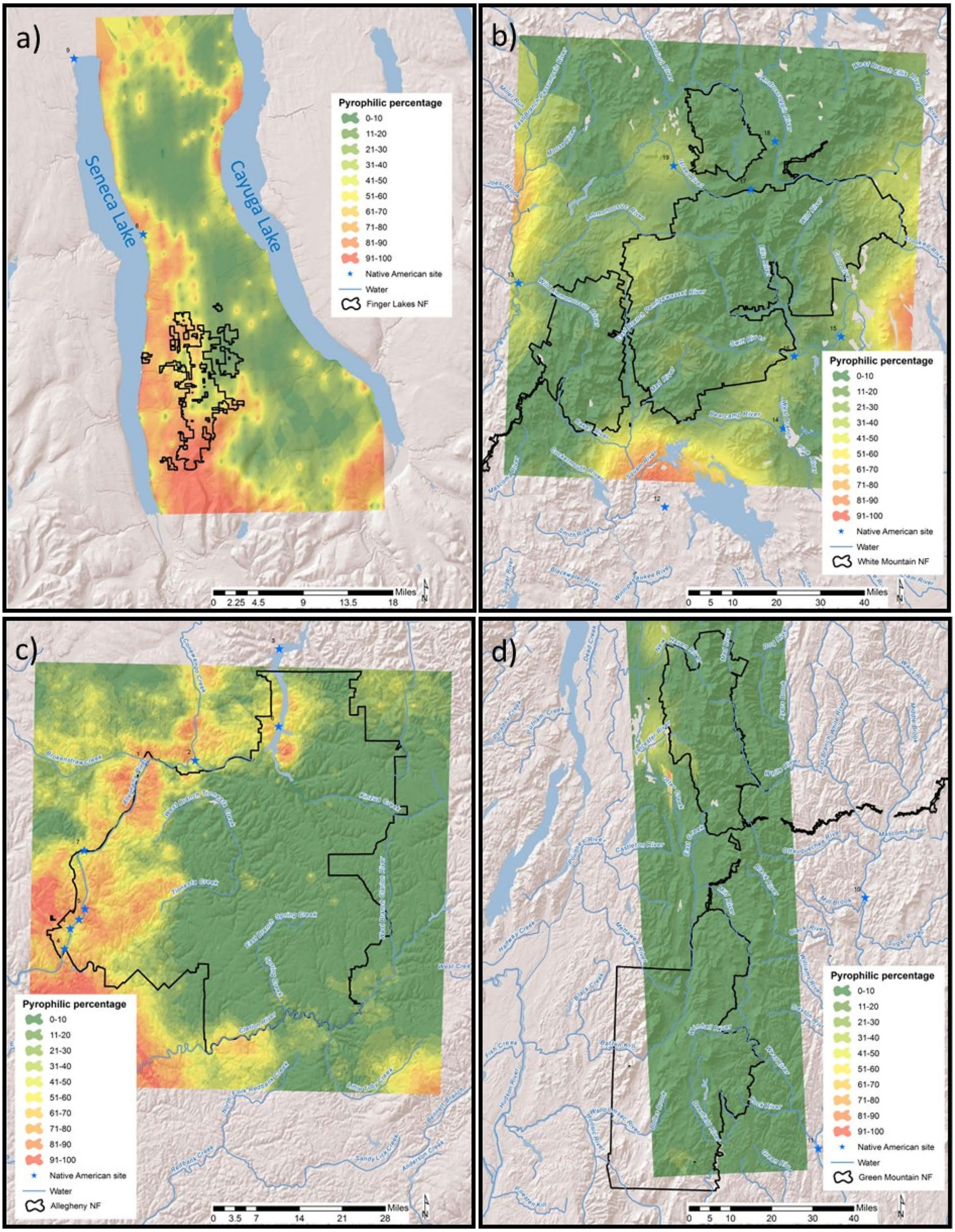

Fig. 2 Pyrophilic percentage interpolated from witness trees on the **a** Finger Lakes National Forest, **b** White Mountain National Forest, **c** Allegheny National Forest, and **d** Green Mountain National Forest (Figs. 6–9 in Thomas-Van Gundy et al. 2015)

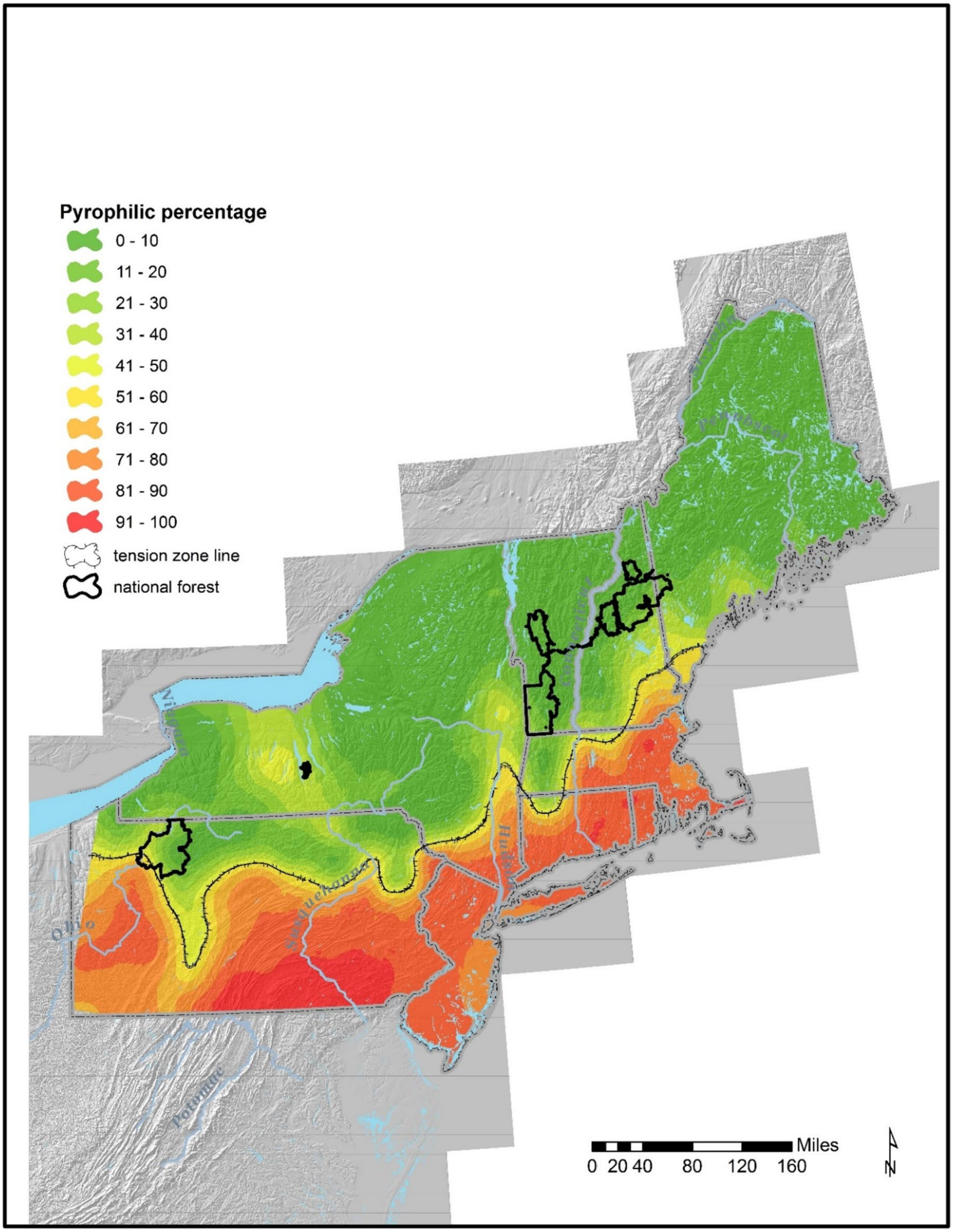

Fig. 3 Pyrophilic percentage as interpolated from town-level witness trees from 701 towns across the northeastern United States. Tension zone line is depicted by the 50 percent pyrophilic contour (Fig. 10 in Thomas-Van Gundy et al. 2015)

a larger regional perspective. Our classification defining pyrophilic and pyrophobic trees has been used to assess human-fire dynamics on vegetation change (Kujawa et al. 2016; Brugam et al. 2016; Fulton and Yansa 2019).

Pyrophilic percentage along the western edge of the eastern deciduous forest

Minnesota represented an interesting test case to map pyrophilic percentage as it encompasses an intermixing of biomes, namely boreal systems in the north, temperate conifer-northern hardwoods in the east, oak-dominated Central Hardwoods in the south, abutting the grasslands of the Great Plains to the west. Each of these biomes embodied unique fire histories in their development and maintenance. To capture this convergence of disparate ecosystems, we used the National Hierarchical Framework of Ecological Units (Cleland et al. 1997) to evaluate pyrophilic percentage at four spatial scales (province, section, subsection, and landtype association). Histograms showing the proportion of area in each pyrophilic percentage class (10-percent classes) were used to categorize the general fire setting of each ecological unit (Thomas-Van Gundy and Nowacki 2016; spatial data available Thomas-Van Gundy and Nowacki 2021). We used this simple, yet unique method to examine ecological units against our pyrophilic percentage maps, noting irregularities and suggesting line improvements based on the prevailing fire setting before European settlement. Our resultant maps and analyses for Minnesota (Fig. 4a), the Superior National Forest (Fig. 4b), and the Chippewa National Forest (Fig. 4c) provided a strong ecological basis for locating areas where long-term burning left an indelible mark on plant composition, structure, and biodiversity and thus where prescribed burning for ecosystem restoration is most appropriate today. Through this analysis, we recommended that the formative role in which fire played in the development and expression of vegetation be a delineation factor in ecological mapping, additive to other factors at various spatial scales. This work helped reinforce the notion that historic fire

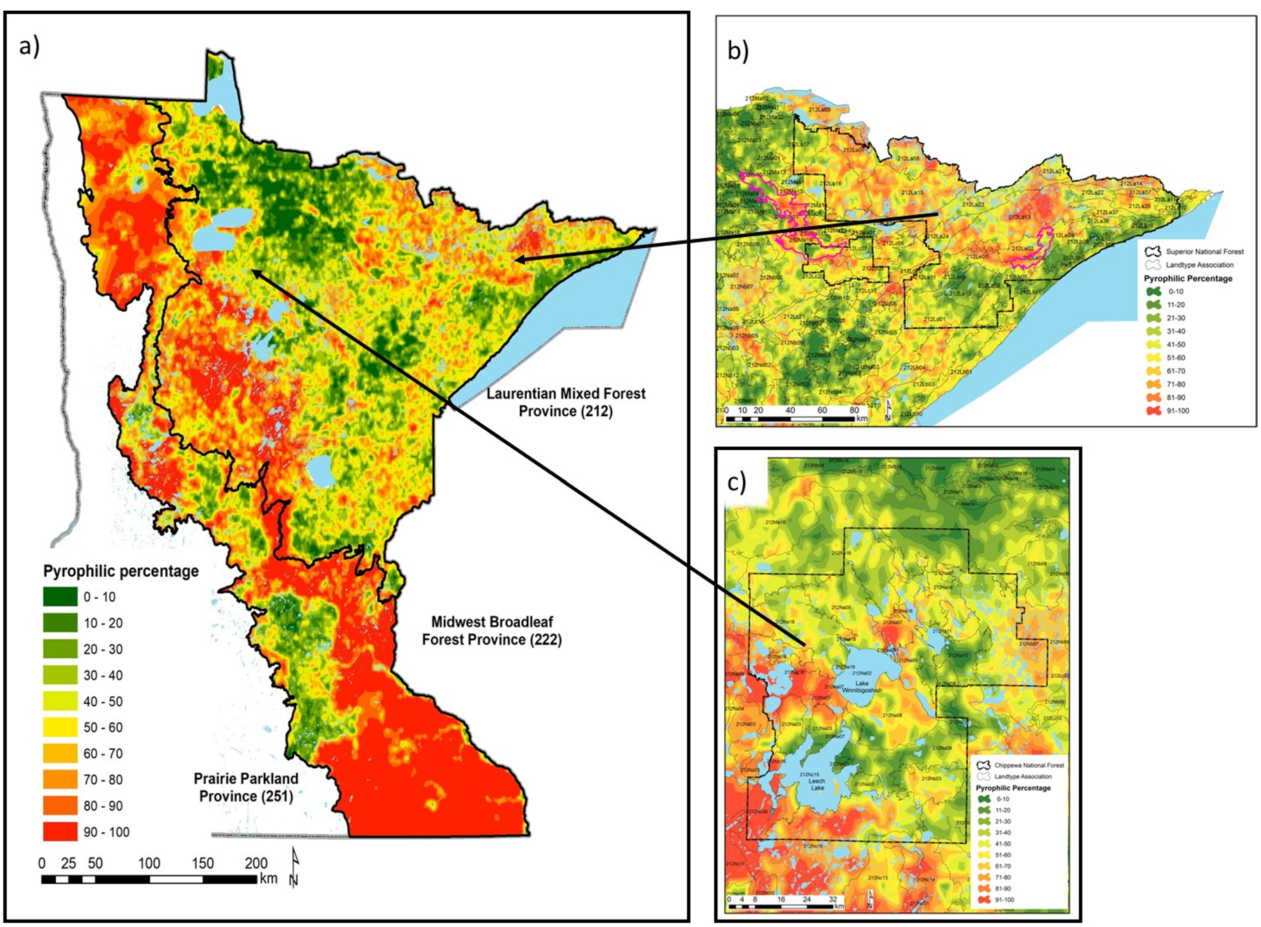

Fig. 4 Pyrophilic percentage maps covering **a** Minnesota with two forest-dominated provinces and prominent landscape features outlined, **b** the Superior National Forest with landtype associations, and **c** the Chippewa National Forest with landtype associations (Figs. 3, 13, and 19 in Thomas-Van Gundy and Nowacki 2016)

was a primary factor in shaping the southern boreal forest ecosystem (Apfelbaum et al. 2017). Moreover, our pyrogenicity classification was employed to quantify the importance of Native American ignitions on past ecosystems (Fern et al. 2020).

Pyrophilic percentage application in land management planning

A Terrestrial Ecosystems Assessment was written for the Wayne National Forest in in southeastern Ohio in preparation of its upcoming Land Management Plan revision (Nowacki et al. 2020). As part of this assessment, a pyrophilic percentage map was created to supplement our understandings of historical fire and its impact of vegetation composition, structure, and successional dynamics (Fig. 5). Based on our output, historic burning was ubiquitous across the Wayne National Forest. The lack of spatial variation displayed in our map was due, in part, to the combined dominance of oak, hickory (*Carya*), and other pyrophilic trees across the landscape, the strong spatial autocorrelation of fire (i.e., areas adjacent to active fire have a high probability of burning as well), and that our analysis was restricted to the national forest, greater variability would be seen across the entire state. This knowledge is exceedingly important as the Wayne National Forest is experiencing tremendous shifts in structure and composition from historically open oak woodlands to closed-canopied forests comprised of shade-tolerant mesophytic competitors (primarily beech (*Fagus*) and maple (*Acer*); Palus et al. 2018) in the absence of fire——a trend affecting most fire-dependent systems throughout the eastern United States (Nowacki and Abrams 2008). The criticality of active management to restore and maintain the oak resource on the landscape is evident, yet apparently lost in messaging with our publics (Radcliffe et al. 2021). Based on ecological theory, maximum biodiversity can be best achieved by emulating the historic disturbance regime (Engstrom et al. 1999; Long 2009), which for oak-dominated Central Hardwoods was recurrent surface burning (Zenner 2016).

One of the best ways to cope with future climate change is to restore the fundamental processes inherent to oak ecosystems that bolster species richness and biodiversity (Iverson et al. 2019; Johnson et al. 2023; Harty 2023). Given the poor condition of current oak ecosystems, both structurally and compositionally, treatments will need to be a combination of thinning and (repeated) burning for optimal results (Albrecht and McCarthy 2006; Greenler and Saunders 2019; Vander Yacht et al. 2019; Yantes et al. 2023); the former to increase light levels to the forest floor and the latter to reduce fire-sensitive competitors presently dominating the understory. We suggest priority sites include those best suited for oak regeneration and restoration, specifically drier and/or infertile sites where the rate and steadfastness of succession are inherently curtailed (Nowacki and Abrams 2008; Iverson et al. 2018).

Where the double Ps meet: pyrophilic percentage and the Prairie Peninsula

The Prairie Peninsula is a wedge-shaped projection extending from the margins of the Great Plains eastward into Indiana (Transeau 1935). Although best known for its emblematic tallgrass prairies, other communities such as shrublands and oak savannas, woodlands, and forests were also important components, forming more of a mosaic reminiscent of a Prairie Archipelago (Sears 1981; Robertson et al. 1997). The foundational roles of climate, fire, and grazing in the genesis and maintenance of this grassland-based ecosystem over millennia are well established (Anderson 2006). Our pyrophilic percentage analyses not only reconfirmed the overwhelming occurrence of historic fire (Thomas-Van Gundy et al. 2020), but also revealed how waterbodies served as important firebreaks on the pre-Euro-settlement landscape (Fig. 6). This phenomenon was particularly evident on the lee (east) sides of north–south running rivers, such as the Mississippi, Illinois, and Root rivers, where trees with pyrophobic tendencies coalesced. Lake Michigan had a profound effect on pre-Euro-settlement fire environments, serving as a massive physical firebreak while casting a moist maritime climate eastward (Fig. 6b). The existence of water-based firebreaks was confirmed by regression analysis, which showed a positive association between pyrophilic percentage and distance to water across all study sites. Pyrophilic percentage was also positively associated with summer potential evapotranspiration, underscoring a relationship between historic fire and climate. Our work demonstrates how witness-tree data can be converted into a useful fire ecology index. While much of the landscape included in our study areas is now in agriculture or urbanized, pyrophilic percentage maps can help guide land managers in the application of fire for restoration, conservation, and forestry purposes (Johnson et al. 2023), especially in the face of climate change (Harty 2023). Our research has been highlighted in the ongoing debate regarding the primacy of climate in controlling vegetation (Briere and Gajewski 2023) vs. humans being an overriding factor (Harty 2023).

Using trees as pyro-indicators to evaluate the Midwestern Tension Zone

The Midwestern Tension Zone (MTZ) is a prominent ecotone where the flora of two major forest types (Northern Mixed Forests and Southern Broadleaf Forests) overlap, striking diagonally across the states of Wisconsin

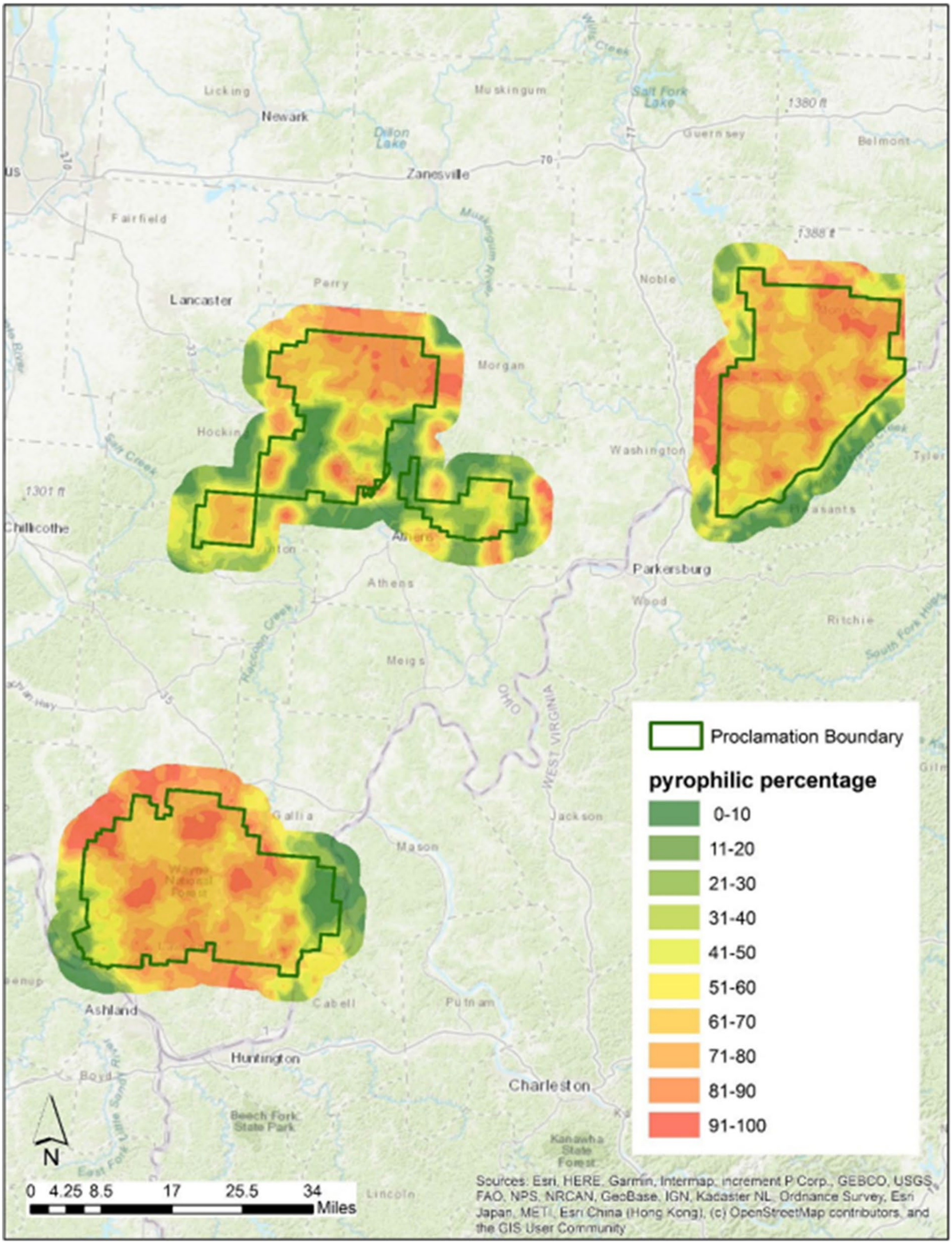

Fig. 5 Pyrophilic percentage map for units of the Wayne National Forest (Fig. 8 in Nowacki et al. 2020)

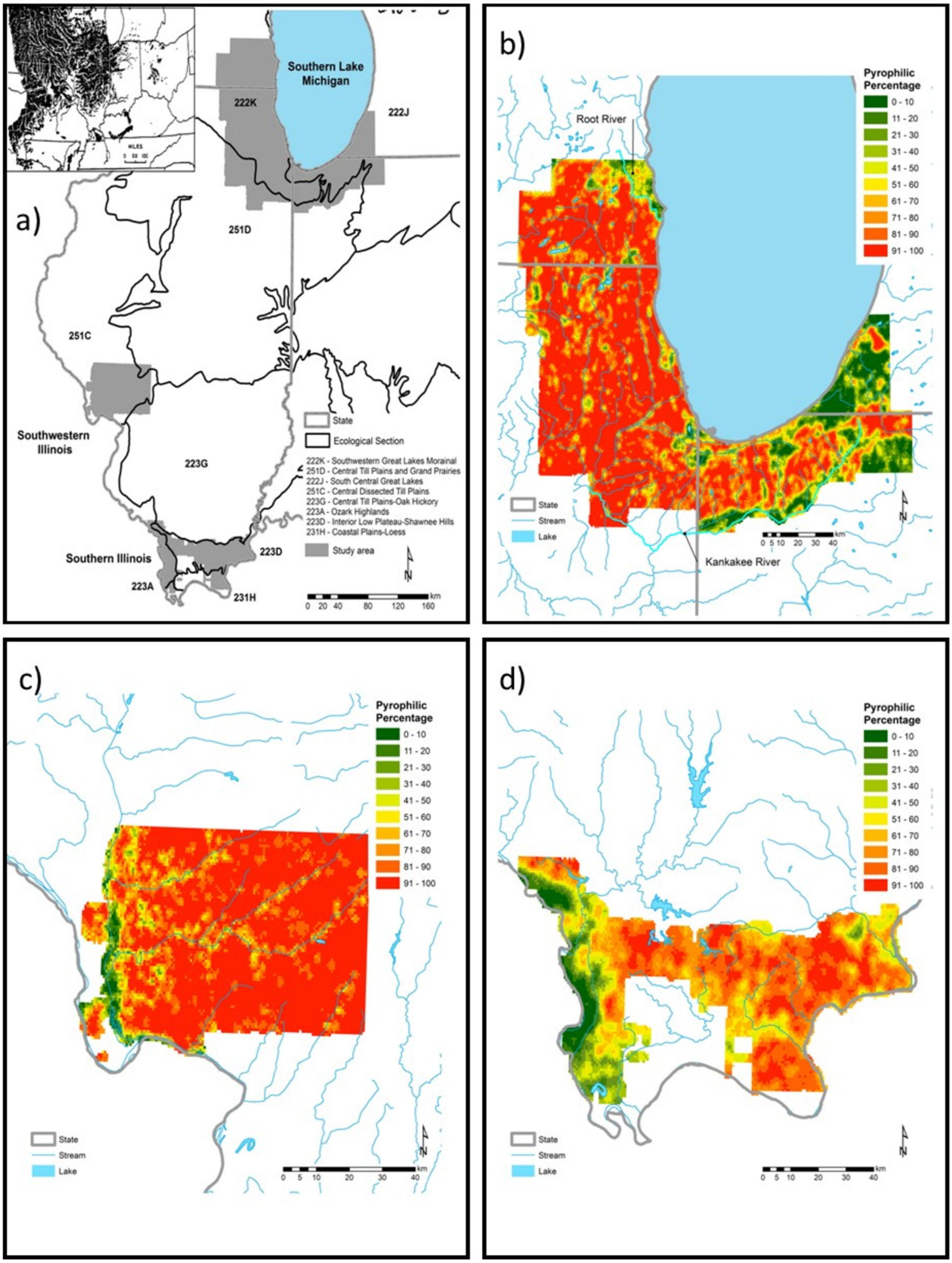

Fig. 6 Composite set of maps showing **a** the study areas [with Ecological Sections superimposed and Transeau's (1935) Prairie Peninsula inset] and interpolated pyrophilic percentage maps for the **b** Southern Lake Michigan, **c** Southwestern Illinois, and **d** Southern Illinois study areas (Figs. 1, 3–5 in Thomas-Van Gundy et al. 2020)

and Minnesota. We employed a novel approach to evaluate environmental controls of the MTZ by converting witness trees into temperature and fire pyro-indicators based on their synecological and autecological traits (Nowacki and Thomas-Van Gundy 2022). Our temperature-based line, representing temperature relations of witness trees, corresponded generally with the MTZ (Fig. 7a). However, in the lee of firebreaks, isolated pockets of cool/cold mesophytic genera occurred south of the MTZ, indicating that other environmental factors might be involved in MTZ expression. A pyrogenic-based line, created by classifying witness trees by fire relations, had two major northward departures from the MTZ where cold-adapted yet pyrophilic northern pines occurred on sandy glacial deposits (Figs. 7b and 8).

Overall, when comparing our witness-tree-based temperature and pyrogenic lines to the original MTZ (as constructed from Buell and Wilbur 1948 for Minnesota and Curtis 1959 for Wisconsin), the best alignment was with the former (Fig. 8). This reconfirms the primacy of climate as the driver of MTZ placement, aligning closely with summer potential evapotranspiration. Historic fire spatially differed on each side of the MTZ, being pervasive south of the MTZ where it supported oak dominance, whereas fire was edaphically relegated to dry, sandy landscapes of pine dominance to the north. Historic fire may have played a secondary role in MTZ placement, shunting it northward (relative to its true climate location) as islands of cool/cold species existed south of the MTZ where firebreaks occurred. Indeed, enclaves of mesic, fire-sensitive trees on the lee (east) side of fire breaks are well documented throughout the Midwestern pre-Euro-settlement landscape (Thomas-Van Gundy et al. 2020).

Climate change and fire suppression will exert future "tension" on the line, forcing uncertain movement across the landscape from these two divergent forces, with projected higher future temperatures pushing the MTZ northward and fire suppression and accompanying mesophication (comprised primarily of cool/cold-based, mesophytic trees) pulling the MTZ southward. Through this analysis, an endpoint to the

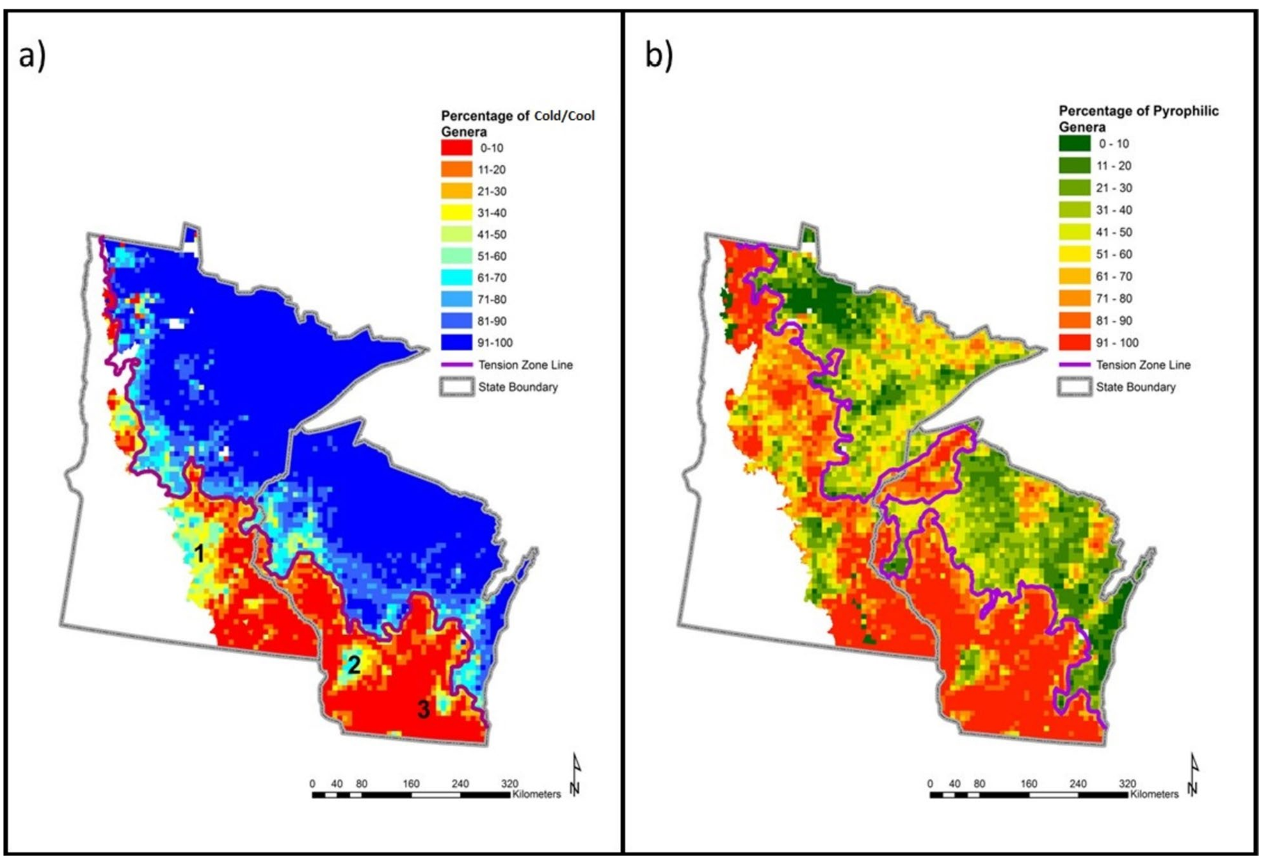

Fig. 7 Spatial display of percentage classes of **a** cool/cold temperature genera and **b** pyrophilic genera. Fifty-percent breakpoints were used to depict temperature- and pyrogenic-based tension zones. Three forested cool/cold outliers include: 1 = Big Woods (MN), 2 = Kickapoo River (WI), and 3 = Rock River (WI) (Figs. 4 and 6 in Nowacki and Thomas-Van Gundy 2022)

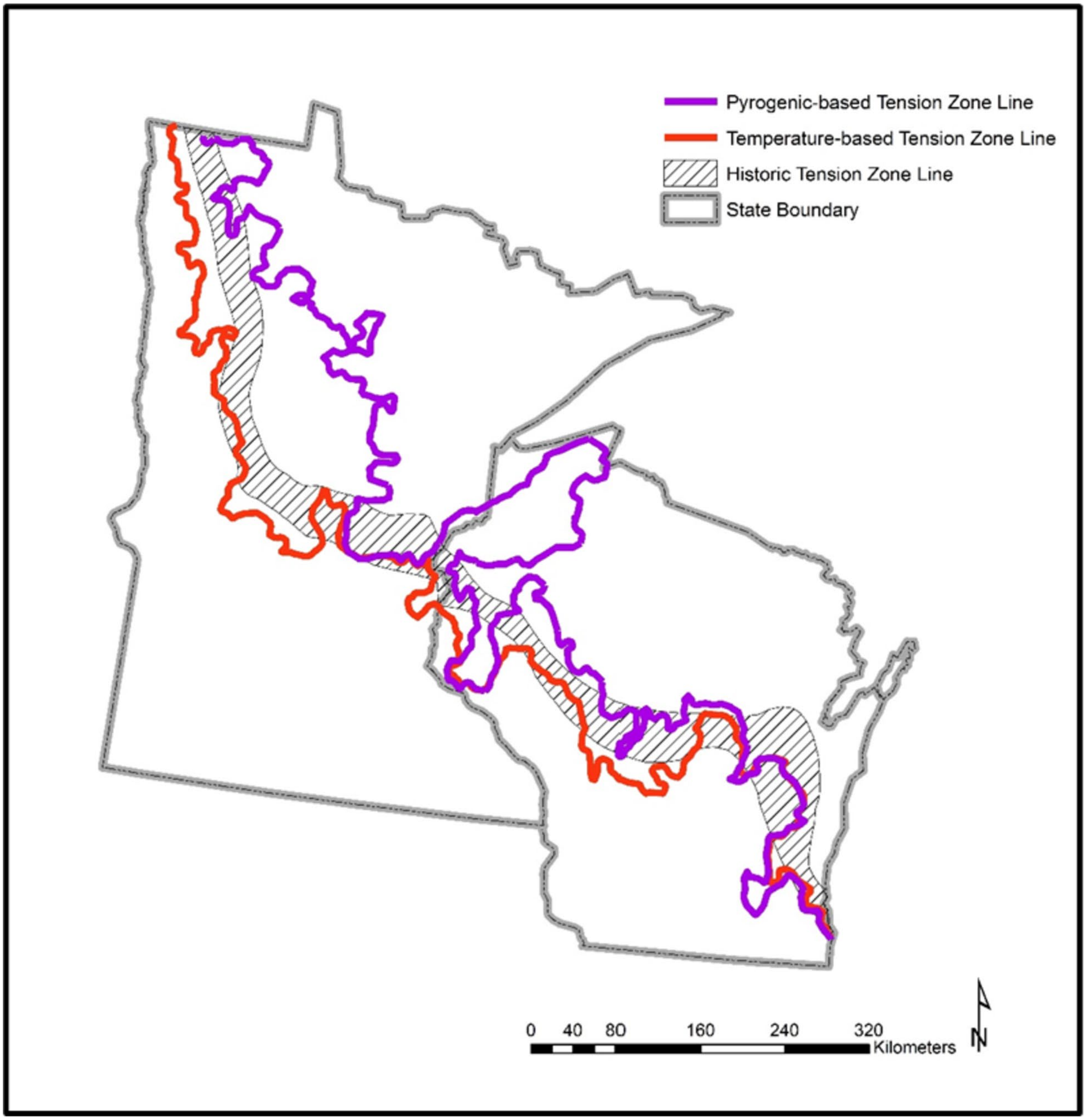

Fig. 8 The original Midwestern Tension Zone (hatched) in comparison to the temperature- and pyrogenic-generated Tension Zones (Fig. 5 in Nowacki and Thomas-Van Gundy 2022)

temperate-based MTZ was identified in northwest Minnesota, which converted over to a Boreal-Prairie Tension Zone northward.

Conclusions

As we have shown, trees listed in deeds and surveys inadvertently serve as ecological data and sentinels of past conditions. By assigning fire relations (pyrophilic vs. pyrophobic) to witness trees, calculating pyrophilic percentage at data points, and applying interpolation, we have produced response surfaces depicting pre-European fire importance for various areas of the eastern United States (Fig. 9). Variations in witness-tree locations and densities are evident when comparing our pyrophilic percentage maps, affecting their resolution and usage. This is especially apparent in maps generated from

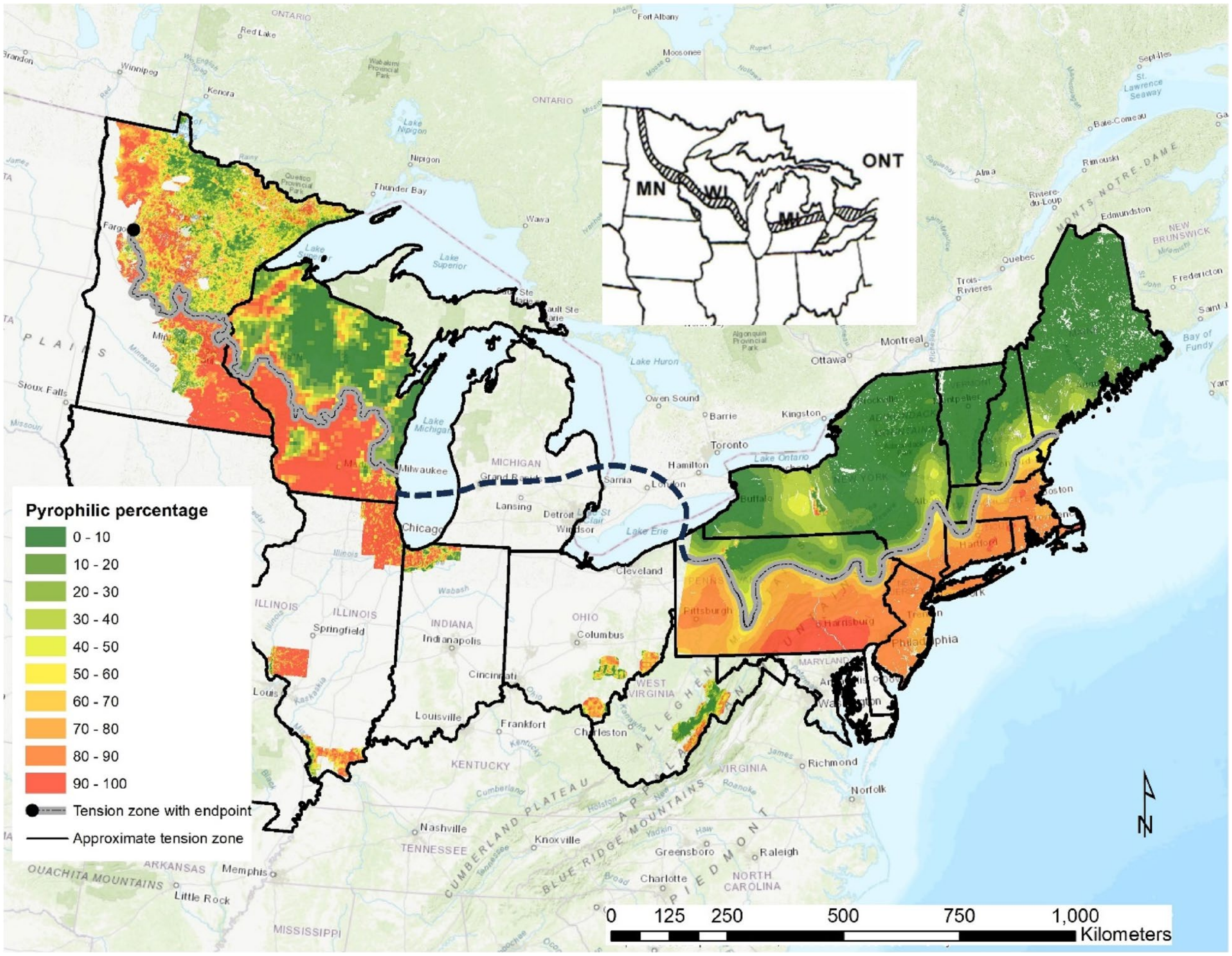

Fig. 9 The compiled map of areas where pyrophilic percentage has been calculated and published by the authors to date

metes-and-bounds surveys (random points often with a singular corner tree) vs. the Rectangular Survey System (systematic points with multiple corner trees). Accordingly, spatial resolution and applicability varies among datasets and any management actions based on these products still require field verification and spatial limits noted.

Through the spatial depiction of fire importance across pre-European landscapes, our products have been successfully used by both researchers and land managers to (1) establish past fire gradients and their relationship to climate, topography, and Native American activities, (2) determine where to use prescribed fire as a silvicultural tool to restore and maintain pyrogenic communities and encourage oak-pine regeneration for forestry purposes, (3) help draw ecological boundaries by acknowledging past fire as an important evolutionary factor, and (4) further investigate tension zones across the eastern United States. In general, contiguous areas of high pyrophilic percentages were concentrated within the oak-dominated Central Hardwood Region, extending from southeastern Minnesota, south through Illinois, and eastward to the Middle Atlantic states and southern New England (Fig. 9). The interface between this and the Conifer-Northern Hardwood Region was clearly captured by our pyrophilic percentage maps, represented by abrupt shifts from pyrophilic to pyrophobic trees and following the tension zone (Thomas-Van Gundy et al. 2015; Nowacki and Thomas-Van Gundy 2022). Smaller areas of higher pyrophilic percentage do occur in the otherwise pyrophobic Conifer-Northern Hardwood Region, associated with Native American villages (Thomas-Van Gundy et al. 2015; Tulowiecki et al. 2022) and/or dry sandy outwash plains (Nowacki and Thomas-Van Gundy 2022).

Abbreviations

GIS Geographic Information System
MTZ Midwestern Tension Zone

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Authors' contributions

GJN wrote the majority of the manuscript. MTVG developed the figures. Both authors contributed to the scope and interpretation of this review article.

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Availability of data and materials

Links to archived data sources are cited in the body of the manuscript.
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Thomas-Van Gundy, M.A.; Nowacki, G.J. 2021. Interpolated fire-adapted tree abundance in pre-settlement forests of Minnesota. Fort Collins, CO: Forest Service Research Data Archive. https://doi.org/10.2737/RDS-2021-0056.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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