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Visualizing the Ecological Importance of pre-Euro-American Settlement Fire across Three Midwestern Landscapes

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Abstract.—Bearing-tree data were used to calculate an index, pyrophilic percentage, depicting the importance of fire before Euro-American settlement on three landscapes, two within the Prairie Peninsula and one outside the region. Based on functional traits, bearing trees were classified as either pyrophilic or pyrophobic, applied to Public Land Survey points, and the pyrophilic percentage was calculated for each point. Kriging was applied to this point database to create a continuous surface of pyrophilic percentages. Regression analysis was used to relate this surface to environmental factors. Regression models created separately for each study area explained 38 to 53% of the variation in pyrophilic percentage. A positive association between pyrophilic percentage and distance to water and summer potential evapotranspiration was consistent across all study sites. The consistently high values and spatial patterns of pyrophilic percentage revealed fire-dominated landscapes interspersed with patches of pyrophobic vegetation. The restriction of pyrophobic areas to the leeside (east) of waterbodies indicated these served as firebreaks in a fire-swept landscape. Lake Michigan must have had a profound effect on pre- Euro-American settlement fire environments, serving as a massive physical firebreak while casting a moist maritime climate eastward. In southern and southwestern Illinois, the Mississippi River and associated tributaries along with an increase in topographic complexity also served as firebreaks, with pyrophobic forests restricted to riparian zones which progressively graded to pyrophilic vegetation on surrounding uplands. Our analysis expands the use of Public Land Survey data by converting bearing trees into a

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meaningful fire ecology index. While much of the landscape included in our study area 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.

INTRODUCTION

The Prairie Peninsula, an area of extensive grasslands that stretched to eastern Indiana (Fig. 1, inset), and surrounding landscapes once harbored a diverse array of plant and animal communities. Although best known for its emblematic tallgrass prairies, other communities such as shrublands and oak savannas, woodlands, and forests were also important components embedded within this floristic region, forming a mosaic perhaps more reminiscent of a Prairie Archipelago (Sears, 1981; Robertson *et al.*, 1997). Its inception was linked to the onset of the Holocene Thermal Maximum Period roughly 8000–9000 y before present (BP); a period when warm dry conditions fostered eastward expansion of Central Plain grasslands into the Midwest (King, 1981; Anderson, 2006). Prairie expansion stalled in eastern Iowa for several thousand years, forming an abrupt prairie-forest ecotone, before proceeding rapidly eastward after 6000 y BP extending into parts of Ohio (Baker *et al.*, 1992, 2002). These warm dry conditions dominated this portion of the Midwest until the Neoglacial Cooling Period ensued ca. 3300 y BP (Abrams and Nowacki, 2015).

Curiously, the largely open and xerophytic vegetation was not supplanted by closed mesophytic forests once cooler and wetter conditions set in during Neoglacial cooling, remaining dominant until Euro-American settlement in the 1800s (King, 1978; Anderson, 2006). The Prairie Peninsula was able to sustain itself over many millennia spanning substantial shifts in climate; this fact points to other contributing factors for this stasis. Gleason (1922) recognized this anomaly and argued Native Americans through burning probably maintained prairies during this latter cool, moist period. Indeed, fire suppression efforts dating back to the mid-1900s have allowed much of today's Midwestern landscape (not in agriculture) to succeed to dense, close-canopy forests of ever-increasing fire-sensitive trees (Adams and Anderson, 1980; Nowacki and Abrams, 2008; Fralish and McArdle, 2009).

We know grasslands and associated ecosystems (shrublands, savannas, and woodlands) are a product of many interacting ecological factors, most importantly climate, topography, fire (including human ignitions), and grazing animals (Anderson, 2006). Subcontinental or regional climate regimes create the general envelope within which most grasslands form, conditions further modified by topography. Specifically, grasslands form within areas having: (1) a climate that has a dry season or short periods of droughty weather, which allow fine fuels to dry out and (2) a flat to slightly rolling terrain (Sauer, 1950). These factors, in turn, facilitate fire occurrence by increasing vegetation flammability and fire receptiveness with seasonal regularity (dryness) and allowing fires to easily spread across large landscapes.

Today, the profound relationship between fire and grassland ecosystems is recognized worldwide (Vogl, 1974; Axelrod, 1985; Bond *et al.*, 2005). Indeed, the role of fire is particularly well established in the pre- Euro-American Midwest (Olson, 1996), with fire frequency and intensity largely controlling a vegetation continuum from prairie through savanna and woodland to forest conditions (Anderson, 1998, 2006). Here, topography and firebreaks like rivers and lakes were critical factors in determining how the prairie-forest mosaic covered the landscape. Grasslands dominated relatively flat surfaces, savanna and woodlands occurred on rolling terrain (*e.g.*, hilltop groves), and forests were located on the most topographically rugged areas (deeply incised blufflands) and/or on lee (east) sides of natural firebreaks. Historically, mesophytic forests (for example, those dominated by *Acer*,

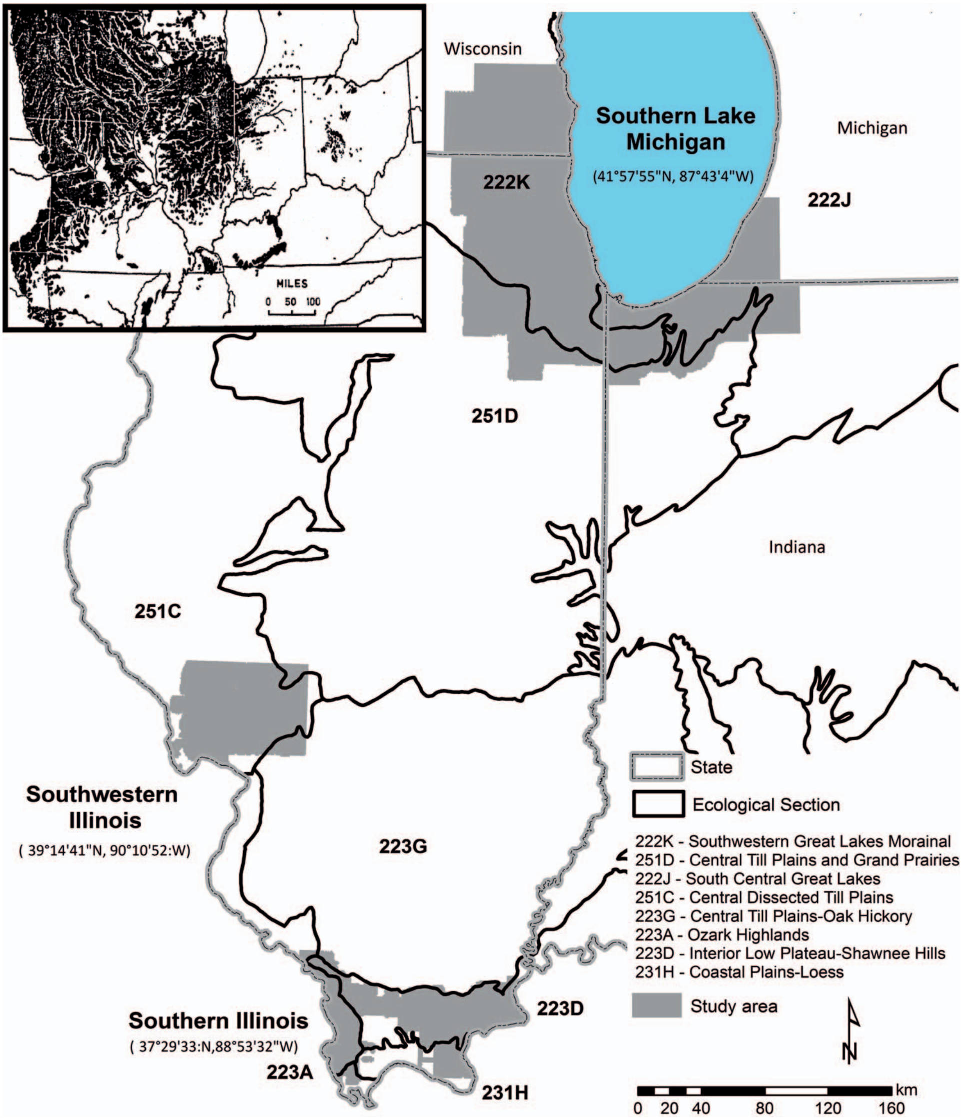

FIG. 1.—The three study areas highlighted in gray with Ecological Sections superimposed. Dark area on the inset map depicts the Prairie Peninsula (Transeau 1935)

Tilia, *Fagus*) were relatively rare and largely restricted to the most fire-protected locations, such as steeply incised, moist ravines (Anderson, 1998, 2006).

Pre- Euro-American fire was frequent (1–3 y), maintaining the former tallgrass prairies of this region, as longer fire return intervals would have resulted in transitions to shrublands (3–8 y) or woodlands (>8 y) (Ratajczak *et al.*, 2014a). The purposes for the deliberate fires of the Native Americans were many but can be summarized as the creation of diverse habitats for humans and the animals important to them (Williams, 2003; *see* also Kilburn and Brugam, 2010 for review). Moreover, once critical fire-return thresholds were crossed and shrublands and woodlands established, positive feedbacks (leading to fire dampening) and hysteresis were most likely evoked, making it difficult for grasslands to return on those sites (Ratajczak *et al.*, 2011, 2014ab). Taken in totality human-caused fire must have been the principal disturbance agent allowing for open grassland-to-woodland conditions to exist, especially considering a current climate that would otherwise support mesophytic forests similar to what previous glacial interstitials exhibited (Teed, 2000; Abrams and Nowacki, 2008).

Across much of the Midwest, fire played a prominent historical role in controlling tree distribution, abundance, and their admixture (Gleason, 1913, 1922; Curtis, 1959; Anderson, 1998; 2006). Since trees have developed functional traits to survive and thrive in such landscapes (Westoby and Wright, 2006; Peterson *et al.*, 2007), they can be used as an indicator of the ecological importance of fire on plant communities (Thomas-Van Gundy and Nowacki, 2013). Using bearing-tree data from early Public Land Surveys, we calculated an index, called pyrophilic percentage, to quantify and display the relative importance of historical fire across landscapes or simply "fire importance" bearing tree species were categorized by their relationships to fire (fire tolerant vs. fire intolerant) then geospatial analyses were run to produce maps depicting the relative importance of pre- Euro-American fire. This characterization is similar to other work involving historical tree data and quantifying functional tree composition over time similar to a recent study in Canada (Danneyrolles *et al.*, 2019). For this exercise pre- existing digital bearing-tree datasets located within or adjacent to the Prairie Peninsula of the Midwest were identified and acquired from several sources.

METHODS

STUDY AREA

We identified three separate study areas centered on the Prairie Peninsula of the Midwest that had well-documented, digitally available, bearing-tree datasets: Southern Lake Michigan (41°57′55″N, 87°43′4″W), Southwestern Illinois (39°14′41″N, 90°10′52″W), and Southern Illinois (37°29′33″N, 88°53′32″W) (Fig. 1). The Southern Lake Michigan study area is located in the ecological sections of Southwestern Great Lakes Morainal, South Central Great Lakes, and small areas in the Central Till Plains and Grand Prairies (Cleland *et al.*, 2007). All three ecological Sections are described as level to gently rolling landscapes underlain by varying amounts of sandstones and shales, with limestone noted for the Central Till Plains and Grand Prairies Section. Ground and end moraines and drumlin fields are found in the Southwest Great Lakes Morainal section, whereas outwash plains define the Southern Central Great Lakes Section. The Southwestern Great Lakes Morainal and South Central Great lakes sections had similar climates, the the former averaging 450 to 900 mm in precipitation and 6 to 11 C in temperature and he latter 750 to 930 mm and 7 to 10 C.

The Central Dissected Till Plains defines much of the Southwestern Illinois study area. This Section includes moderately dissected rolling plains with loess and till over shales, sandstones, and carbonate bedrock and average precipitation of 760–1020 mm and mean temperatures of 10 to 13 C. Small areas of the Central Till Plains-Oak Hickory section are found in this study area where landforms are flat plains with differing drainage patterns depending on depth of till. Precipitation in this section averages 1120 to 1120 mm with mean temperatures of 13 to 14 C. A small portion of the study area is also found in the Central Till Plains and Grand Prairies described above.

The Southern Illinois study area includes the Interior Low Plateau-Shawnee Hills Section (annual precipitation of 1140 to 1120 mm and average temperatures of 13 to 14 C), an area with a variety of landforms including sandstone bluffs, steep-sided ridges, and hills with broad valleys. Bedrock is mainly level-bedded sandstones with some limestone. The Ozark Highlands Section (annual precipitation of 1020 to 1220 mm and average temperatures of 13 to 16 C) is found on the west side of this study area and is described as a high plateau of steep hills and low rolling hills. Loess deposits are widespread in the entire Section over dolomite and sandstone bedrock. Small areas of the Coastal Plains-Loess Section are found in this study area consisting of irregular plains and gently rolling hills, with steep bluffs near the Mississippi River.

Bearing-tree data.—Existing electronic, georeferenced, point data of bearing-tree locations and their associated species/genera were gathered for the three study areas from a variety of sources. Bearing tree data for the Illinois counties in the Southern Lake Michigan study area are documented in McBride and Halsey (2015) and Paciorek and others (2016). In the Southern Lake Michigan study area, up to four quarter-section and section bearing trees were recorded for each point during surveys from 1821 to 1840 depending on county. Vegetation community type was also listed for each corner and the initial dataset included 28,082 points. In the Southwestern Illinois study area, up to two quarter-section and section bearing trees and occasional line trees were tallied at each of 9807 points (Kilburn *et al.*, 2009, Brugam *et al.*, 2016) with the counties surveyed between 1819 and 1820. In the datasets for the Southern Illinois study area, up to two quarter-section and section bearing trees were recorded at 4976 points in 1806 and 1807 (Anderson and Anderson, 1975; McBride and Bowles, 2008; Fralish and McArdle, 2009). The Southern Lake Michigan study area covered approximately 2,254,616 ha, the Southwestern Illinois study area 504,110 ha, and the Southern Illinois study area 537,063 ha.

Bearing trees from the Prairie Peninsula Region were a reflection of frequent, widespread burning, with this relationship equal to or stronger than to climate (King, 1978). Capitalizing on this relationship, we categorized bearing-tree species or genera as either pyrophobic or pyrophilic based on their responses to fire and specifically to a disturbance regime of repeated fire (Appendix 1) (*see* Thomas-Van Gundy and Nowacki, 2013 for more details). The presence or absence of a species or genera on a landscape can provide clues to the ecological processes that created the conditions for that species to occur. The ability to infer disturbance regimes from species occurrence data is expanded when more species are included over a larger area. We used a number of synecological and autecological traits taken from literature and the Fire Effects Information System (https://www.feis-crs.org/feis/) when classifying species or genera. Traits used to assign pyro class included: bark thickness on mature trees, preference for fire-prepared seedbeds, xerophytic (often associated with fire) or mesophytic (often disassociated with fire) tendencies, sprouting response after repeated topkill, and leaf and wood characteristics that either encourage (thick water-repellant, and curled leaves that allow air movement through leaf litter; slow decaying wood) or discourage (thin, moisture-retaining, and flat-lying leaves; rapid decaying wood) surface fire (Abrams, 1992; Nowacki and Abrams, 2008, 2015; Varner *et al.*, 2016). With this simple categorization, there is no intent to determine the strength of any individual relationship between a species and fire regime. For example jack pine is as dependent on fire as bur oak is for successful regeneration, although they arise from different fire regimes. We do not consider fire dependent trees occurring in different fire

TABLE 1.—Classification of original survey points by pyrophilic percentage

	Southern Lake Michigan	Southwestern Illinois	Southern Illinois
Percent pyrophilic	Number of points (percentage of total)		
0	6083 (21.7)	1386 (14.1)	987 (19.8)
25	6 (0.02)		
33	3 (0.01)		
50	1036 (3.7)		1171 (23.5)
67	5 (0.02)		
75	13 (90.05)		
100	20,936 (74.5)	8421 (85.9)	2818 (56.6)
total	28,082	9807	4976

regimes a limitation as we are interested in mapping gradients of the ecological importance of fire, not fire regimes per se. To that end it is the actual spatial mix of pyrophilic and pyrophobic trees from numerous data points that allows our approach to successfully capture gradients of fire importance across landscapes.

Pyrophilic percentages were calculated for each survey point by dividing the number of pyrophilic trees by the total number of trees (pyrophobic and pyrophilic) and multiplying by 100. If prairie was listed as an entry in the tree name column in a dataset or as a vegetation type in the Southern Lake Michigan study area, and no other tree species or genera information was included, that point was coded as pyrophilic (100%). All other vegetation types and points with no trees listed were coded as pyrophobic (*e.g.* a wet area with no trees was coded as 0% pyrophilic). Table 1 shows the results of this categorization of the original survey points for each study area.

Interpolation or spatial extrapolation can be applied to point data to depict and assess, possibly unforeseen, broad-scale ecological patterns and processes (Miller *et al.*, 2004). For our study we used ordinary kriging in ArcMap10.3.1 to create a continuous surface of the pyrophilic percentage from the point-based, bearing-tree data. The input data were not transformed and no spatial trends were used for the predictive interpolation. We used the optimized model setting which seeks to minimize the root mean square error in the model and chose a stable model with no anisotropy (no change based on direction, just on distance). The interpolated pyrophilic percentage was calculated using a moving window of a maximum of five neighboring points and a minimum of two; the window size varies as the nearest five points are found automatically. The resulting grid spatial data files (cell sized approximately 800m by 650m; size chosen to mimic spacing of input corner points) were converted to polygon files for easier display and manipulation.

These interpolated areas were then used to create new point data layers for statistical analysis by assigning the grid cell pyrophilic percentage to grid cell centroids. This sampling of the newly created surface by grid cell centroids resulted in 44,233 points for the Southern Lake Michigan area, 9623 points for the Southwestern Illinois study area, and 10,036 points for the Southern Illinois study area. These newly generated points, which are not in the same location as the original corner points, were then used as sample locations for gathering data from topographic, climate, and soils data grids for statistical analysis. The advantage of using interpolated data over the original point-based pyrophilic percentages for environmental analyses is that the new interpolated percentages range from 0 to 100 and can be considered continuous whereas the original input corner data are either 0, 33, 25, 50, 67, 75, or 100%.

The interpolated data represent a model of the tree species composition in 1800–1840 in the study areas.

Environmental data and analyses.—To explore the possible drivers of the patterns of pyrophilic percentage across the study areas, we examined a variety of topographic, climate, and soil variables. The topographic variables, including compound topographic index (CTI), heat load index (HLI), slope (as a percent), topographic roughness index (TRI), cosine-transformed aspect (Beers *et al.*, 1966), and elevation; were all derived from a 90m digital elevation model. The CTI variable is a measure of site wetness and is a function of slope and the upstream contributing area. Variation in slope within a moving window of three cells (90m DEM) was used to calculate the TRI. To capture the relative amount of solar radiation and temperature a slope receives, a HLI was calculated using the methods of McCune and Keon (2002). These three indices were calculated in ArcMap using the Geomorphometry and Gradient Metrics toolbox version 2.0. (Evans *et al.*, 2014).

Select climate data were acquired from the PRISM Climate Group data set for the time period of 1981–2010 (PRISM Climate Group, 2014). Specifically, we used the 30 y normal dataset, a set of average annual conditions over the most recent three full decades. We acquired the 800 m resolution data for mean temperature and total precipitation for the months of May, June, July, August, and September for the study area. These individual grids were then averaged to create means for growing season only (Fig. 2). PRISM data were modeled from weather station data using a digital elevation model as the predictor grid (Daly *et al.*, 2008) and while differences between gridded products and an independent climate record have been found at high elevations and along coastlines, PRISM data are well-supported for use at the landscape-scale (Beier *et al.*, 2012). While these climate data are obviously not from the same time period as the bearing tree data and this could result in mischaracterizing trends between climate and our interpolated pyrophilic percentage, PRISM data are the best spatially explicit climate data available for use.

Potential evapotranspiration (PET) was calculated for the conterminous US using the Hamon equation and defined as the combined amount of water expected to evaporate and transpire from a vegetated surface with no restrictions other than atmospheric demand (Lu *et al.*, 2005). First, monthly temperature data for 1981–2010 were acquired from the PRISM data set (PRISM Climate Group, 2014). Then, monthly sunlight hours for each raster grid cell (4 km) were calculated using methods found in Allen *et al.* (1998). We used a C factor (or k proportionality, a unitless co- efficient) calculated using methods from McCabe *et al.* (2015) and gridded evapotranspiration tables from Farnsworth and Thompson (1982) to estimate PET in mm. Data from the months of June, July, and August were selected to create summer PET (Fig. 2).

Soils data were developed from gridded USDA-NRCS Soil Survey Geographic (gSSURGO) datasets for states in the study areas (https://gdg.sc.egov.usda.gov/; Soil Survey Staff, 2016a). Files for individual states were joined together through the mosaic to new raster function in ArcGIS with a cell size of 10 m. Each cell is assigned a unique key, the map unit key, for identification and link to the associated database (Soil Survey Staff, 2016b). We queried the SSURGO dataset for cation exchange capacity, soil drainage class, soil taxonomic particle size, and available water storage for each map unit within the study areas. Cation exchange capacity (CEC for the top 25 cm) was calculated for the dominant map unit by percentage of area (Soil Survey Staff, 2016b). Soil drainage class was assigned based on the dominant condition found within the soil map unit. Available water storage capacity (AWS for the top 150 cm) was calculated as a weighted average of map unit components (Soil Survey Staff, 2016c).

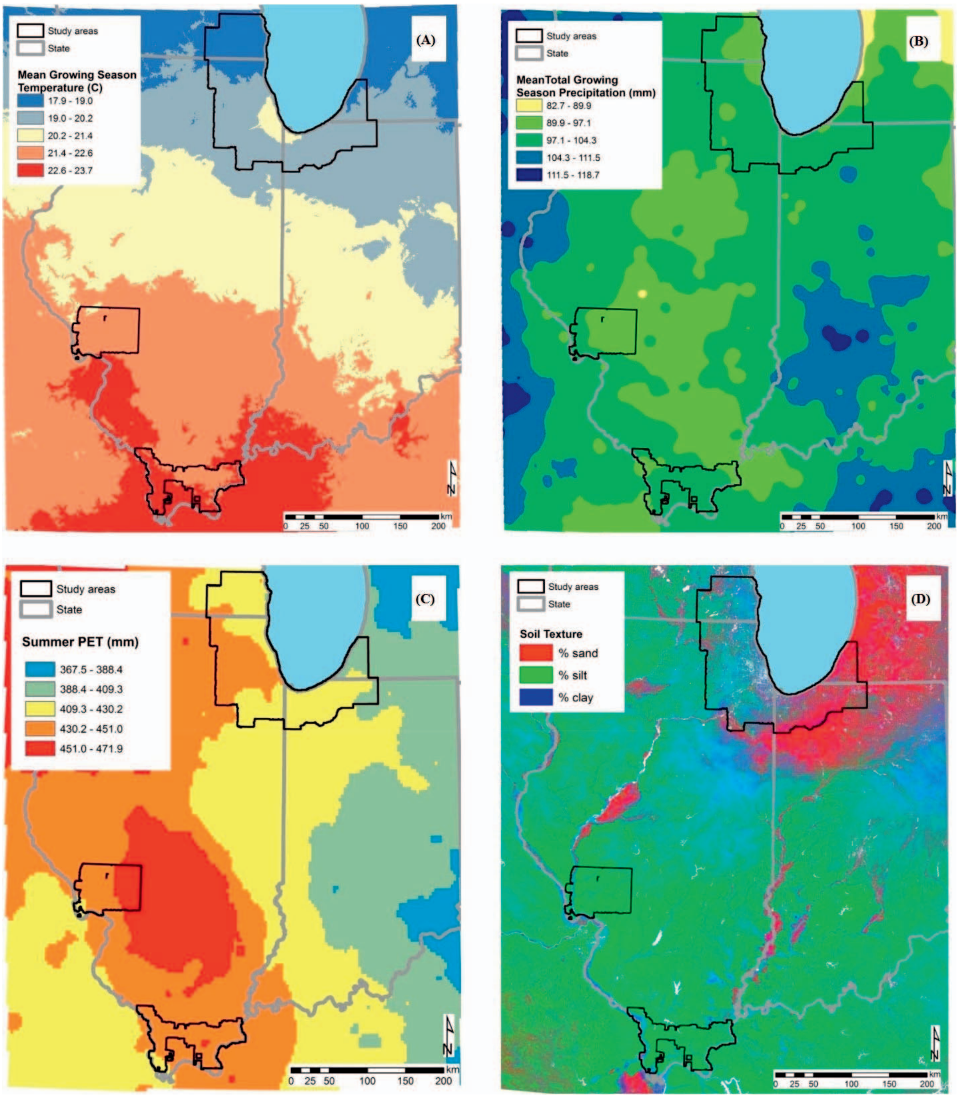

FIG. 2.—Thirty-year (1981–2010) climate normals for the study areas, (**A**) mean growing season temperature (**C**), (**B**) mean growing season precipitation (mm), (**C**) summer potential evapotranspiration (PET, mm), and (**D**) soil texture (Ramcharan *et al.,* 2018)

Soil drainage class categories were converted to an ordinal variable with increasing values indicating increasing wetness. The seven drainage classes from the gSSURGO data for soils in the study area were ranked as follows: excessively drained - 1, somewhat excessively drained - 2, well drained - 3, moderately well drained - 4, somewhat poorly drained - 5, poorly drained - 6, and very poorly drained - 7. Similarly, soil taxonomic particle size classes were ranked to create an ordinal variable ranging from fine clays - 1 to coarse sands - 5 (Appendix 2).

The water features data layer from the National Atlas of the United States (ESRI and US Geological Survey) was used to calculate distance to water (rivers, streams, and lakes) from each sample point. ArcMap was used to assign each sample point a latitude and longitude for statistical analysis. This resulted in a final list of explanatory variables of: CTI, TRI, HLI, slope (as a percent), aspect (Beers transformed), latitude, longitude, elevation (m), distance to water (m), AWS, CEC, drainage class, particle size class, summer PET (mm), mean growing season temperature (degrees C), and mean growing season precipitation (mm).

The locations of the new points created from the interpolated data described above, not the original survey points themselves, were used as sample locations to create input explanatory variables for correlation and regression analyses. We used correlation matrices from principle components analysis (PROC PRINCOMP, SAS Enterprise Guide® 2016) to determine how correlated our response variables were with each other before assessing their relationship with pyrophilic percentage. An *a priori* absolute value of 0.4 was used as a measure of highly correlated variables; highly correlated pairs of variables were reviewed and the derived variable was dropped or a variable was retained if it was highly correlated with several other variables– for example if slope and CTI were correlated, CTI was dropped and slope retained. Each study area was evaluated separately.

To explore the relationships between pyrophilic percentage and the topographic, climatic, and soils variables we used regression analysis (PROC REG, SAS Enterprise Guide® 2016) with pyrophilic percentage as the dependent variable. Explanatory variables included in the regression models were those determined not to be highly correlated with other explanatory variables based on the principle components assessment (Table 2). All variables used in the analysis were continuous. All noncorrelated variables were included in the regression models with no selection or elimination and regression models were developed and run separately for individual study areas. Standardized regression co- efficients were calculated.

RESULTS

For comparison we performed regression analyses on pyrophilic percentages calculated at individual section and quarter-section points and from the points sampled from the interpolated surfaces from the original point data. Similar trends in significant explanatory variables were found for all three areas, however, model fits (adjusted R^2 values) were lower for the original bearing tree point-based data compared to analyses made based on sample points from the interpolated surfaces, therefore the latter was chosen and is presented here (Table 2).

Southern Lake Michigan.—When viewing the actual bearing-tree point data used for interpolation we noted most corners in the western sector (WI and IL) had a high pyrophilic percentage, whereas a mix of high and low of pyrophilic percentages occurred eastward (IN and MI). When kriged, these patterns become vividly apparent (Fig. 3) with pyrophilic percentages generally grading from high (west) to low (east) across the study area, with large patches of pyrophobic landscapes (green) concentrated in the eastern sector. The pyrophobic patches are located near large river systems (*e.g.*, Kankakee River and Marsh) and on the leeward (east) side of Lake Michigan. A distinct firebreak, consistent with the literature, occurred in southeastern Wisconsin where the western boundary of an isolated pyrophobic landscape matched exactly with the Root River along much of its course.

TABLE 2.—Regression model statistics for the three study areas

	Southern Lake MI adjusted R^2 = 0.3766		Southwestern IL adjusted R^2 =0.3784		Southern IL adjusted R^2 = 0.5283	
Variable	Standardized estimate	Pr > |t|	Standardized estimate	Pr > |t|	Standardized estimate	Pr > |t|
Heat load index (HLI)	0.00024249	0.9526	0.00782	0.3553	−0.01253	0.0982
Slope (as a percent)	−0.00672	0.1107	−0.11307	<.0001	0.02621	0.0011
Aspect (cosine transformation)	0.00019780	0.9606	0.00564	0.4896	−0.01288	0.0779
Distance to water (m)	0.01935	<.0001	0.14508	<.0001	0.22151	<.0001
Drainage class	−0.12832	<.0001				
Available water storage (AWS in mm)	0.00348	0.4476	0.04431	<.0001	0.00016387	0.9832
Summer potential evapotranspiration (PET) (mm)	0.60864	<.0001	0.28791	<.0001	0.45124	<.0001
Mean growing season temperature (C)	−0.01445	0.0058	−0.01350	0.1334		
Mean growing season precipitation (mm)	−0.10464	<.0001				
Particle size class			0.06173	<.0001	−0.02489	0.0013
Elevation (m)			0.37251	<.0001	0.35725	<.0001

In this study area latitude, longitude, and elevation were found to be highly correlated with summer PET, mean growing season temperature, and mean growing season precipitation; slope was found to be highly correlated with TRI and CTI; AWS was correlated with CEC; and particle size class correlated with longitude and summer PET (data not shown). Based on these correlations, environmental factors used in the regression analysis were reduced to include distance to water, AWS, drainage class, HLI, slope, summer PET, mean growing season temperature, mean growing season precipitation, and aspect.

The regression model explained 38% of the variation in this dataset with distance to water and summer PET having statistically significant ($P < 0.0001$) positive associations with pyrophilic percentage (Table 2). Mean growing season precipitation and drainage class had statistically significant negative associations with pyrophilic percentage. Site wetness increases as drainage class value increases, meaning higher pyrophilic percentages were found on drier sites.

Southwestern Illinois.—High pyrophilic percentages dominated throughout the area based on bearing-tree point data, which, when interpolated, resulted in much of the area in high pyrophilic percentage classes (Fig. 4). Low pyrophilic percentages (green) were located within the Illinois and Mississippi river corridors, with bands of intermediate levels of pyrophilicity (yellow) along bluffs and east-west tributaries (Macoupin and Apple Creeks) on the otherwise strongly pyrophilic upland plain (red).

Principle component analysis showed latitude and longitude were highly correlated with the PRISM climate data variables. Also, drainage class, CEC, and slope were highly correlated as were slope and TRI (data not shown). Therefore, subsequent regression analysis of the relationship of

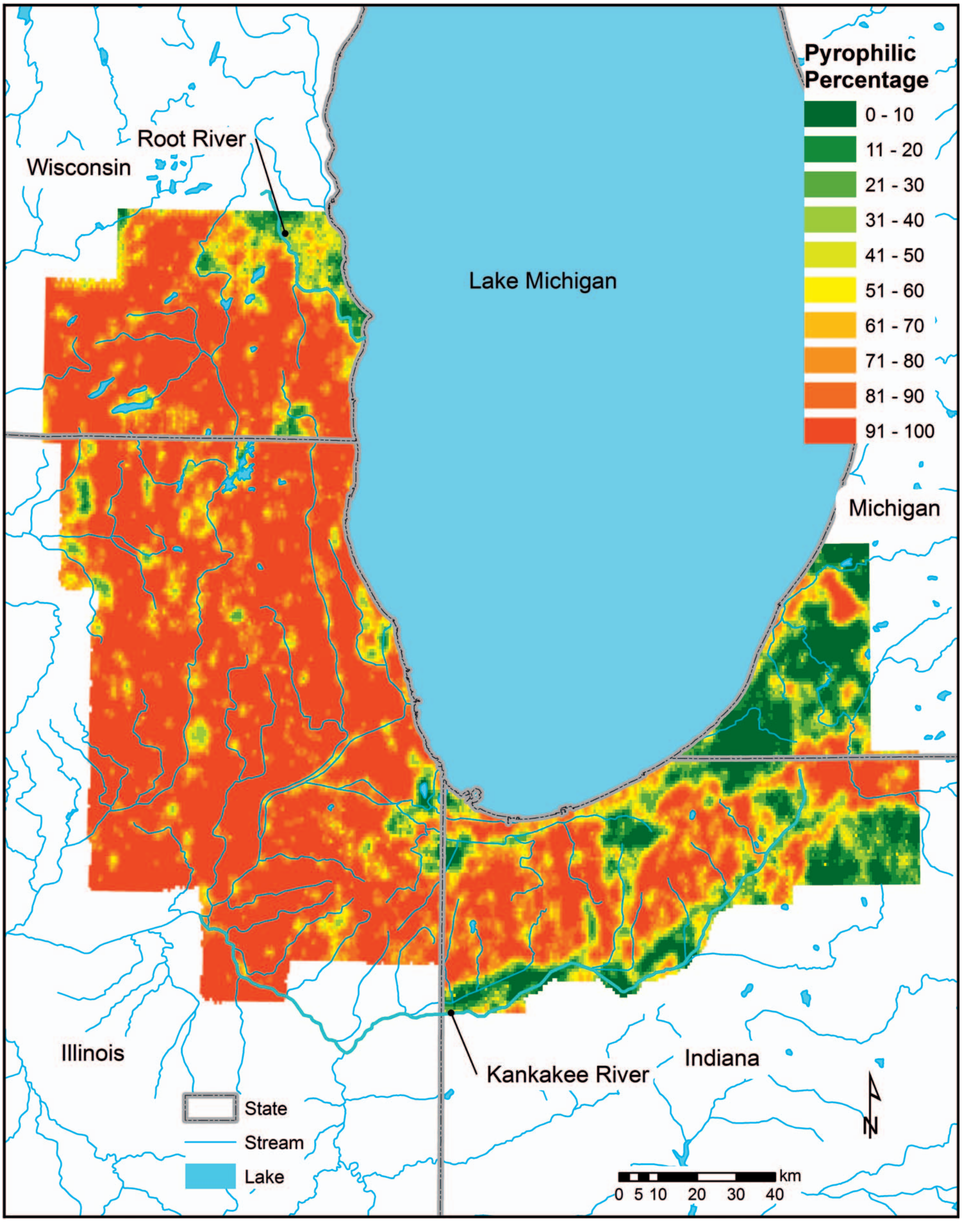

FIG. 3.—Interpolated pyrophilic percentage for the Southern Lake Michigan study area

pyrophilic percentage to explanatory variables were made on AWS, slope, HLI, particle size class, elevation, distance to water, summer PET, mean growing season temperature, and aspect. The resulting model explained about 38% of the variability with significant positive associations between pyrophilic percentage and distance to water, AWS, summer PET, particle size, and

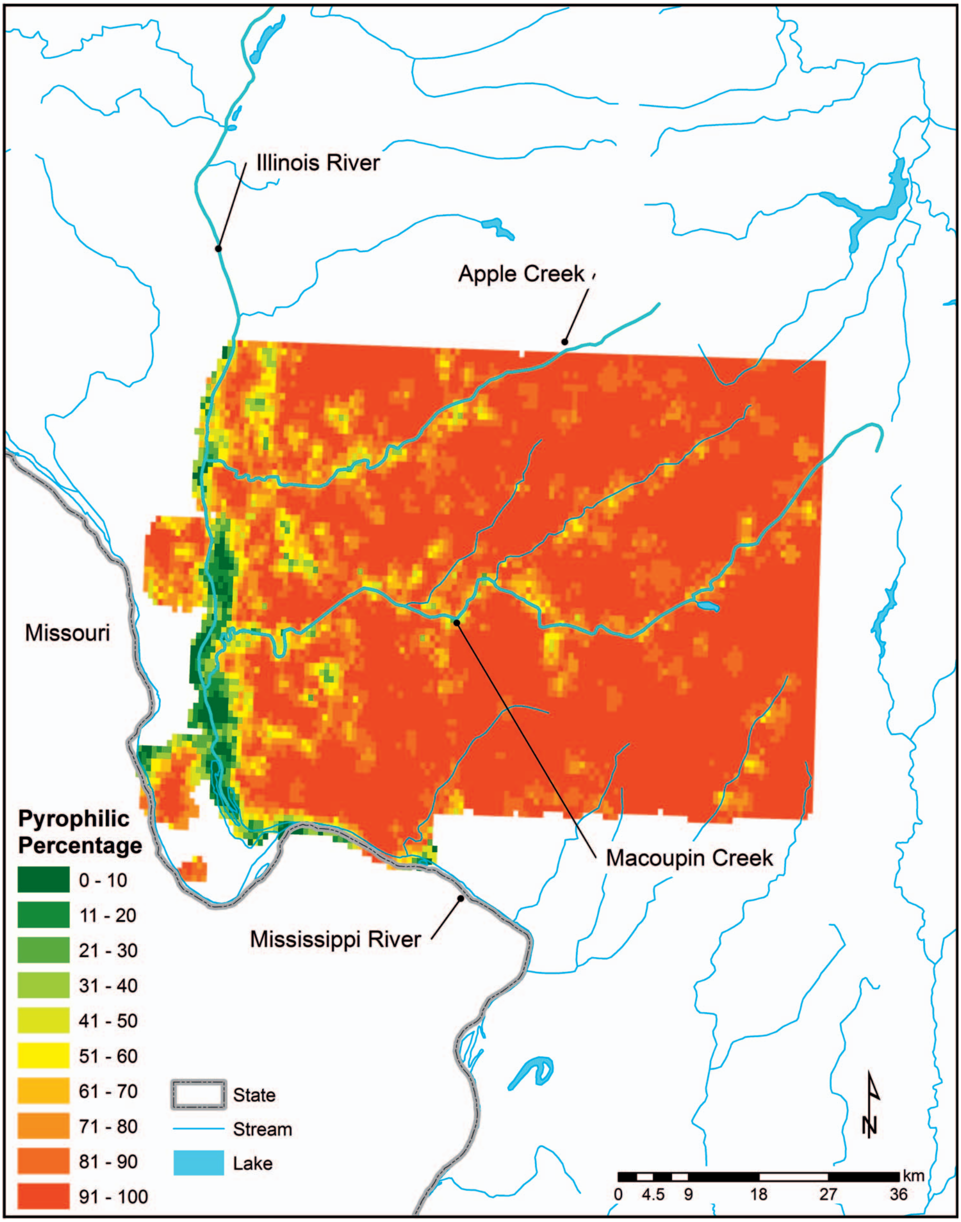

FIG. 4.—Interpolated pyrophilic percentage for the Southwestern Illinois study area

elevation (Table 2) with the strongest effects found for summer PET and elevation. Slope was found to be negatively associated with pyrophilic percentage in this model.

Southern Illinois.—Based on actual bearing-tree data at corner points, high pyrophilic percentages were abundant over most of the area, with pyrophobic points concentrated

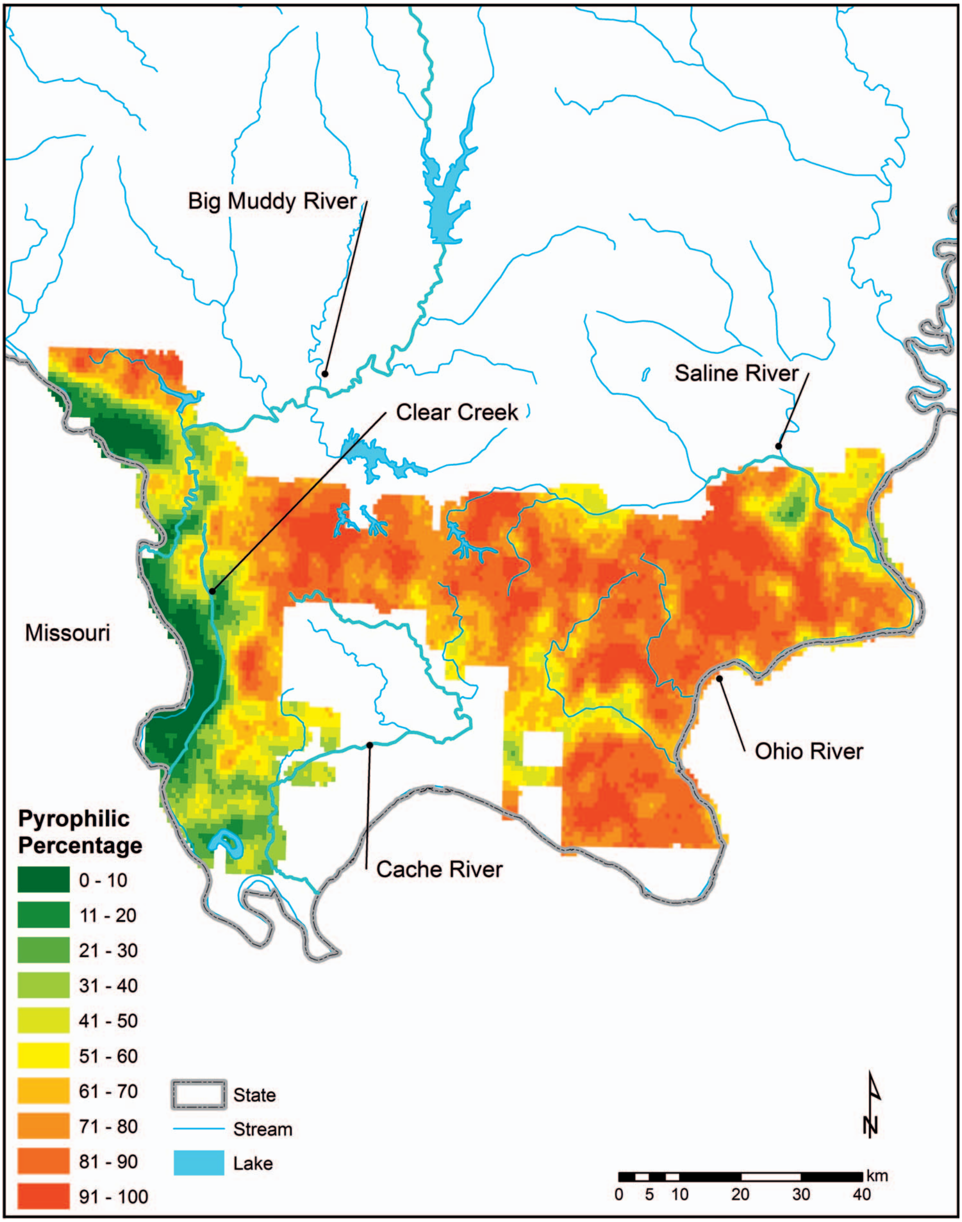

FIG. 5.—Interpolated pyrophilic percentage for the Southern Illinois study area

along the western border. When interpolated, an apparent pyrophilic gradient was revealed, with low pyrophilic percentages along the Mississippi River and associated tributaries (Cache River, Clear Creek, and Big Muddy River) and high pyrophilic percentages spanning uplands to the East (Fig. 5). In the far eastern sectors near the Ohio

River, pyrophilicity again drops along isolated stretches of the Saline River and Eagle Creek.

As in the other study areas, latitude and longitude were found to be highly correlated with summer PET and mean growing season temperature and summer PET was correlated with mean growing season precipitation. Slope was found to be highly correlated with CTI, TRI, and drainage class, and drainage class was also highly correlated with CEC. Elevation was found to be highly correlated with drainage class and mean growing season temperature. Subsequent regression analysis of the relationship of pyrophilic percentage to explanatory variables were made on HLI, slope, AWS, elevation, particle size class, distance to water, summer PET, and aspect. The resulting model explained 53% of the variation in pyrophilic percentage across this study area, with distance to water, summer PET, and elevation being significantly ($P < 0.0001$) positively associated with pyrophilic percentage (Table 2). Slightly weaker relationships where found with slope (positive; $P = 0.0011$) and soil particle size (negative; $P = 0.0013$), therefore indicating increasing pyrophilic percentage with increasing slope and decreasing particle size (Appendix 2).

DISCUSSION

Our analysis provided a new visualization of fire importance across the Prairie Peninsula. The ubiquity of high pyrophilic percentages across our study areas is consistent with literature stating that fire was a key disturbance agent in and around this region (Gleason, 1913; Transeau, 1935; Williams, 1981; Nuzzo, 1986; Olson, 1996; Anderson, 2006). The spread of landscape fire driven by prevailing westerly winds accounts for expansive uplands possessing pyrophilic vegetation as well as the restriction of pyrophobic vegetation along the leesides of major north-south waterbodies (Gleason, 1913; Goder, 1956; Neuenschwander, 1957). Firebreak size must be an important factor controlling patch size and configuration, as Lake Michigan casts an unexpectedly large pyrophobic shadow on its leeside. Although regression models differed somewhat among the three study areas, pyrophilic percentages were consistently aligned with increasing summer PET, elevation (when included in regression models), and distance to water. These environmental associations coupled with the patterns displayed in our pyrophilic percentage maps point towards the prevalence of large fires punctuated by occasional firebreaks.

Prior to the Holocene Thermal Maximum (HTM), mixed mesophytic forests dominated the rich, loess-derived surfaces of central Illinois (Anderson, 1998; 2006). Here, repeated burns fostered by HTM warming made for a dramatic conversion from fire-sensitive mesophytic forests to open grasslands (Anderson, 1998; 2006). Once established fires moved with ease across flats and slightly rolling terrain within the Prairie Peninsula, forming the topographic base of the vast grasslands. We also see the Prairie Peninsula has a connection to climate, centered on where summer PET is highest in the Region (>400mm; *see* Fig. 2c). Historically, fire barriers, such as north-south-oriented rivers and streams, lakes, wetlands, steep bluffs and cliffs, decreased fire intensity to such an extent as to allow trees to become established (Anderson, 1998; 2006). It was in these fire shadows where pyrophobic conditions were documented in our analysis, namely along the Mississippi River and its principal tributaries (*e.g.*, Illinois River), on the leeside of Lake Michigan, and within the vast Grand Kankakee Marsh. Apparently, grassland fires encountered few barriers across north-central Illinois, routinely burning all the way to the western shores of Lake Michigan except in a few locations (*e.g.*, Root River).

Southern Lake Michigan.—A distinct transition in pyrophilic percentage flanks the southern end of Lake Michigan, changing from a highly pyrophilic, grassland-dominated landscape in the west to a progressively pyrophobic, treed landscape eastward. This transition reflects the significant regional effect of Lake Michigan on past vegetation types and fire regimes, the latter driven by prevailing westerlies. Lake Michigan had a two-fold effect: (1) serving as a vast firebreak while (2) casting a maritime (moist) influence to its east (*see* potential evapotranspiration; Fig. 2c), resulting in an apparent "fire shadow", although with indistinct boundaries. Oddly, this pyrophobic "fire shadow" east of Lake Michigan was superimposed on high concentrations of coarse-textured sands – surfaces that elsewhere are normally associated with dryness and high fire receptivity (compare Figs. 2d and 3). This implies cool/moist maritime climates can suppress fire occurrence on edaphic surfaces (nutrient poor, well-to-excessively drained sands) that would normally support fire.

Riparian-based firebreaks were also embedded in this study area, although manifested at a smaller spatial scale. Most vivid were those along the Kankakee River (IN) and Root River (WI), which had contrasting river orientations (Fig. 3). The east-west Kankakee River historically meandered through a vast, lake-pocked, freshwater marshland and wooded swamp (Jackson, 1997). The hardwood swamps embedded within the Grand Kankakee Marsh were dominated by green ash (*Fraxinus pennsylvanica*), with cottonwood (*Populus deltoids*), sycamore (*Platanus occidentalis*), black ash (*F. nigra*), silver maple (*Acer saccharinum*), and elm (*Ulmus*) associates (Bacone and Campbell, 1980). The prevailing wet conditions within the river basin undoubtedly greatly limited fire, with its leading, arrow-like western edge near the IL-IN border steering oncoming fire around the floodplain. Instead of having a pyrophobic signature that largely conformed to its floodplain, the more north-south-oriented Root River of southwestern Wisconsin was a stark firebreak whereby half of the floodplain historically burned. Here, recurrent fire maintained a mix of prairies and oak savannas right up to the waterway's western edge (also *see* Fig. 1 of Goder, 1956). From its eastern bank onward to Lake Michigan, pyrophobic upland forests of American beech (*Fagus grandifolia*) and sugar maple (*Acer saccharum*) prevailed. Goder (1956) attributed this sharp change in vegetation from prairie to arboreal forest to the direct halting of fires at the west bank of the Root River. This sharp contrast is typical of north-south rivers running through the Prairie Peninsula, with trees often concentrated, some with mesophytic tendencies, on the lee sides of streams (Leitner *et al.*, 1991; Anderson, 1998; 2006). For instance this same phenomenon occurs along the Des Plaines River in northwestern Illinois (Moran, 1978), but due to the sparseness of mesophytic (pyrophobic) trees along its eastern flanks, it was poorly captured at the spatial scale of our analysis.

Within the Southern Lake Michigan study area, species-level habitat modeling by Bowles *et al.* (2015) showed slope, elevation, and topographic variability were the best predictors of habitat, however, the responses differed by species group. In their work species modeled included an oak group (black oak, (*Quercus velutina*), bur oak, (*Q. macrocarpa*), red oak, (*Q. rubra*), white oak (*Q. alba*)) and American beech, basswood, (*Tilia americana*), elm, and sugar maple as another contrasting group, creating essentially two categories, xerophytes and mesophytes. That the two groups responded differently to site variables, and with the mesophytic group responding consistently within group, suggests a shared characteristic for species within these groups – that being fire-tolerance (Bowles *et al.,* 2015). Other assessments made county-by-county in the Southern Lake Michigan study area show presettlement prairie dominated this area and the numbers of mesic tree species increased with increasing slope and in proximity to firebreaks (Bowles *et al.*, 2015). In these assessments using tree density as a proxy for fire regime, the bearing trees show the landscape-fire relationships and transitions from prairie to barrens or open forest to closed forest. Our interpretation of the same bearing trees and prairie points is another way to display this transition without delineating the area into community types or by using tree density as a surrogate for fire importance.

Southwestern Illinois.—The pyrophobic forests were largely restricted to the riparian corridors of the Illinois and Mississippi rivers (Fig. 4), with pyrophilic vegetation dominating surrounding bluffs and upland plains. This fire gradient corresponds to compositional changes from cottonwood-hackberry (*Celtis occidentalis*)-box elder (*Acer negundo*) on islands (importance values of 55%, 35%, and 27%, respectively) through pin oak (*Q. palustris*)-elm-cottonwood on floodplains (45%, 26%, and 20%, respectively) to white oak-black oak-hickory (*Carya*) on uplands (76%, 61%, and 23%, respectively) as reported by Nelson *et al.* 1998. These rivers, specifically the Illinois and tributaries in our study area, likely fostered the presence of pyrophobic vegetation by serving as firebreaks coupled with their low-lying wet condition. The positive associations of pyrophilic percentage with particle size and AWC initially seem counterintuitive but make sense considering that coarse-textured soils (low AWC) dominate riparian zones and grade to loess-derived silt loams (high AWC) on bluffs and beyond. Here, the small, east-running tributaries that paralleled the prevailing direction of the wind from the west did not serve as effective fire barriers.

Our work parallels past research that has documented prairies on level to gentle surfaces and forests on steeper slopes with fire-intolerant species found on the steepest slopes (Brugam *et al.*, 2016; Kilburn and Brugam, 2010). Although we did not delineate vegetation communities in our assessment of pyrophilic percentage, we see a similar association with pyrophilic percentage being negatively correlated with slope (*i.e.*, greater numbers of pyrophobic species were found on steeper slopes), although the relatively low explanatory power in the overall model (R^2=0.38) indicates unexplained or unexamined factors contribute most to model variability.

Southern Illinois.—This study area possessed similar characteristics as in Southwestern Illinois with pyrophobic vegetation concentrated along the Mississippi River and larger tributaries and pyrophilic vegetation on the bordering uplands. The increase in pyrophilicity with topographic position is stark, particularly along the immediate margins of floodplains. It corresponds closely to increases of presettlement white and black oak on north-facing slopes from terrace (combined importance value of 30%) to lower slope, upper slope, and ridgetop positions (64%, 84% and 78%, respectively) (Fralish *et al.*, 1991). Interestingly, and in contrast to Southwestern Illinois, here pyrophilic percentage increased with slope steepness and was significant in our regression analysis. This area is outside the Prairie Peninsula and possesses higher topographic complexity than the other study areas, which may explain this difference in the effect of slope on pyrophilic percentage.

Jones and Anderson (2011) determined that importance values for two species groups, xerophytes and mesophytes, did not differ significantly among open and closed forests or among open forests and savannas in this area however, there were significant differences between closed forests and savanna. In this area, again outside the Prairie Peninsula, savanna and closed forests are the opposite ends of the fire regime spectrum. Jones and Anderson (2011) found no association of community type with aspect or slope but did see a weak association with elevation. We found that slope and elevation were correlated with increasing pyrophilic percentages, but the strongest correlation was with summer PET (correlation analysis, data not shown, r =–0.56).

CONCLUSION

Use of pyrophilic percentage as a grouping of tree species based on a shared response to fire disturbance allows for an integrated new view of landscapes and possible identification of transitions between pyrophilic (*e.g.*, savannas and woodlands) and pyrophobic (*e.g.*, closed-canopy, mesophytic, and hydrophilic forests) systems. Although we did not assign a pyrophilic percentage that would depict structural transitions, it is reasonable to assume that as pyrophilic percentage (an index of the ecological importance of fire) decreases, tree density increases and a higher percentage of closed-canopy forest developed. As such pyrophilic percentage may serve a broader purpose as a multifaceted ecological index.

Our assessment of potential drivers of pyrophilic percentage resulted in models that explained 38 to 53% of the variation. Missing from the variables examined is some measure or proxy for the influence of Native American land use on these landscapes (Dorney, 1981; McClain and Elzinga, 1994; Abrams and Nowacki, 2008). In future analyses we could incorporate distance to known Native American village sites and travel routes as an influence index as applied to historical tree maps in Pennsylvania (Black *et al.*, 2006) and New York (Tulowiecki and Larsen, 2015; Fulton and Yansa, 2019) and what we have done previously for the northeastern US (Thomas-Van Gundy *et al.,* 2015).

Other possible factors for poor regression model performance include the edaphic and climate variables selected in the analyses. Perhaps the greatest difficulty stems from the indiscriminate nature of past fire, which burned across vast areas in this region at different frequencies and intensities, oftentimes with little regard to changing edaphic conditions. For example prairies routinely extended from dry upland to wetland conditions and across multiple, contrasting soil types (Lindsey, 1961). One consistent and prominent factor controlling fire patterns and importance, however, was the existence of major waterbodies that served as firebreaks, which effectively subdued or blocked fire and led to the development of pyrophobic systems on their lee (eastward) sides. While much of the landscape included in our study areas is now in agriculture or other developed land use, pyrophilic percentage maps can help guide land managers in the application of fire for restoration, conservation, and forestry purposes. Our maps could be used to help prioritize areas for prescribed fire or aid in delineating boundaries for burn units.

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APPENDIX 1.—Species or genus of trees listed in bearing tree datasets and their assigned pyrogenicity. All species/genera were not found in all datasets

Species/genus	Pyrogenicity
Acer	Pyrophobic
Acer negundo	Pyrophobic
Acer saccharum	Pyrophobic
Aesculus	Pyrophobic
Asimina triloba	Pyrophobic
Betula	Pyrophobic
Betula nigra	Pyrophobic
Betula papyrifera	Pyrophilic
Carpinus caroliniana	Pyrophobic
Carya	Pyrophilic
Carya illinoensis	Pyrophilic
Carya ovata	Pyrophilic
Carya texana	Pyrophilic
Cercis canadensis	Pyrophobic
Celtis occidentalis	Pyrophobic
Cornus	Pyrophilic
Crataegus	Pyrophobic
Diospyros virginiana	Pyrophobic
Fagus grandifolia	Pyrophobic
Fraxinus	Pyrophobic
Fraxinus americana	Pyrophobic
Fraxinus nigra	Pyrophobic
Gleditsia triacanthos	Pyrophobic
Gymnocladus dioicus	Pyrophobic
Juglans	Pyrophobic
Juglans cinerea	Pyrophobic
Juglans nigra	Pyrophobic
Juniperus virginiana	Pyrophobic
Larix	Pyrophobic
Liquidambar styraciflua	Pyrophobic
Liriodendron tulipifera	Pyrophobic
Magnolia acuminata	Pyrophobic
Malus	Pyrophobic
Morus	Pyrophobic
Nyssa aquatica	Pyrophobic
Nyssa sylvatica	Pyrophilic
Ostrya virginiana	Pyrophobic
Pinus	Pyrophilic
Pinus resinosa	Pyrophilic
Pinus strobus	Pyrophilic
Platanus occidentalis	Pyrophobic
Populus	Pyrophobic
Populus deltiodes	Pyrophobic
Populus tremuloides	Pyrophilic
Prunus serotina	Pyrophobic
Prunus	Pyrophobic
Quercus	Pyrophilic
Quercus alba	Pyrophilic

APPENDIX 1.—Continued

Species/genus	Pyrogenicity
Quercus coccinea	Pyrophilic
Quercus falcata	Pyrophilic
Quercus lyrata	Pyrophilic
Quercus macrocarpa	Pyrophilic
Quercus muehlenbergii	Pyrophilic
Quercus marilandica	Pyrophilic
Quercus nigra	Pyrophilic
Quercus palustris	Pyrophilic
Quercus rubra	Pyrophilic
Quercus stellata	Pyrophilic
Quercus velutina	Pyrophilic
Robinia pseudoacacia	Pyrophilic
Sassafras albidum	Pyrophilic
Salix	Pyrophobic
Taxodium distichum	Pyrophobic
Thuja occidentalis	Pyrophobic
Tilia americana	Pyrophobic
Ulmus	Pyrophobic
Ulmus rubra	Pyrophobic
Other	Pyrophobic

APPENDIX 2.—Soil taxonomic particle size class rankings and pseudo variable assignment

Taxonomic particle size	Assigned value
sandy-skeletal	5
sandy or sandy-skeletal	5
sandy	5
coarse-loamy over sandy or sandy-skeletal	4
sandy over loamy	4
sandy over clayey	4
coarse-loamy	4
coarse-loamy over clayey	4
loamy-skeletal	3
loamy	3
coarse-silty over sandy or sandy-skeletal	3
coarse-silty	2
coarse-silty over clayey	2
fine-loamy over clayey	2
fine-loamy over sandy or sandy-skeletal	2
fine-loamy	2
clayey skeletal	2
clayey over sandy or sandy-skeletal	1
clayey over loamy	1
fine-silty	1
clayey	1
fine	1
very fine	1