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Sharp Savanna-forest Transitions in the Midwest Followed Environmental Gradients but are Absent from the Modern Landscape

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ABSTRACT.—Historically, closed eastern forests transitioned into open savannas and prairies in the U.S. Midwest, but this transition is poorly understood. To investigate the eastern boundary of the prairie-forest ecotone, we conducted a case study of historic and modern vegetation patterns of the Yellow River watershed in northwest Indiana. Historic vegetation came from the Public Land Survey notes collected in the early 1800s, whereas modern vegetation came from the Forest Inventory Analysis and USGS National Land Cover Database. We mapped vegetation data using GIS to reconstruct the region's past and current forest composition and structure. We also mapped climate, topography, and soil composition across the watershed to investigate the relationship between historic vegetation and environmental gradients. We found a sharp transition in the presettlement forest structure and composition, with dense deciduous forests in the eastern portion of our study area and open oak savannas in the west. The savanna ecosystem dominated in sandy well-drained soils and was at a slightly lower elevation than the adjacent closed forest. Modest environmental changes accompanied major vegetation changes in the past, which might suggest fire and hydrological patterns helped maintain the sharp ecotone. By contrast the modern forest shows no difference in tree density and composition across the watershed, which is consistent with major land use and hydrology changes in the watershed since settlement. On the modern landscape, land that was historically closed forest now has higher agricultural productivity compared to land that was historically savanna, whereas the historic savanna currently supports more mesic forest. These results suggest the environmental gradient continues to subtly shape the landscape. Though land use change has largely removed the closed mixed hardwood forests and oak savannas from this area, a better understanding of the historic vegetation and the conditions that supported it can help inform land management and restoration, as well as reveal ecological processes that drive vegetation transitions.

INTRODUCTION

The Midwestern prairie-forest ecotone, where the Prairie Peninsula historically met the eastern deciduous forest biome, has been well-studied but is still not well understood. Specifically, studies have investigated the patterns of the transitions between prairies, savannas and forests, as well as the factors that shape them (Transeau, 1935; Curtis and

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McIntosh, 1951; Manogaran, 1983; Rodgers and Anderson, 1979; Haney *et al.*, 2008; Paciorek *et al.*, 2016). Edgar Nelson Transeau (1935) first mapped the range of the Prairie Peninsula and provided an overview of its vegetation, climate, and soils patterns. Moving westward across the region, climate drives a continuum of increasingly fire and drought-adapted tree species and lower stem density (Anderson, 1998; Danz *et al.*, 2011). But at smaller scales where climatic differences are negligible, these ecosystems can have discrete boundaries and patchy distributions (Transeau, 1935; Kilburn, 1959; Almendinger, 1992). Both large and small-scale studies along the boundary describe close relationships between soil type and vegetation (Kilburn, 1959; Lindsey *et al.*, 1965). But others have found modest or negligible associations between ecosystem and soil transitions, suggesting processes such as hydrological seasonality and fire disturbance can amplify the effects of small differences in soil and topography on vegetation (Grimm, 1984; Whitney and Steiger, 1985; Almendinger, 1992; Danz *et al.*, 2011). Furthermore, emerging research shows environmental characterizations poorly predict vegetation in some savanna-forest transitions, and these studies propose internal feedbacks can hold these ecosystems as alternative stable states in similar environments (Staver *et al.*, 2011; Ratajczak *et al.*, 2014). These diverging descriptions of the Midwestern ecotone and its accompanying environment highlight the need for more studies at a detailed scale.

Many studies document the ecotone's northern ranges in Minnesota and Wisconsin (Grimm, 1984; Almendinger, 1992; Umbanhowar, 2004; Hanberry *et al.*, 2012), western regions in Illinois (Bowles and Jones, 2004; Fahey *et al.*, 2012), and southern reaches in Illinois and Missouri (Weaver, 1960; Batek *et al.*, 1999; Brugam *et al.*, 2016), but at its wet climatic extreme in the east, the ecotone boundary is comparatively understudied. This is an important knowledge gap, as vegetation-environment relationships along the boundary appear to be spatially variable. Environmental features such as morainic uplands, for example, have been linked to both oak-dominated (generally more dry-adapted) and beech-maple (more mesic) associations in nearby regions in Illinois and Indiana (Cowles, 1901; Fuller, 1925; Abrams, 2003). Understanding these vegetation-environment relationships becomes especially critical as ecosystem ranges and composition shift in response to environmental change throughout the region (Fahey *et al.*, 2012). In particular, transitional ecosystems such as oak savannas have already shifted towards closed-canopy forests comprised of more mesic species within the last century, threatening the exceptional biodiversity supported by the grass-tree mosaic habitat of savannas (Leach and Givnish, 1999; Nowacki and Abrams, 2008; Philippe *et al.*, 2011). Oak-savanna ecosystems are therefore increasingly rare (Nuzzo, 1986; Hoekstra *et al.*, 2005). Conservation agencies want to understand the environmental conditions that best support savannas, as well as identify optimal areas for restoration to connect scattered patches (Fahey *et al.*, 2015). Though little remnant vegetation remains, historical land survey datasets from the early 19th century capture a snapshot of this region's landscape before Euro-American settlement. These data afford the opportunity to explore the eastern regions of this vegetation transition in order to guide preservation and restoration efforts.

This study examines the historic vegetation transition, underlying environmental gradient, and modern land cover of the eastern region of the ecotone. We used 19th century Public Land Surveys (PLS) data for the Yellow River watershed in northwest Indiana, a region that lies on the eastern boundary of the Prairie Peninsula, as outlined by Transeau (1935; Fig. 1A). This ecotone map breaks the region into an eastern forest and western prairie region without detailing the sharpness of the transition, and it does not address vegetation and environment patterns specific to the mesic eastern edge of the transition. We

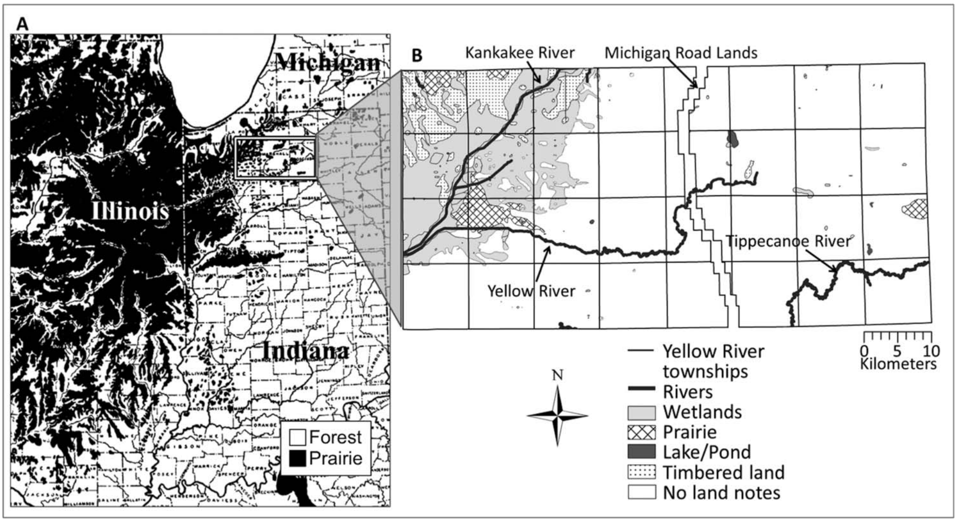

FIG. 1.—Study Area. (**A**) Transeau's (1935) depiction of the prairie before Euro-American settlement, with study area outlined. (**B**) Yellow River watershed study area and the digitized surveyor-drawn plat maps of the region. The area is composed of 32 townships (thick black outline). Surveyors described wetlands (marsh or swamp; light gray), timbered land (stipple), and prairie (crosshatch), but for most areas the plat maps do not give land cover data (white). The north-south break between the townships represents the Michigan Road Lands, not included in this study. Permission to use the Transeau (1935) image granted by John Wiley & Sons, Inc. publishing company

compare this original vegetation pattern with climate, soil, and topography gradients and with current forest and land use patterns, and in so doing answer three questions:

(1) Do the historic land survey (PLS) data show a sharp or gradual transition from closed mesic forest to open oak savanna?
(2) Do environmental covariates correspond to the vegetation shift in space?
(3) Are these vegetation gradients still visible on the modern landscape?

Based on Transeau's coarse map of the region and on the general pattern of discontinuous vegetation changes between grassland, savanna, and forest (Nowacki and Abrams, 2008), we hypothesized the PLS surveys would show a discrete structural and compositional boundary between eastern deciduous forest and western oak savanna. Additionally, fine-textured morainal soils and sandy outwash soils have been linked to beech-maple and oak-hickory associations, respectively, near our study area (Kenoyer, 1933; Lindsey *et al.*, 1965). This watershed historically experienced spring flooding as part of the larger Grand Kankakee Marsh system (Ivens *et al.*, 1981). This hydrology could either encourage fire by increasing herbaceous fuel buildup (Higgins *et al.*, 2000) or discourage fire by extending wet seasons (van Langevelde *et al.*, 2003). Though these hydrological drivers have shown diverse relationships with vegetation (*see* Whitney and Steiger, 1985; but also Anderson and Anderson, 1975; Rodgers and Anderson, 1979), we predict that the historic oak savanna distribution correlates with well-drained soils and lower elevation, factors that drove historic fire and flooding regimes. Finally, we investigate if legacies of this ecotone are still present on the modern landscape, which has been heavily deforested, drained for agriculture, and partially urbanized. We expect that soil and land attributes determined historic vegetation by shaping fire and hydrology, processes disrupted on the modern landscape. Therefore, compared to the historic conditions, we expect much weaker or absent relationships between edaphic factors and modern vegetation.

METHODS

STUDY AREA

Our study area in northwest Indiana is a 3000 km^2 rectangular region (N:41.31, S:41.1., E:–85.5 and W:–86.56) encompassing the Yellow River watershed, an important tributary to the Kankakee River (Fig. 1B). The Yellow River runs just under 100 km long, with an original natural length estimated to be three times longer (Chicago Sanitary District, 1895). It drains 1127 km^2 across the region (Jonas and Little, 2010). The river flows southwest and drains six northern Indiana counties: Elkhart, Kosciusko, Marshall, La Porte, Starke, and St. Joseph. Currently, the study area includes both sparsely populated (county population ~23,000 people) and heavily populated (county population >250,000 people) counties (United States Census Bureau, 2015). Due to the watershed's irregular shape, two other rivers run through portions of our rectangular study system. The Kankakee River runs through the northwest corner, and the headwaters of the Tippecanoe run through the southeast corner. At the time of the historic surveys, the State of Indiana procured and set aside a mile-wide, north-south strip of the watershed for the construction of the Michigan Road (hereby referred to as the Michigan Road Lands), which is now U.S. Highway 31 (Prather, 1943). This area was surveyed differently from other PLS surveys used in our analyses (*see* below) and is not included in the dataset. The upper part of the Yellow River watershed is characterized by clay soils, whereas the lower third is sandy glacial outwash (Jonas and Little, 2010), and most of the basin is overlain with sand (Thompson, 1886). The Kankakee watershed, which includes the Yellow River, is mostly level plains and depressions, and many parts were either seasonally or partially inundated (Woods *et al.*, 2006). Continental glaciation in northwest Indiana formed wetlands that are not found in the Illinois side of the watershed (Ivens *et al.*, 1981).

The Yellow River's hydraulics, and consequently the region's hydrology, have been significantly altered by development and agriculture (Christopher B. Burke Engineering, 2012). The eastern portion of the Yellow River was dredged and straightened in the early 1900s, rerouting the extensive marsh waters into a straight channel and draining the land for cultivation. The new human-made channel, dug only 2.5 m wide instead of the proposed 6 m, led to severe erosion and deposition of silt and sand (Downey *et al.*, 1909). The Yellow River contributes the largest load of sand to the Illinois River due to high load of suspended sediment from its watershed as well as heavy erosion of its sandy banks (Jonas and Little, 2010). There has been recent interest in restoring the hydrological health of the region and bringing back native fauna (Christopher B. Burke Engineering, 2012; The Nature Conservancy, 2017).

DATA SOURCES

To reconstruct the presettlement vegetation of the watershed, we used Public Land Surveys (PLS) conducted by the Government Land Office between 1829 and 1837. PLS records were obtained from the Indiana State Archives. The PLS system divided the land into townships comprised of 36 sections, each one square mile in area. Surveyors set posts at half-mile intervals and documented each post's position by noting one to four trees—

recording the species' common name, diameter, azimuth, and distance from the post. When possible, we list trees at the species level, but when ambiguity exists in historic common names, we combine genera or, in cases such as poplar/tulip poplar, use higher classifications. These notes provide a "snapshot" of the landscape when the region was relatively undisturbed by European settlement. The surveyors also scaled tracts of land to be sold by drawing plat maps for each township, in which they outlined water and non-tree land features such as prairie (Rohrbough, 1968). The Yellow River watershed encompasses 32 townships. Tree data at mile ("corner post") and half-mile ("quarter post") intervals from the PLS surveys were entered into a database by the McLachlan lab at the University of Notre Dame. The USGS Lake Michigan Ecological Station digitized the plat maps (Fig. 1B). This dataset has some limitations, such as the inability to capture seasonality, potential sampling differences across multiple surveyors, and the possibility of bias in tree selection. However, by excluding subjectively recorded "line" trees (recorded along survey lines but not at survey posts) and studying a sufficiently large area, these data can be a powerful tool to reconstruct historic vegetation (Liu *et al.*, 2011; Manies and Mladenoff, 2001). Some of these surveyor biases in density are corrected (*see* methods below).

We compiled several datasets to establish both the region's environmental gradient and modern landscape (*see* Supplemental Material https://github.com/PalEON-Project/YellowRiver_Indiana, Table S1, for full list and description). We used 30 y Normal Mean Temperature and 30 y Normal Precipitation rasters (calculated for the years 1981-2010, both at a resolution of 800 m; from PRISM Climate Group, http://prism.oregonstate.edu). Although we know climate has changed since the mid-1800s, we do not expect the spatial pattern within the study area to have changed significantly since the time of the presettlement surveys. We used a digital elevation map (DEM) with a 10 m resolution from the USGS National Elevation Dataset (data available from the U.S. Geological Survey). From the Soils Survey Geographic Database (SSURGO) we procured spatial soils data (sand, silt, clay, organic matter, available water content [AWC], and hydraulic conductivity in saturated soil [Ksat]). Though detailed soil data is not available from the time of the historical surveys, we do not expect the patterns associated with the parent material (*i.e.*, soil texture) to vary considerably through time. Despite alterations to the rivers' floodplains and significant land-use change, we found textural differences in modern soils that are consistent with glacial patterns (Jonas and Little, 2010; *see* Results). We therefore consider this modern dataset representative of historic edaphic conditions and useful for exploring historic vegetation-environment relationships. The SSURGO dataset also included indices for current land use, such as National Commodity Crop Productivity Index (NCCPI), soil erodibility, and categorical drainage class assessments. We used the National Land Cover Database (NLCD) 2006 Land Cover layer, a 30 m grid modeling land cover in Indiana with 15 land use categories (Fry *et al.*, 2011). This layer provided the distribution of developed land, agricultural land, and modern forest.

We obtained plot-level tree species and size data from the U.S. Forest Service Forest Inventory and Analysis (FIA) for the most recent plot inventory (2009–2014). Though the PLS and FIA datasets have different survey methods that complicate comparisons between them, these two surveys have been effectively used to model forest changes in the Midwest after Euro-American settlement (Friedman and Reich, 2005; Deines *et al.*, 2016; Goring *et al.*, 2016).

Data were visualized and variables were extracted to tree locations in ArcGIS 10.4 (ESRI, Redlands, CA) and statistical analyses were conducted in R 3.2.1 (R Core Team, Vienna, Austria). All R code is available in GitHub at: https://github.com/PalEON-Project/YellowRiver_

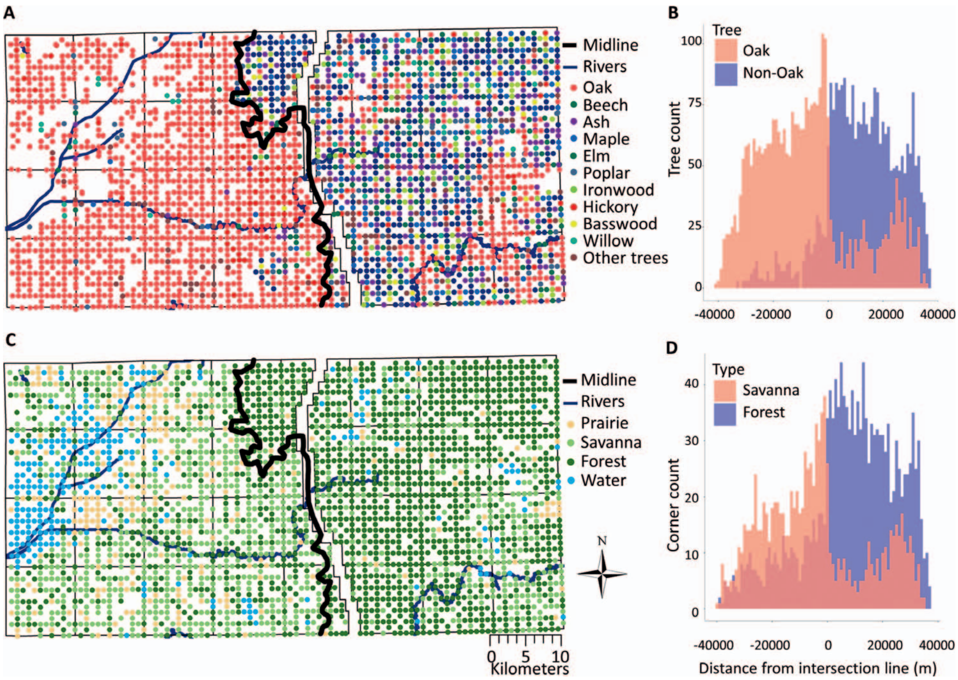

FIG. 2.—(**A**) Yellow River watershed presettlement tree composition. (**B**) Corresponding overlay histogram showing the distribution and overlap of oak (orange) and non-oak (purple) trees, according to each tree's minimum Euclidean distance (m) from the black midline that bisected the study area. (**C**) Tree density (stems/ha) at each corner with (**D**) the corresponding overlay histogram of distribution east and west of the midline. Corners were classified as savanna (orange) or forest (purple), based on the divisions in Anderson and Anderson (1975)

Indiana and data files are archived with LTER's Network Information System (NIS) Data Portal (https://portal.lternet.edu/nis/mapbrowse?scope=msb-paleon&identifier=18&revision=0).

DATA ANALYSIS

Historical prairie-forest transition.—We located trees from the referenced corner points to their surveyed locations by calculating the radian degree and distance from post in Python (package: Arcpy). We mapped all corner trees in the watershed, as well as all survey corners without a tree recorded. When the presettlement trees were mapped by species, there was a clear dominance of oaks in the western half of the watershed, and an abrupt switch to mesophytic associations in the eastern half (Fig. 2A).

To spatially quantify the east-west composition divide, we used a distance-buffer generation tool in ArcGIS to create a radius of 0.5 mi around each tree. Overlapping radii from adjacent trees from the same taxonomic group (oak or nonoak species) were dissolved to form two continuous "buffer" areas of similar vegetation type. The western buffer was composed of near-continuous oak vegetation, while the eastern buffer was dominated by several mesophytic tree taxa. Because the buffer distance did not permit the buffer groupings to combine tree areas on opposite sides of the mile-wide Michigan Road

Lands, two small but distinctly nonoak groupings just west of the Michigan Road Lands were added to the main nonoak region (*see* Supplemental Fig. S1 at https://github.com/PalEON-Project/YellowRiver_Indiana). We then created a midline between the two buffer boundaries either where they overlapped or, in the case of the Michigan Road Lands where they didn't overlap. We used this line as the border between the two ecotypes: an oak area in the west (n = 2633 trees) and a mesic area in the east (n = 3059 trees). We removed corners with no data, or corners which were illegible in the PLS notes from our analyses (n = 15). Corners with no trees listed and where the corner post was set in a mound were classified as "prairie." Corners with no trees listed because of an aboveground water feature (*e.g.*, swamp, marsh, lake, creek, river, etc.) were classified as "water." We had a total of 3004 tree, water, and prairie data points in the section west of the midline and 3122 points in the section east of the midline. To assess whether this division method was representative of the ecotone shift observed on the tree map, we calculated the percentages of each taxon in each of the two composition areas (Table 1). Because of the potentially important variation in fire and flood tolerances among oak species, we further separated trees within the oak area by species and mapped them in ArcGIS to visualize any trends in species distribution (*see* Supplemental Fig. S2 at https://github.com/PalEON-Project/YellowRiver_Indiana).

We calculated tree density (stems/ha) from PLS survey corners from the distances, diameters and azimuth compass bearings recorded for the nearest two trees, following the Morisita II plotless density estimator methods described in Goring *et al.* (2016) and using correction factors specific to Indiana (C. Cogbill, Harvard Forest, pers. comm.). These correction factors account for biases in the representation of smaller (~12–20 cm diameter) trees, azimuthal censoring of trees near cardinal directions, and surveyor bias in nearest tree selection (Goring *et al.*, 2016; Cogbill *et al.*, 2018; Morisita II estimation and specific correction factors located in GitHub repository). Corners with only one or zero trees recorded were considered to be of low density and were entered as zero density. Corners were designated as savanna (0.5–47 stems/ha) or forest (>47 stems/ha) in accordance with divisions used in Anderson and Anderson (1975). Average tree-density values were compared for corners east and west of the midline to compare vegetation structure in the two areas using a two-sample *t*-test. We excluded corners classified as water features to avoid an artificially low density estimate. Average tree diameter at breast height (dbh), as recorded by the surveyors, were also compared for trees in the east and west areas with a two-sample *t*-test. The distance from the midline to each data point was used to assess the east-west distribution of both species composition classes (oak and nonoak), and vegetation structure classes (savanna and forest).

Environmental covariates of the vegetation shift.—We spatially overlaid soil survey (SSURGO), elevation, and climate (PRISM) values to the PLS trees mapped in ArcGIS. For the eastern and western vegetation areas, we calculated average values for climate, soil characteristics and topography, and compared them using two-sample *t*-tests. We also compared drainage-class designations within each area by calculating the percentage of data points in each class on either side of the dividing line.

Using principal component analysis, we identified correlations between the environmental variables tested in this study. The variables included were: temperature, precipitation; elevation; sand, silt, and clay content; and scores for available water content (AWC) and hydraulic conductivity in saturated soil (Ksat). We compared the average first component scores for data points in the east and west regions with a two-sample *t*-test. We present results from the original data, but an arcsine transformation to minimize negative

TABLE 1.—Historic and modern vegetation. Pre-settlement (PLS data) and modern (FIA) average tree density (stems/ha), tree diameter (cm), and species representation (by percent of trees) within each buffer. Taxa with over 2% composition were included. Density and tree diameter differed historically between the two areas, but not on the modern landscape

	Historic (PLS)		Modern (FIA)	
	West	East	West	East
Average stem density	47 ± 3	183 ± 7	112 ± 22	161 ± 32
Average diameter	40.3 ± 0.3	39.8 ± 0.4	33.3 ± 1.2	35.5 ± 1.7
Taxa				
Ash	0.6	12.6	1.0	10.8
Basswood	0.4	2.5	—	—
Beech	0.4	21.2	—	—
Black gum	0.3	0.5	6.7	—
Cherry	0.1	0.3	21.0	9.2
Elm	1.2	9.3	2.9	15.4
Hickory	4.2	3.4	3.8	—
Ironwood	0.1	4.4	—	—
Maple	0.6	9.9	15.2	30.8
Oak	87.4	23.4	26.7	6.2
White	47.8	14.6	8.6	—
Black	20.4	0.8	7.6	—
Yellow[1]	8.4	0.7	—	—
Red	6.1	2.7	—	3.1
Bur	2.8	3.5	—	—
Pin	1.1	0.2	10.5	
Other hardwood[2]	2.2	4.7	17.1	46.2
Pine	0.0	—	3.8	—
Poplar[3]	1.7	5.7	—	21.5
Willow	0.8	2.1	1.9	—

[1] According to White (2005) yellow oak could be chinkapin oak (*Q. muehlenbergii*) or black oak (*Q. velutina*)

[2] Other hardwoods include: Alder, Buckeye, Birch, Hackberry, Black/Honey Locust, Mulberry, Sycamore, Tamarack, and Walnut. These taxa all represented less than 2% composition in each vegetation area (*i.e.*, eastern and western regions of the historic and modern forests)

[3] Due to the ambiguity in the common tree names used in the PLS records, Poplar could be tulip poplar (*Liriodendron tulipifera*) or aspen (*Populus spp.*)

skew yielded similar results. The east-west distribution of elevation and first component scores at each data point were assessed by their distance from the midline.

Characterizing the modern landscape.—We were interested in whether the historical east-west vegetation boundary corresponded to patterns on the modern landscape. We analyzed current forest cover from the FIA dataset to compare the modern vegetation composition, density and tree diameter (dbh) across the watershed. Within the historic eastern and western vegetation areas, we calculated plot-level density and tree diameter and compared the averages with a two-sample *t*-test. We evaluated current land use in each half of the watershed by calculating the number of historical tree and corner data points in each land use category. Using the SSURGO soils data, we also compared the average overall National Commodity Crop Productivity Index (NCCPI) rating, as well as the soils erodibility factor, for the two areas using two-sample *t*-tests.

RESULTS

STARK COMPOSITIONAL AND STRUCTURAL VEGETATION SHIFT IN HISTORIC VEGETATION

Reconstruction of the watershed's presettlement forest showed a clear dominance of oak taxa (87.4% oak species) in the west, which included white oak (*Quercus alba*), red oak (*Q. rubra*), yellow (Chinkapin) oak (*Q. muehlenbergii* or possibly *Q. velutina*), black oak (*Q. velutina*), burr oak (*Q. macrocarpa*), pin oak (*Q. palustris* or *Q. ellipsoidalis*), and jack oak (*Q. ellipsoidalis).* Individual oak species were not distributed in a way that suggested an ecological gradient (*see* Supplemental Fig. S2 at https://github.com/PalEON-Project/YellowRiver_Indiana).

The eastern portion of the study area was a mixed forest dominated by oak (*Quercus* spp.), beech (*Fagus grandifolia*), ash (*Fraxinus* spp.), elm (*Ulmus* spp.), and maple (*Acer* spp.) and to a lesser degree included alder (*Alnus* spp.), basswood (*Tilia americana*), birch (*Betula* spp.), black gum (*Nyssa sylvatica*), buckeye (*Aesculus* spp.), cherry (*Prunus* spp.), hackberry (*Celtis occidentalis*), hickory (*Carya* spp.), ironwood (*Carpinus caroliniana* and *Ostrya virginiana*), locust (*Robinia pseudoacacia* or *Gleditsia triacanthos),* mulberry (*Morus* spp.), pine (*Pinus* spp.), poplar (*Populus* spp.), sycamore (*Platanus occidentalis*), tamarack (*Larix larcina*), tulip poplar (*Liriodendron tulipifera*), walnut (*Juglans* spp.), willow (*Salix* spp.), and unidentified hardwoods (Fig. 2A, Table 1).

The composition shift followed a discrete increase in tree density moving eastward (Fig. 2C). Tree density was significantly higher in the eastern area than in the west (mean [m $\pm$ SE]; West: 47 $\pm$ 3 trees/ha; East: 183 $\pm$ 7 trees/ha; $P < 0.001$; df = 3097). These average densities for the western and eastern ecotypes are consistent with Anderson and Anderson's (1975) definition of savanna and forest, respectively. There was no difference in tree diameter between the two areas (mean dbh [cm] $\pm$ SE; West: 40.3 $\pm$ 0.3; East: 39.8 $\pm$ 0.4 cm; $P = 0.3$; df = 5672). The structural and compositional shifts in vegetation are both spatially synchronous and sharp (Fig. 2B, D).

Upon mapping the vegetation structure and composition, a small region within the eastern area, clustered around the headwaters of the Tippecanoe River, appeared to resemble the western oak side based on taxa and structure metrics (*see* Supplemental Fig. S3 at https://github.com/PalEON-Project/YellowRiver_Indiana). This oak-dominated subregion in the east was selected using the same buffer tool and radius distance, yielding a 280 km^2 oak "island" including n = 617 trees and n = 322 survey corners (Fig. S3). When we compared the composition and structure of the small oak island within the larger eastern mesophytic area with the two main vegetation regions (the western oak region and the eastern mixed-forest region), the eastern oak island was dominated by oaks (62.3%) but had up to 7% representation of some mesophytic taxa such as beech and elm. An ANOVA, followed by a Tukey HSD post-hoc test, showed that average tree density in this eastern oak island differed significantly from both the main eastern mixed-forest and western oak vegetation types ($F[2,3411] = 166.5$; all comparisons $P < 0.01$; mean oak island 88 $\pm$ 9 trees/ha; *see* Supplemental Fig. S4a at https://github.com/PalEONProject/YellowRiver_Indiana).

ENVIRONMENTAL CHARACTERIZATION OF THE LANDSCAPE

Climate across the watershed was not significantly different ecologically. Although the average temperature was statistically higher in the eastern area (mean [C $\pm$ SE]; West: 9.85 $\pm$ 0.001; East: 9.92 $\pm$ 0.001; $P < 0.001$; df = 6124) and the precipitation higher in the west (mean [mm] $\pm$ SE) West: 1010.4 $\pm$ 0.2; East: 1005.7 $\pm$ 0.3; $P < 0.001$; df = 6124), we suspect the difference is due to sample size and is not ecologically significant because the difference between the means is very small.

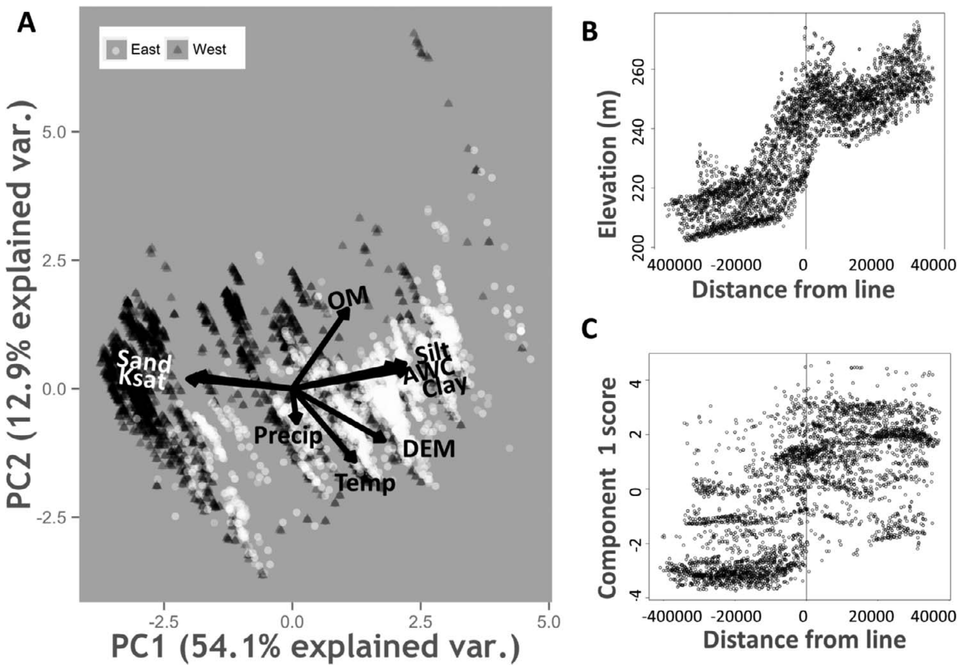

FIG. 3.—Environmental gradient of the watershed. (**A**) Principal component analysis biplot showing the variance explained by the first principal component (54.1%) and second principal component (12.9%). High sand content and Ksat (hydraulic conductivity in saturated soil) scores are associated with trees in the western oak area (gray triangles), whereas high elevation, silt and clay content and available water content are associated with trees in eastern mixed hardwood area (white circles). (**B**) Elevation and (**C**) First principal component scores are shown at the minimum Euclidean distance (m) from the black midline that bisected the study area (Fig. 2)

The elevation in the watershed varied significantly between the two historic ecotypes. Trees in the west were at a significantly lower average elevation than trees in the east (mean (m ± SE); West: 222.0 ± 0.2; East: 251.7 ± 0.1; $P < 0.001$; df = 6124). This moderate 30 m difference followed the vegetation transition (Fig. 3B, *see* Supplemental Fig. S5 at https://github.com/PalEON-Project/YellowRiver_Indiana) and is the most significant topographical feature in this flat region.

In the west 148 corners were classified as prairie and 223 were classified as water features. In the east there were 17 prairie corners, and 46 corners were water features. These survey notes suggest differing extents of low tree-density area and hydrological features between the regions. These observations were reinforced when each point location was matched to the soil survey natural drainage condition and the percentage of trees in each drainage category was compared in the two areas. More points in the western oak region were in drained areas (*i.e.*, the SSURGO categories of excessively drained, somewhat excessively drained, well drained, and moderately drained; West: 50.8 vs. East: 33.7%).

Results from the principal component analysis linked soil characteristics with the vegetation shift seen in the watershed. The first component accounted for most (54.1%) of the variance, with the second and third components explaining only 12.9% and 11.2%, respectively. The western oak area had low first component scores, which were associated with high sand content and Ksat scores – factors that facilitate soil drainage (Fig. 3A, *see* Supplemental Table S2 at https://github.com/PalEON-Project/YellowRiver_Indiana). High clay and silt content, high AWC scores, and higher elevation contributed most strongly to high first component scores and were associated with the eastern mesophytic forest (mean [m] ± SE; West: –1.53 ± 0.03; East 1.47 ± 0.02; $P < 0.001$; df = 6124). Because our vegetation division was an east/west divide, we plotted the scores of the first principal component in relation to their east/west distance relative to the midline. This showed a distinctly different eastern and western environment, and a transition that was spatially synchronous with the vegetation division (Fig. 3C). For the eastern oak island region, the average PC component 1 (0.55 ± 0.06) was intermediate between that of the larger east and west regions. An ANOVA showed average PC component 1 score varied significantly between the west, east, and smaller eastern oak area ($F[2, 6740] = 2692$, $P < 0.001$; *see* Supplemental Fig. S4b).

CURRENT LANDSCAPE

The amount of wooded area has decreased drastically on the modern landscape. From the National Land Cover database, few presettlement data points to the east (11.5%) and west (4.9%) of the midline are currently classified as deciduous forest. FIA survey data showed no difference in the east and west side of the study area in tree diameter (dbh) or stem density (mean dbh [cm ± SE]; West: 33.3 ± 1.2; East: 35.5 ± 1.7; $P < 0.28$; df = 168; mean stem density [stems/ha ± SE]; West: 112 ± 22; East: 161 ± 32; $P < 0.23$; df = 18; Table 1). Across the watershed, remaining vegetation has stem densities indicative of closed forest (i.e., stem density >47 stems/ha, Anderson and Anderson, 1975). Mesophytic species now dominate in both regions. The historically dominant taxa in the presettlement vegetation, oak and beech, have both decreased markedly on the modern landscape (Table 1).

Crop productivity ratings were higher in the east than the west (mean [m] ± SE; West: 0.53 ± 0.28; East 0.68 ± 0.22; $P < 0.001$; df = 6124). This difference was reinforced when current land use was assessed in the watershed. More PLS data points in the east fall in modern cultivated cropland (West: 33.7% vs. East: 38.1%), whereas the western vegetation area includes more modern forested land (West: 11.5% vs. East: 4.9%; Fig. 4).

DISCUSSION

Based on the historical vegetation data, we found a sharp contrast in both composition and structure, delineating a discrete savanna-forest transition within the Yellow River watershed. The closed forest in the east had several well-represented mesophytic species. It was compositionally and structurally distinct from the open savanna in the west, which had over 75% oak composition. This is similar to the results of early vegetation surveys in nearby areas (Kenoyer, 1933; Elton, 1970; Bowles and McBride, 2001), and it provides detail to Transeau's (1935) simpler prairie-forest division of the watershed. Our results outline sharp boundaries between savannas and forest in the locality, rather than a gradual, continuous forest change on the prairie-forest boundary that has been demonstrated in places such as Wisconsin (Curtis and McIntosh, 1951). This does not preclude the possibility of a larger gradient that other regional-scale studies have described, in which broad climate gradients can differentially affect vegetation (Grimm, 1984; Anderson, 1998). However, at this eastern edge of the Prairie Peninsula, the shift from the moderately drought-tolerant white oak to beech-maple dense forest was a sharp transition.

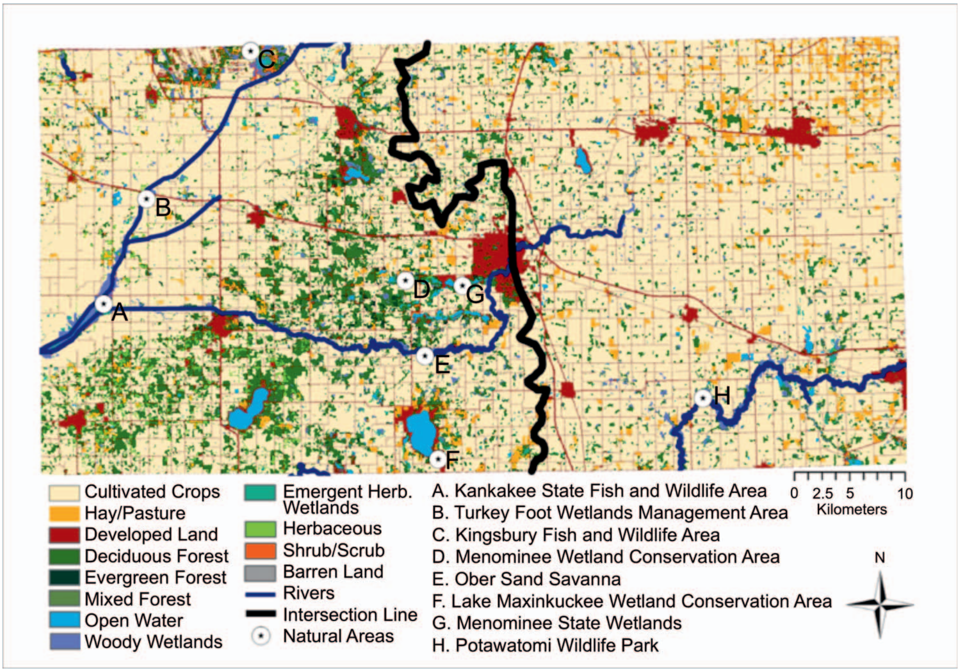

FIG. 4.—Modern-day land use. 2006 land use of the Yellow River watershed in each historic vegetation area (overlaid with the black midline that separates the east mixed forests from the west oak savannas in the PLS maps). The eastern area historically had more trees in area but is now cultivated cropland (light yellow; West: 33.7% vs. East: 38.1%) whereas the historical western savanna now includes more modern deciduous forested land (green; West: 11.5% vs. East: 4.9%). Nature preserves, parks and other green spaces within the study region are marked with black stars in white circles

An environmental gradient tracked the historic vegetation shift in the watershed. Poorly drained fine-textured soils in the east give way to sandy well-drained soils in the west. These results support previous research that has associated white oaks with coarse-grained soils (Kenoyer, 1933; Haney *et al.*, 2008). Yet these studies also noted closed mesophytic forest on sandy soil where fire was excluded, suggesting a strong but not absolute association of soil with vegetation type. Likewise, the vegetation-soil relationship was not tight throughout the Yellow River watershed: we identified a small island of open oak vegetation within the eastern ecosystem, in an intermediate, but generally mesic environment. This pattern would be expected if soil influences vegetation composition and structure principally through its interaction with fire (Grimm, 1984). The large savanna region in our study area was in a glacial outwash plain and was significantly lower in elevation than the eastern forest (Jonas and Little, 2010). This elevation difference closely follows the vegetation transition and is fairly sharp and could have served as a partial firebreak. However, the elevation difference is unlikely to be large enough to act as a complete firebreak, especially because moderate uphill slopes generally encourage fire (Whelan, 1995; Anderson, 1998) and does not appear to completely explain the historically sharp ecotone.

Unlike historic vegetation, modern vegetation in our analysis does not change with soil and elevation. We found that woodlands in the oak savanna area have closed and become more mesophytic since the presettlement surveys. These structural and compositional changes are accompanied by some environmental alterations: the Grand Kankakee Marsh system was drained at the turn of the century, and fire suppression has changed vegetation in northwest Indiana and throughout the Great Lakes region (Downey *et al.*, 1909; Paulson *et al.*, 2016). This descriptive case study cannot demonstrate ecological mechanisms, but the distinct historic and modern vegetation patterns suggest the modest environmental gradient in the watershed may be amplified by the region's hydrology and fire ecology. Brewer and Vankat (2004) describe how, in Ohio open oak systems, lower elevation and wetter conditions aid herbaceous plant undergrowth during spring floods, and this growth fuels late-season burns and keeps tree density low. Similarly, flood and fire processes such as these may help maintain savanna conditions in the low, sandy, seasonally wet region described in this study. This hypothesis would explain why vegetation followed soil and elevation differences in the past but ceased to do so once spring flooding was prevented and fires were suppressed. These processes may have also supported the small eastern oak island in the clay-heavy uplands. Despite sharing a similar soil environment to the closed forest around it, the oak island's proximity to the Tippecanoe River headwaters and slightly lower elevation may have allowed for spring inundation and subsequent herbaceous fuel buildup for fires. Further study is needed to evaluate the importance of these processes in our study system and across the ecotone and to test these hypotheses mechanistically.

This study site adds to a larger exploration of the prairie-forest ecotone, and its patterns appear distinct from drier western sites. For example, Thomas and Anderson (1990), as well as Brugam *et al.* (2016), associated oak savannas with uplands in Illinois. Abrams (1992) proposed drier upland sites select more strongly for oak species adapted to less water, low nutrients, and frequent fire, but our eastern upland site may be too wet for such an upland-oak association to occur. Other studies in Indiana conclude that seasonal flooding decreases fire effects in pin oak stands, as it confers protection from spring fires (Haney *et al.*, 2008). This contrasts with the amplifying role of fall fires in driving vegetation described in Brewer and Vankat (2004). Danz *et al.* (2011) suggests the relationships between vegetation and the environment are diverse spatially and at different scales. This proposition could explain the different patterns found along the ecotone, and it emphasizes the value of local, detailed studies of the prairie-forest boundary, such as this one.

Despite drastic changes to tree composition, forest structure, and the environment since the mid-1800s, we found evidence that the pattern of the historical ecotone is subtly preserved on the modern landscape. Contrary to our prediction, there was more cropland in the eastern section, on soil that was rated to be more productive. Furthermore, more land in the west has remained or has reverted to deciduous forest, although with a different composition and structure compared to the early 1800s. Other studies along this boundary have suggested sandy, low-nutrient soils were able to support high forest productivity but have deteriorated after agricultural disturbances (Reich *et al.*, 2001). The reason the two historic ecosystems are currently characterized by similar closed forest but distinct differences in crop production is still unclear. This surprising result does, however, reinforce that the landscape's history may be of particular interest to land managers and those involved in maintaining or restoring natural areas.

Though little land in our study area is currently forested, there are still several preserves and natural areas throughout our study area (Fig. 4). Although the whole watershed is heavily farmed, organizations such as the Nature Conservancy and the Soil and Water Conservation Districts work with private landowners in our study area who wish to restore natural habitats on their farms (A. Kautz, Elkhart Soil and Water Conservation Districts, pers. comm.). Depending on the goals of these projects, historical land cover information may aid decision-making. Chicago Wilderness, for example, works to manage, connect, and expand remnant savanna ecosystems in Illinois and have recently expanded their work in Indiana, where historical information such as we present here may optimize those efforts (Fahey *et al.*, 2015). Furthermore, transitions of savannas to closed forest present an example of hysteresis, in which feedbacks such as wetter ground and exclusion of flammable herbaceous vegetation on the modern landscape make it difficult and costly to revert to the original ecosystem (Staver *et al.*, 2011). This process may be slower and less severe on drier sites, so considering environmental gradients may help target restoration efforts to particularly favorable sites (Nowacki and Abrams, 2008). This detailed look at the savanna-forest ecotone explores the factors shaping this area's historic landscape mosaic, and it suggests that this vegetation history may still have implications for the modern landscape.

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