Reconstructing Vegetation Past: Pre-Euro-American Vegetation for the Midwest Driftless Area, USA

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ABSTRACT

Historical reference conditions provide important context for creating ecological restoration and management plans. The U.S. 19th Century Public Land Survey (PLS) records provide extensive ecological information for constructing such reference conditions. We used PLS records to reconstruct pre-Euro-American tree species cover class and vegetation structure types for the Midwest Driftless Area, a 55,000 km² region currently experiencing multiple conservation threats. We related cover classes to soil texture, topographic roughness, and distance from waterway. Our analyses revealed that the landscape of the Driftless Area was mostly composed of savanna, with two large patches of closed forest and smaller, scattered patches of closed forest, open woodland, and prairie. The Driftless Area was heavily dominated by a variety of oak communities, with bur (*Quercus macrocarpa*), white (*Q. alba*), and black (*Q. velutina*) oak by far the most dominant species across the region. A variety of non-oak communities occurred within the closed forest patches, along rivers, or in smaller areas near the periphery of the region. The prevalence of savanna and oak communities indicates that fire played a key role in mediating historical landscape patterns and ecosystem processes in the region. Variation in soil texture, topographic roughness, and distance from waterways additionally contributed to the diversity of cover classes present prior to Euro-American settlement. Restoration practitioners can use our reconstructions to inform regional and site-specific restoration planning. Because oaks tend to be foundational species within ecosystems and are currently in decline throughout the Driftless Area, restoration activities that encourage these species are urgently needed.

Keywords: historical reconstruction, oak savanna, reference conditions, U.S. Public Land Survey (PLS), vegetation mapping

Ecological restoration efforts often seek to enhance the resilience and sustainability of ecosystems by directing them toward conditions that fall within their historical range of variability (HRV), as measured by composition, structure, and/or function (Landres et al. 1999, Keane et al. 2009). HRV focuses not on a single condition, but indicates the range of conditions possible within a given environmental context (Swetnam et al. 1999) and over a geographical extent relevant to management goals (Landres et al. 1999, Keane et al. 2009). The first steps in using information on HRV to restore ecosystems involves the identification of reference conditions and the development of knowledge regarding the processes that contributed to development of those conditions and their variability across landscapes (Landres et al. 1999).

There are several means by which reference conditions can be determined, including the study of contemporary ecological reference areas (e.g., prairie remnants, old-growth forest reserves); elements of past ecosystems as preserved in the contemporary environment (e.g., tree rings, fossilized pollen or charcoal layered in lake sediments); human records of ecosystem conditions (e.g., accounts of explorers, land survey records, landscape paintings or photographs); or by simulating past dynamics using ecological models (Egan and Howell 2001). The U.S. General Land Office's original Public Land Survey (PLS) records have been widely used to reconstruct past vegetation and disturbance dynamics, assess vegetation change over time, and contribute to the general understanding of HRV (Schulte and Mladenoff 2001). PLS records provide one of the most thorough and extensive descriptions of vegetation in the U.S. for the period just prior to Euro-American settlement (Schulte and Mladenoff 2001). While some inconsistencies and biases have been documented within the survey records (Bourdo 1956, Manies et al. 2001, Liu et al. 2011), PLS data provide a reasonable representation of pre-Euro-American vegetation when they are used in a relative way, over broad spatial scales, and in combination with other historical data sources (Schulte and Mladenoff 2001).

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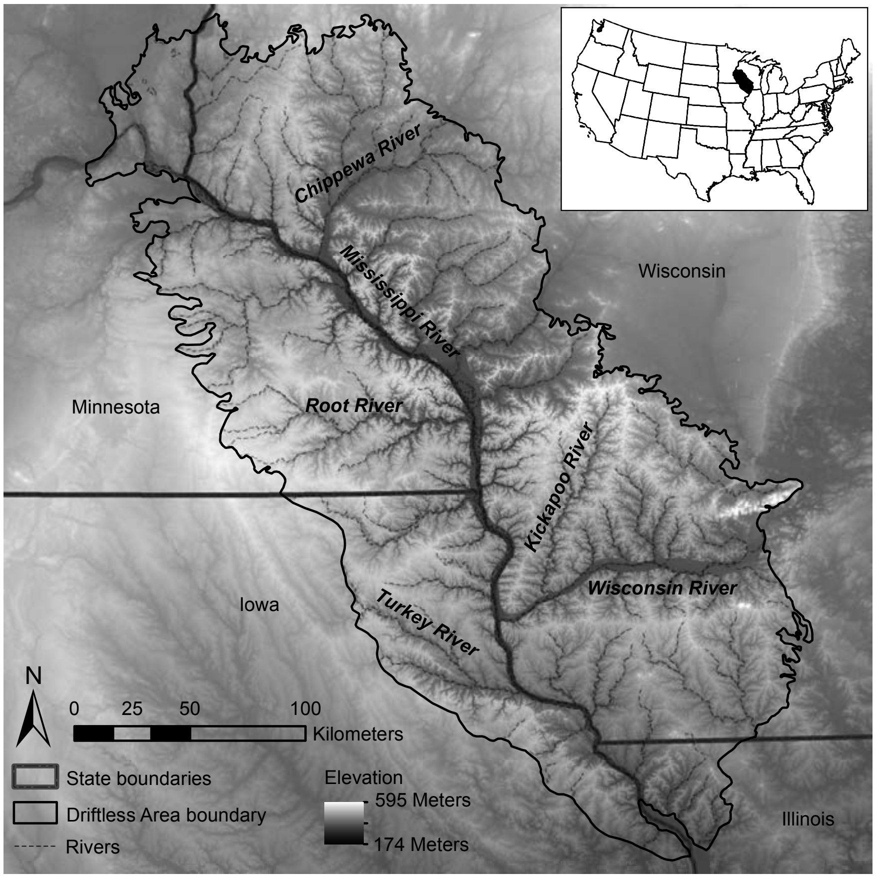

Figure 1. Elevation and major rivers of the U.S. Midwest Driftless Area; inset shows the location of the Driftless Area in the U.S. Elevation obtained from National Elevation Dataset (USGS 1999).

We sought to reconstruct pre-Euro-American vegetation and identify reference conditions for the Driftless Area of the U.S. Midwest using PLS data. This 55,000 km² region is composed of portions of southwestern Wisconsin, southeastern Minnesota, northeastern Iowa, and northwestern Illinois (Figure 1) not covered by glacial ice during the Late Wisconsin glaciation of the Quaternary Period (Hobbs 1999). Because it escaped this most recent glacial advance, the region has high levels of topographic variation and contains a distinctive array of plant communities and several preglacial relict species absent from surrounding regions (Curtis 1971, USFWS 2006). Native vegetation communities in the region are experiencing dramatic ecological change due to habitat loss and fragmentation; lack of fire; introductions of exotic plants, pests, and diseases; climate change; and high rates of deer herbivory, among other reasons (Rooney and Waller 2003, Schulte et al. 2008, Taft et al. 2009, Knoot et al. 2010, Fan et al. 2013). Of particular concern is the widespread replacement of oak forests, woodlands, and savannas by late-successional mesic hardwood forests (Rhemtulla et al. 2009, Knoot et al. 2010).

Government agencies and non-governmental organizations recognize the need for restoration in the Driftless Area (ILDNR 1998, WIDNR 2005, MNDNR 2006, USFWS 2006, IADNR 2007, NRCS 2013), though efforts have tended to be piecemeal and uncoordinated, partly because the Driftless Area falls under multiple state jurisdictions (T. Knoot, Wisconsin DNR, unpub. data). A consistently derived set of reference conditions, along with an understanding of the factors that influenced their formation, may facilitate successful restoration in the Driftless Area. In our study, we addressed this need with the following objectives: 1) to reconstruct pre-Euro-American tree composition and vegetation structure in the Driftless Area; and 2) to relate tree composition to potential environmental drivers. Our overarching goal was to inform the development of HRV reference benchmarks for use in Driftless Area restoration planning.

Methods

Study Area Description

The climate of the Driftless Area is continental (mean annual precipitation = 82 cm) with hot, humid summers (mean July temperature = 22.3°C) and cold, dry winters (mean January temperature = –9.7°C; Wendland et al. 1992). The topography of the Driftless Area is steeply dissected by numerous rivers and small, coldwater streams, with elevations ranging from 176 m to 523 m (USGS 1999). The Mississippi and Wisconsin Rivers are two major rivers that dissect the region (Figure 1). Bluffs along the Mississippi River can span 150 m from base to top. The average slope is 11.8% (± 14.1 SD), but slopes of 10–40% are frequently encountered and sometimes exceed 100% (USGS 1999). The dominant soil texture in the southern and western portions of the Driftless Area is mainly silt, with more sandy soils in the north, on the eastern edge, and along some rivers; clay soils are rare (NRCS 2010).

Public Land Survey Records

PLS records provide the earliest (mid-1800s) spatially explicit data on landscape conditions in the Driftless Area. Surveyors delineated 1.6 km by 1.6 km sections by marking section corners and quarter corners (halfway between section corners) with a monument and recording information on two to four nearby witness trees, noting tree species, diameter, and distance from the corner. Stewart

(1935) and Bourdo (1956) provide full descriptions of the survey and ecological information contained within. We used a geodatabase compiled by Grubh (2010), who digitized and georeferenced the original PLS witness tree records for the Iowa and Illinois portions of the Driftless Area and combined them with previously georeferenced PLS records for the Wisconsin and Minnesota portions of the Driftless Area. Of the 105,233 witness tree records contained in the geodatabase, 12.9% were ambiguously identified only to the genus level across ten genera. Using methods developed by Mladenoff and others (2002), Grubh (2010) systematically differentiated 25.3% of ambiguously identified trees to species within four genera that were well-represented across the dataset, including oak (*Quercus*), maple (*Acer*), pine (*Pinus*), and ash (*Fraxinus*). The remaining ambiguously identified witness trees, including aspen (*Populus*), birch (*Betula*), elm (*Ulmus*), and hickory (*Carya*), remained in the dataset, classified by genus. American hornbeam (*Carpinus caroliniana*) and hophornbeam (*Ostrya virginiana*) were additionally classified together as "ironwood."

Classification of Historical Tree Species Cover and Vegetation Structure

We used relative dominance of the 28 most commonly recorded tree genera or species (hereafter referred to as species) to categorize cover types. For each survey section, we calculated basal area of all witness trees associated with the section corners and quarter corners along the section perimeter. We calculated relative dominance (RD) of tree species for each section using the following formula:

$$RD = \left(\frac{\sum_{j=1}^{m} \text{basal area}_{ij}}{\sum_{i=1}^{n} \sum_{j=1}^{m} \text{basal area}_{ij}} \right) \times 100$$

where m is the number of individuals of a given species, n is the overall number of species in a section, and basal area_{ij} is the basal area of individual j of species i.

We used the two-step cluster analysis method developed by Schulte and others (2002), which uses the iterative FASTCLUS procedure followed by hierarchical agglomerative clustering within SAS (SAS v. 9.3, SAS Institute, Cary, NC), to categorize the section-level relative dominance data into tree species cover classes. We chose a cutoff of < 0.05 increase in R^2 to determine the number of output clusters from FASTCLUS. Hierarchical agglomerative clustering was used to statistically define and graphically depict relationships between the clusters identified through FASTCLUS. We pruned the resulting dendrogram to eliminate rare or spurious groups so that each final cluster contained at least 1% of the total number of sections. Clusters that did not pass the 1% rule were combined with the most closely related cluster. We named the final cover classes following the criteria: 1) single-species cover classes were named for clusters where the most dominant species had greater than 40% relative dominance and was at least twice as dominant as the next ranking species; 2) double-species cover classes were named for clusters that did not meet the first criteria and where the sum of the relative dominance of the two highest ranking species was greater than 60% and individually were at least twice as dominant as the third-ranking species and; 3) for clusters that did not meet the first two criteria, mixed-species cover classes were named after the four most dominant species. Sections that had no witness trees recorded on them were excluded from the cluster analysis because they had no relative dominance values associated with them, and were given a "No Trees" cover class designation.

We based our classification of vegetation structure on tree density, which we calculated using a modified version of the point-centered quarter method applied to PLS data (Bolliger et al. 2004). Tree density (trees/ha) was calculated with this method for each section and quarter corner using distances of trees from survey points and averaged to derive a density estimate for each section. We classified sections with similar tree densities into the following structural categories: prairies, having less than 0.5 trees/ha; savannas, having 0.5 to less than 47 trees/ha; open woodlands, having 47 to 99 trees/ha; and closed forests, having greater than 99 trees/ha (Anderson and Anderson 1975).

Statistical Analysis of Cover Class Associations with Environmental Factors

We analyzed the relationships between tree species cover classes and three environmental factors: soil texture, topographic roughness, and distance from waterway (Figure 2). Environmental data were processed in ArcGIS (v. 10.0, ESRI, Redlands, CA). Soil texture was identified from the SSURGO database (NRCS 2010), from which we recorded the majority textural class (sand, silt, clay) for each section. We calculated topographic roughness for each section as the ratio of the three-dimensional surface area to the planar surface area (Stambaugh and Guyette 2008), based on the 10-m digital elevation model (USGS 1999). We created categories for topographic roughness by splitting the data into equal-sized quantiles: low (< 1.002383), medium (1.002383–1.009251), medium-high (1.009252–1.026601), and high (> 1.026601). Distance from waterway was measured from the center of the section to the closest waterway; waterway data were obtained from the National Atlas of the United States (2005) and included only higher-order perennial streams as displayed at the 1:2,000,000 scale. Distance from waterway was categorized into the following classes, based on equal-sized quantiles rounded to the nearest tenth of a kilometer: < 1.5 km, 1.5 km–3.2 km, 3.3 km–5.5 km, and > 5.5 km.

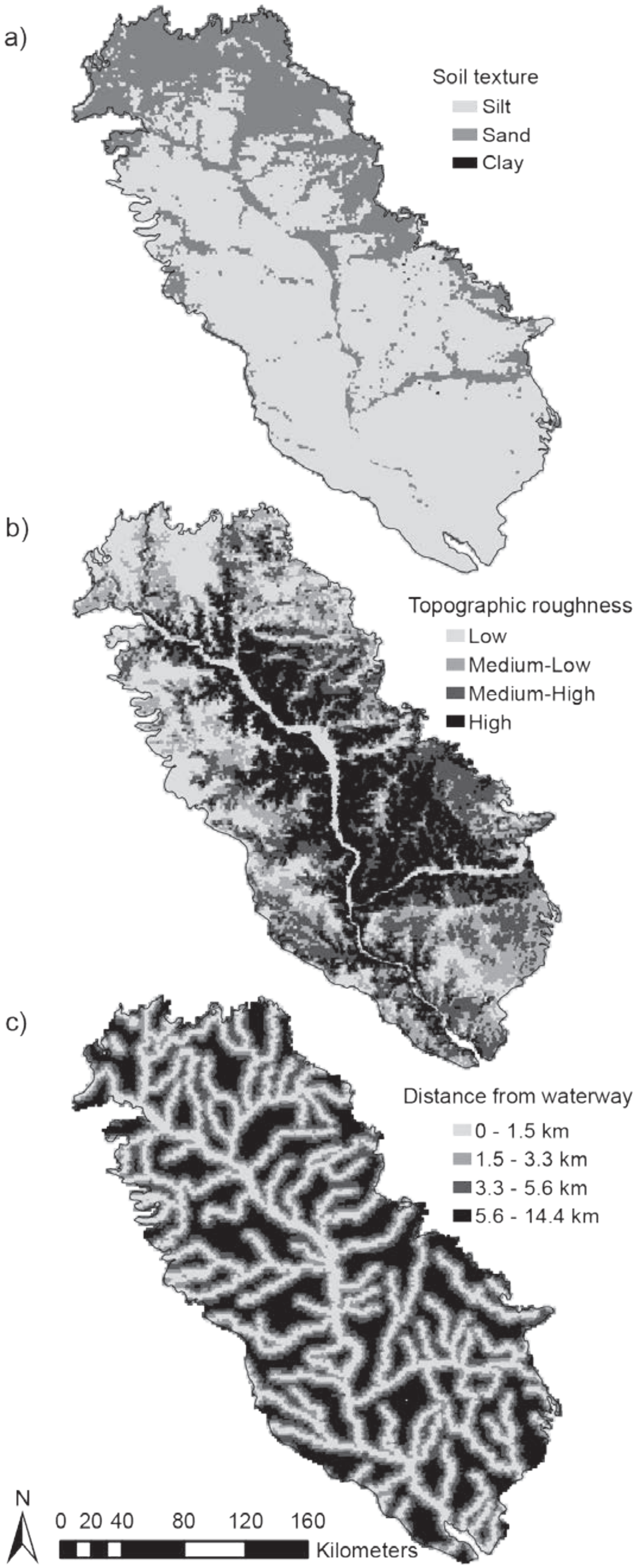

Figure 2. U.S. Midwest Driftless Area: a) soil texture, b) topographic roughness, and c) distance from waterway classes. Each cell represents a Public Land Survey-designated section.

We analyzed relationships between tree species cover classes and environmental factors using contingency table analysis and standardized residuals (Haberman 1973, Strahler 1978). Contingency table analysis has been used in several studies to analyze the relationship between PLS data and environmental factors (Whitney 1982, Whitney 1986, Leitner et al. 1991, Black et al. 2002), while others have used regression models (Iverson et al. 1988, Batek et al. 1999). We tallied the sections based on cover class and the associated environmental factor category. Tallies were conducted separately for the three environmental factors and used in contingency table analyses; the maximum likelihood ratio (G-test) was used to test whether significant relationships existed between each cover class and each environmental factor ($\alpha = 0.05$). Because only eight sections had clay as the majority soil type, we excluded those sections from the contingency table analysis for soil. We calculated standardized residuals for the environmental factors and cover classes that were significantly related to evaluate relationships between the environmental factor categories and cover classes (Haberman 1973, Strahler 1978). These standardized residuals allow relationships between the different cover classes to be compared to one another in a relative manner (Haberman 1973). We classified associations between cover classes and environmental factors as strong (> 10), moderate (5–10), and weak (< 5) based on the absolute value of the standardized residual. Positive standardized residual values indicate a positive relationship and vice versa. All statistical operations were performed in SAS (v. 9.3, SAS Institute, Cary, NC).

Results

Bur oak (*Quercus macrocarpa*), white oak (*Q. alba*), and black oak (*Q. velutina*) were the most commonly recorded tree species in the Driftless Area, collectively accounting for 72.6% of all

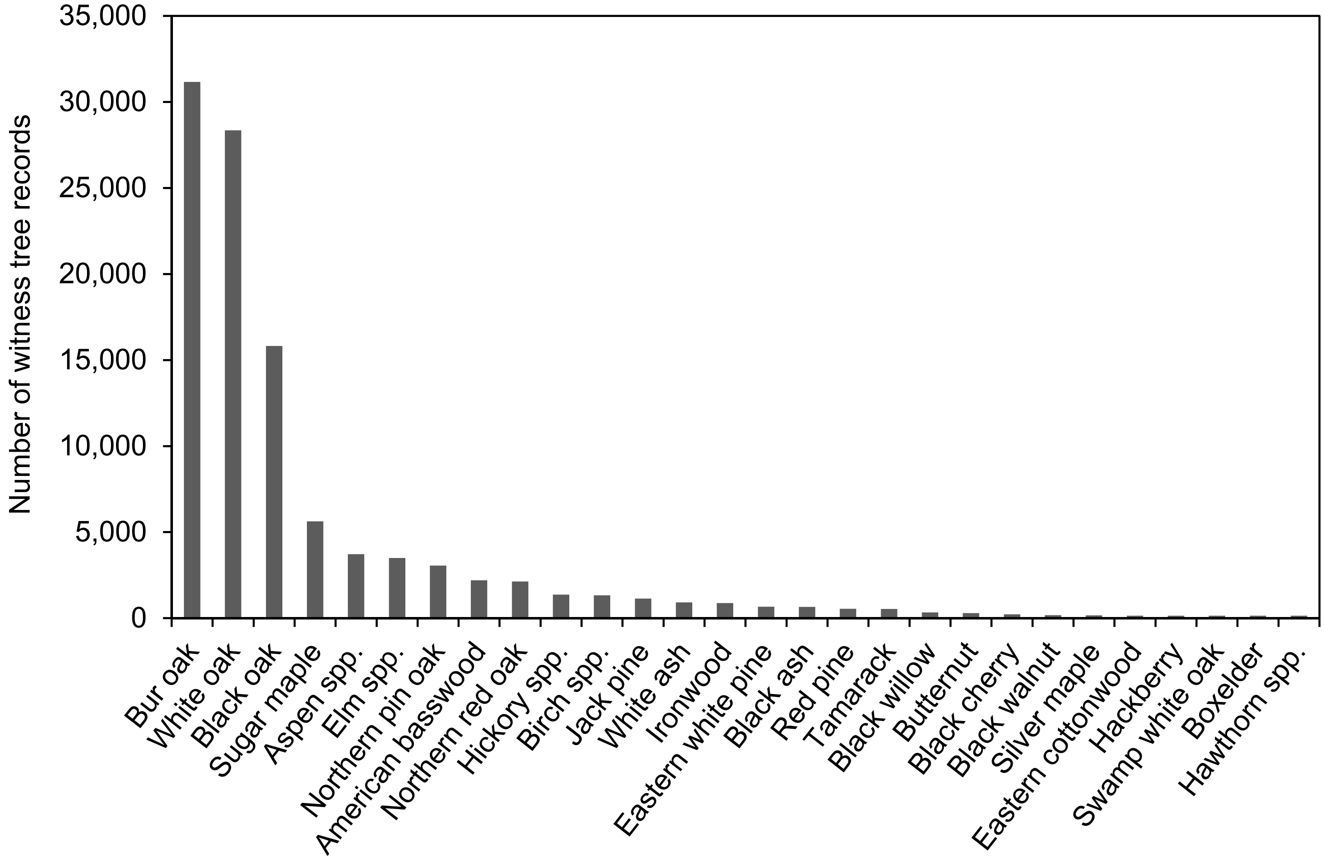

Figure 3. Frequency of witness trees recorded in the original Public Land Survey records for the U.S. Midwest Driftless Area. Taxa comprising greater than 0.04% of the data shown here. 'Ironwood' represents a combination of American hornbeam (*Carpinus caroliniana*) and hophornbeam (*Ostrya virginiana*).

witness trees (Figure 3). These species, along with less common northern pin oak (*Q. ellipsoidalis*), northern red oak (*Q. rubra*), and swamp white oak (*Q. bicolor*), occurred throughout the region, though the relative dominance of each species varied geographically (Figure 4, page 423). Sugar maple (*Acer saccharum*), elm species, American basswood (*Tilia americana*), ironwood, butternut (*Juglans cinerea*), black cherry (*Prunus serotina*), and black walnut (*Juglans nigra*) all occurred largely in two distinct areas, one between the Kickapoo and Wisconsin Rivers and the other just to the north of the Mississippi River in western Wisconsin. Sugar maple and elm species also occurred along the Mississippi River corridor. Other deciduous species occurred mainly along river corridors, particularly birch species, white ash (*Fraxinus americana*), black ash (*Fraxinus nigra*), black willow (*Salix nigra*), silver maple (*Acer saccharinum*), eastern cottonwood (*Populus deltoides*), hackberry (*Celtis occidentalis*), and boxelder (*Acer negundo*). Tamarack (*Larix laricina*) and the three pine species, jack (*Pinus banksiana*), red (*P. resinosa*), and eastern white pine (*P. strobus*), were largely confined to northeastern part of the Driftless Area. Aspen species occurred throughout the Driftless Area and was dominant in northern portions of the region.

Vegetation Cover Type Classification

Cluster analyses on tree relative dominance values produced 19 initial clusters (Figure 5, page 425) Pruning the dendrogram so that each cluster contained at least 1% of the cells resulted in 14 final cover classes (Table 1, page 424). There were eight oak-dominated cover classes, accounting for 85.5% of the Driftless Area (Figure 6a, page 426). Most cover classes were scattered throughout the region, but some concentrated in certain areas. The White Oak cover class was most common in the southeast; Bur Oak commonly occurred in the western portion of the Driftless Area; a large patch of Northern Pin Oak was found immediately south of the Wisconsin River; Red Oak-White Oak was concentrated near the eastern edge; White Oak-Sugar Maple-Basswood-Elm often occurred adjacent to the Sugar Maple cover class. The Sugar Maple cover class was clustered in two distinct areas east of the Mississippi River, one in the north and one in the southeast, and also occurred in smaller patches in the west and along the Mississippi River. Also occurring adjacent to these maple-dominated areas was the Elm cover class. The Birch-White Ash-Sugar Maple-Elm cover class occurred in the north, as well as along the middle portion of the Mississippi River. The Aspen and pine cover classes, Jack Pine-Red Pine and White Pine, occurred mainly in the northern to northeastern portions of the Driftless Area.

Vegetation Structure Classification

Classification of vegetation structure based on stem density revealed that the Driftless Area was historically dominated by savannas, making up 69.4% of the area, interspersed with closed forests, open woodlands, and prairies (Figure 6b, page 426). Closed forests, at 15.3% of the Driftless Area, mainly occurred in two large patches—one in the north and one in the southeast—although smaller patches of closed forest were scattered throughout the region. Open woodlands, which made up 8.6% of the area, were scattered in small patches throughout savanna and along the edges of closed forest. Prairie occurred in only 6.9% of the Driftless Area in a number of large patches adjacent to savanna, except for a large patch in the north abutting closed forest.

Oak-dominated cover classes were largely associated with savannas, most with greater than 70% of their sections designated as savanna (Figure 7, page 427). Jack Pine-Red Pine and White Pine cover classes were also associated with savanna, with 75.6% and 71.4% of their sections designated as savanna, respectively. The cover class with the greatest percentage of sections in closed forest was Sugar Maple (69.1%). White Oak-Sugar Maple-Basswood-Elm, Aspen, Elm, and Birch-White Ash-Sugar Maple-Elm cover classes were associated with both closed forest and savanna. The percentage of sections in open woodland was low for all the cover classes, ranging from 3.6% (Bur Oak-White Oak) to 16.9% (White Oak-Sugar Maple-Basswood-Elm). The No Trees cover class had 100% of its sections occurring in prairie. Otherwise, there was very little of the other cover classes occurring in prairie, ranging from 0 (Red Oak-White Oak) to 4.6% (Northern Pin Oak).

Vegetation-Environment Associations

All cover classes were significantly related to each of the environmental factors (Table 2, page 427). Standardized residuals illustrate the relationship between cover classes and environmental factors (Figure 8, page 428). White Oak was strongly associated with silt-dominated soils and had a strong negative association with short distance from waterways; Bur Oak showed a similar association with silt-dominated soils and was associated with far distance from waterways, but these associations were weak. White Oak was strongly associated with medium-high and high topographic roughness and had a strong negative association with low topographic roughness while Bur Oak was strongly associated with low and medium topographic roughness and had a strong negative association with high topographic roughness. The combined Bur Oak-White Oak class was moderately associated with medium and medium-high topographic roughness and had a strong negative association with low topographic roughness. The Black Oak, Northern Pin Oak, and Red Oak cover classes were associated with sandy soils, medium-high to high topographic roughness, and farther distance from waterways, though these associations were relatively weak for Northern Pin Oak and Red Oak. The remaining oak-dominated cover classes—Bur Oak-Black Oak-White Oak-Aspen and White Oak-Sugar Maple-Basswood-Elm—were associated with closer distances to waterways; the association was strong for Bur Oak-Black Oak-White Oak-Aspen. Bur Oak-Black Oak-White Oak-Aspen was moderately associated with sandy soils. White Oak-Sugar Maple-Basswood-Elm was strongly associated with high topographic roughness and had a strong negative association with low topographic roughness. The Sugar Maple cover class showed weak associations for silt-dominated soils and short distance from waterways; Sugar Maple was also moderately associated with high topographic roughness and had a moderate negative association with medium topographic roughness. The Elm cover class was strongly associated with short distance from waterways. Aspen, Birch-White Ash-Sugar Maple-Elm, Jack Pine-Red Pine, and White Pine cover classes were all strongly associated with sandy soils. Aspen and Birch-White Ash-Sugar Maple-Elm were strongly associated with low topographic roughness and strong and moderate negative association with high topographic roughness, respectively; Jack Pine-Red Pine and White Pine were moderately associated with low topographic roughness and had a moderate negative association with high topographic roughness. Birch-White Ash-Sugar Maple-Elm was strongly associated with short distance from waterways and Jack Pine-Red Pine and White Pine were moderately so. The sections without trees were strongly associated with low topographic roughness and had strong negative associations with medium-high and high topographic roughness. The sections without trees were also moderately associated with sandy soils and had a moderate negative association with short distance from waterways.

Discussion

Our reconstruction of pre-Euro-American vegetation for the Driftless Area depicts a landscape dominated by savanna and a variety of oak communities. The cover class and vegetation structure maps are consistent with other work from this region, including qualitative reconstructions using PLS witness tree records and surveyor notes to map vegetation in Minnesota (Marschner 1974), Wisconsin (Finley 1976), Iowa (Anderson 1996), and Illinois (Anderson 1970). These early reconstructions also depict the Driftless Area as dominated by oak savannas, with several large patches of closed forest and prairie in roughly the same locations as we found. Despite

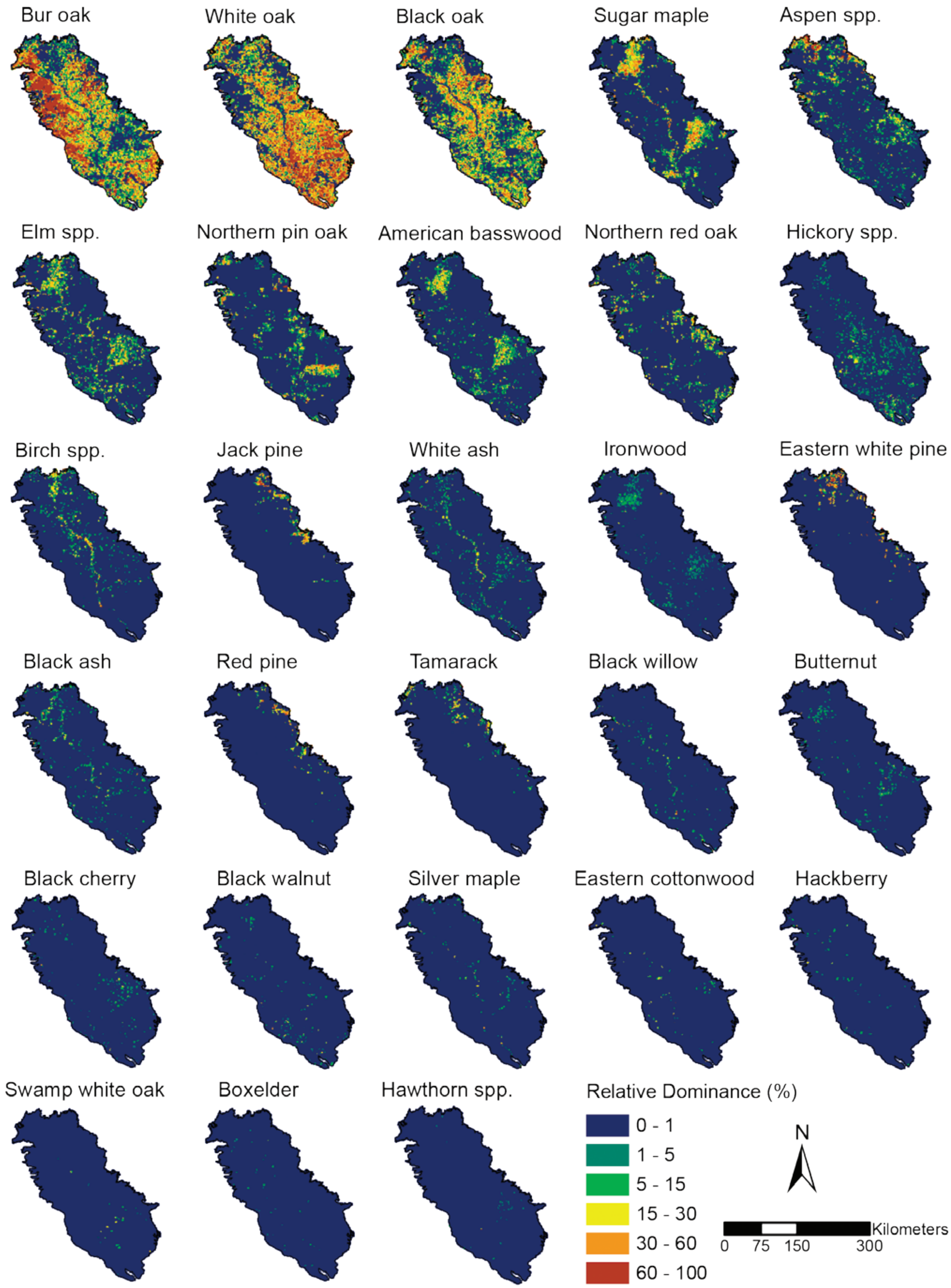

Figure 4. Relative abundance maps of the 28 most commonly recorded witness trees in the original Public Land Survey (PLS) records for the U.S. Midwest Driftless Area. Each cell represents a PLS-designated section.

Table 1. Average relative dominance of tree species within tree species cover classes. Bold indicates the average relative dominance value of the species used in the cover class name.

	Cover Class													
Tree Species	White Oak	Bur Oak	Bur Oak-White Oak	Black Oak	White Oak-Sugar Maple-Basswood-Elm	Bur Oak-Black Oak-White Oak-Aspen	Northern Pin Oak	Red Oak-White Oak	Sugar Maple	Elm	Aspen	Birch-White Ash-Sugar Maple-Elm	Jack Pine-Red Pine	White Pine
Jack pine	0.1	0.1	0.1	0.4	0.3	0.9	0.9	0.6	0.1	0.1	0.4	0.1	**37.7**	5.3
Red pine	0.1	0.1	0.1	0.2	0.3	0.5	0.4	0.7	0.1	0.1	0.2	0.0	**28.6**	4.0
Eastern white pine	0.1	0.1	0.1	0.1	0.9	0.8	0.3	0.2	0.5	0.7	0.6	1.3	3.9	**55.1**
Tamarack	0.1	0.1	0.2	0.5	0.3	6.5	0.6	0.1	0.2	0.1	1.0	0.2	2.3	1.9
Aspen spp.	1.3	0.7	0.8	1.9	4.5	**8.5**	2.8	4.3	1.3	2.3	**67.1**	1.1	2.1	3.4
Eastern cottonwood	0.0	0.0	0.1	0.1	0.2	0.5	0.0	0.1	0.2	0.3	0.0	4.5	0.0	0.0
Black willow	0.1	0.1	0.1	0.1	0.2	0.5	0.1	0.1	0.5	0.6	0.3	6.1	0.0	0.0
Black walnut	0.1	0.0	0.1	0.1	0.4	0.3	0.0	0.0	0.5	0.5	0.0	0.2	0.0	0.0
Butternut	0.1	0.0	0.0	0.1	0.7	0.5	0.0	0.2	0.9	0.8	0.1	0.2	0.0	0.1
Black cherry	0.1	0.0	0.0	0.1	0.5	0.5	0.1	0.1	0.1	0.5	0.2	0.0	0.0	0.0
Hickory spp.	0.8	0.3	1.0	1.1	1.0	2.4	0.7	0.4	0.6	0.4	0.1	0.6	0.0	0.0
Ironwood	0.1	0.0	0.1	0.1	0.9	0.6	0.0	0.3	1.7	1.0	0.1	0.5	0.0	0.2
Birch spp.	0.2	0.3	0.4	0.6	1.4	1.9	0.9	0.3	2.6	2.7	1.3	**28.6**	0.4	2.4
White oak	**69.2**	3.4	**34.1**	20.1	**36.0**	**8.8**	19.2	**27.3**	8.7	9.2	7.1	3.1	5.2	7.9
Bur oak	9.1	**85.5**	**44.7**	14.9	4.3	**26.7**	16.9	10.7	3.3	8.0	5.4	4.1	8.7	5.1
Swamp white oak	0.0	0.0	0.0	0.0	0.3	0.2	0.0	0.0	0.2	0.2	0.0	0.2	0.0	0.0
Northern red oak	1.5	1.2	0.9	0.5	1.9	1.9	0.6	**41.7**	1.3	1.1	2.4	0.9	1.7	0.8
Black oak	11.8	5.8	13.6	**55.8**	8.0	**16.5**	5.3	6.1	3.7	5.0	5.6	2.6	6.0	3.3
Northern pin oak	1.7	1.1	1.7	1.0	0.9	2.5	**48.7**	1.3	0.1	0.6	2.4	0.5	1.7	1.1
Elm spp.	1.1	0.5	0.8	0.8	**8.1**	6.3	0.8	1.5	8.3	**43.5**	1.6	**7.4**	0.8	2.9
Hackberry	0.0	0.0	0.0	0.0	0.1	0.5	0.0	0.0	0.1	0.8	0.1	0.1	0.0	0.0
Hawthorn spp.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.1	0.0	0.0
Sugar maple	1.1	0.2	0.3	0.8	**14.8**	4.1	0.5	2.1	**49.3**	9.3	2.1	**14.0**	0.3	3.5
Silver maple	0.0	0.0	0.0	0.1	0.5	0.6	0.1	0.0	0.6	0.9	0.6	1.6	0.1	0.2
Boxelder	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0
American basswood	0.7	0.2	0.4	0.4	**10.2**	4.3	0.4	1.1	11.1	6.4	0.8	2.0	0.2	1.6
White ash	0.2	0.1	0.1	0.2	1.5	1.3	0.2	0.4	2.2	2.1	0.3	**14.5**	0.1	0.2
Black ash	0.2	0.1	0.1	0.2	1.4	1.6	0.2	0.2	1.8	2.4	0.1	5.6	0.2	0.7
Number of sections	5077	3668	3206	2851	1271	983	523	493	946	554	456	348	389	374

the similarities, these earlier maps are inconsistently derived and offer very general or no information on tree species composition. In a more quantitative approach, Bolliger and others (2004) used the same methods presented here to map tree species cover classes and vegetation structure for the entire state of Wisconsin. Our results are similar to theirs for the Wisconsin portion of the Driftless Area; however, since our analysis covered a smaller, more ecologically distinct area (Albert 1995), we were able to more precisely depict the variety of tree communities present in the Driftless Area. For example, we describe eight oak-dominated cover classes specifically occurring in the Driftless Area, whereas Bolliger and others (2004) found only five oak-dominated cover classes more generally occurring throughout the entire state of Wisconsin. Thus, our reconstruction of pre-Euro-American vegetation provides an improvement over past efforts for the Driftless Area by identifying consistently derived, species-specific reference conditions at a finer scale and quantifying their associations with key environmental variables.

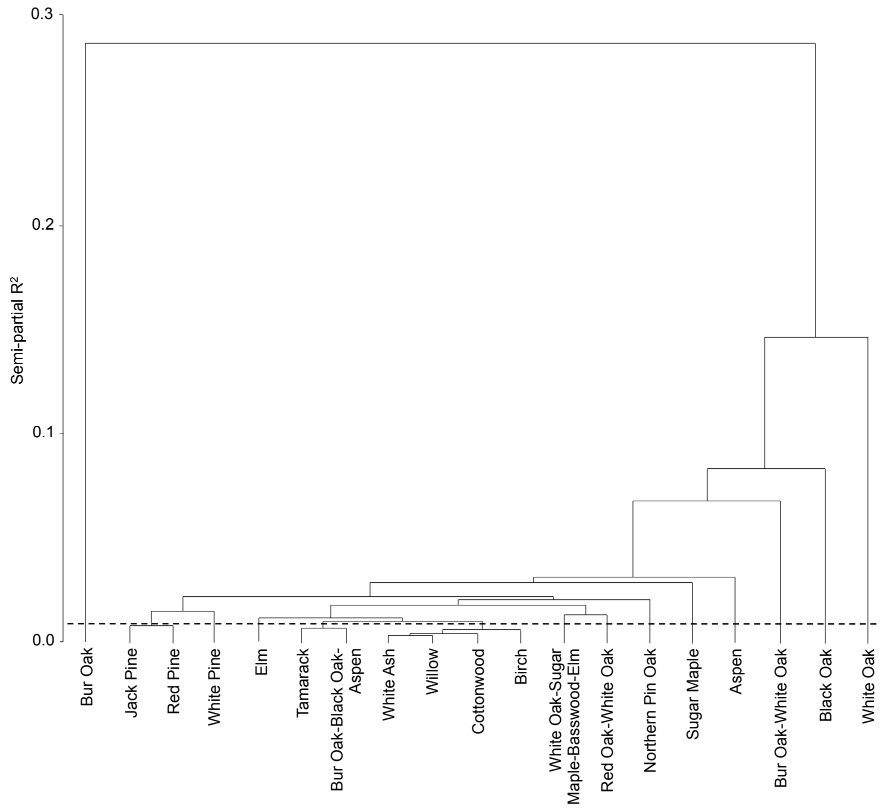

Figure 5. Dendrogram resulting from hierarchical agglomerative clustering. Each branch represents one of the nineteen clusters output from FASTCLUS. The dashed line shows pruning level where the clusters contained at least 1% of total sections.

Tree Community Diversity

While dominated by oak species, our reconstructions of Driftless Area vegetation illustrate a complex landscape containing a variety of species assemblages, oak and non-oak. This diversity is likely due to a complex assortment of interacting factors (i.e. abiotic environment, disturbance history, disturbance regime, past community composition and structure, climate, etc.; Kline and Cottam 1979, Grimm 1983, Swanson et al. 1988, Foster et al. 1998, Umbanhower 2004), which we cannot fully address given the scale of PLS data (Schulte and Mladenoff 2005). Nevertheless, our study points to two elements that likely played a role in determining species composition and contributed to the Driftless Area's HRV: disturbance and environmental conditions.

The preponderance of oak and, in particular, savanna supports previous assessments that suggest fire was widespread in the Driftless Area prior to Euro-American settlement (Curtis 1971, Davis 1977). Savanna was likely maintained by low intensity fire with a frequent return interval of 5–15 years (Dickmann and Cleland 2002), which created favorable conditions for the persistence of relatively fire-resistant, shade-intolerant oak species (Abrams 1992). Six of the eight oak-dominated cover classes were highly associated with savanna and were dominated by species that display some degree of resistance to fire (Burns and Honkala 1990). Associations with environmental factors varied among these cover classes, suggesting that, while frequent low-intensity fire maintained oak savanna habitat in general, environmental conditions played a role in separating oak species into different cover classes. Indeed, the Driftless Area's characteristically undulating topography generates a range of environmental conditions, predisposing the region to potentially support a diverse set of tree communities (Curtis 1971).

The biological requirements and limitations of tree species directed the compositional response to environmental conditions. Some oak species, such as black oak and northern pin oak, are limited to particular growing conditions: both are fairly intolerant of shade, drought tolerant and resistant to fire, and grow well in sandy, xeric soils (Curtis and McIntosh 1951, Burns and Honkala 1990). In the Driftless Area, these two species dominated cover classes that generally occurred in areas that displayed xeric qualities: sandy soil, high topographic roughness, and far distance from waterways. White oak and bur oak are more versatile. These two species tolerate a wide range of

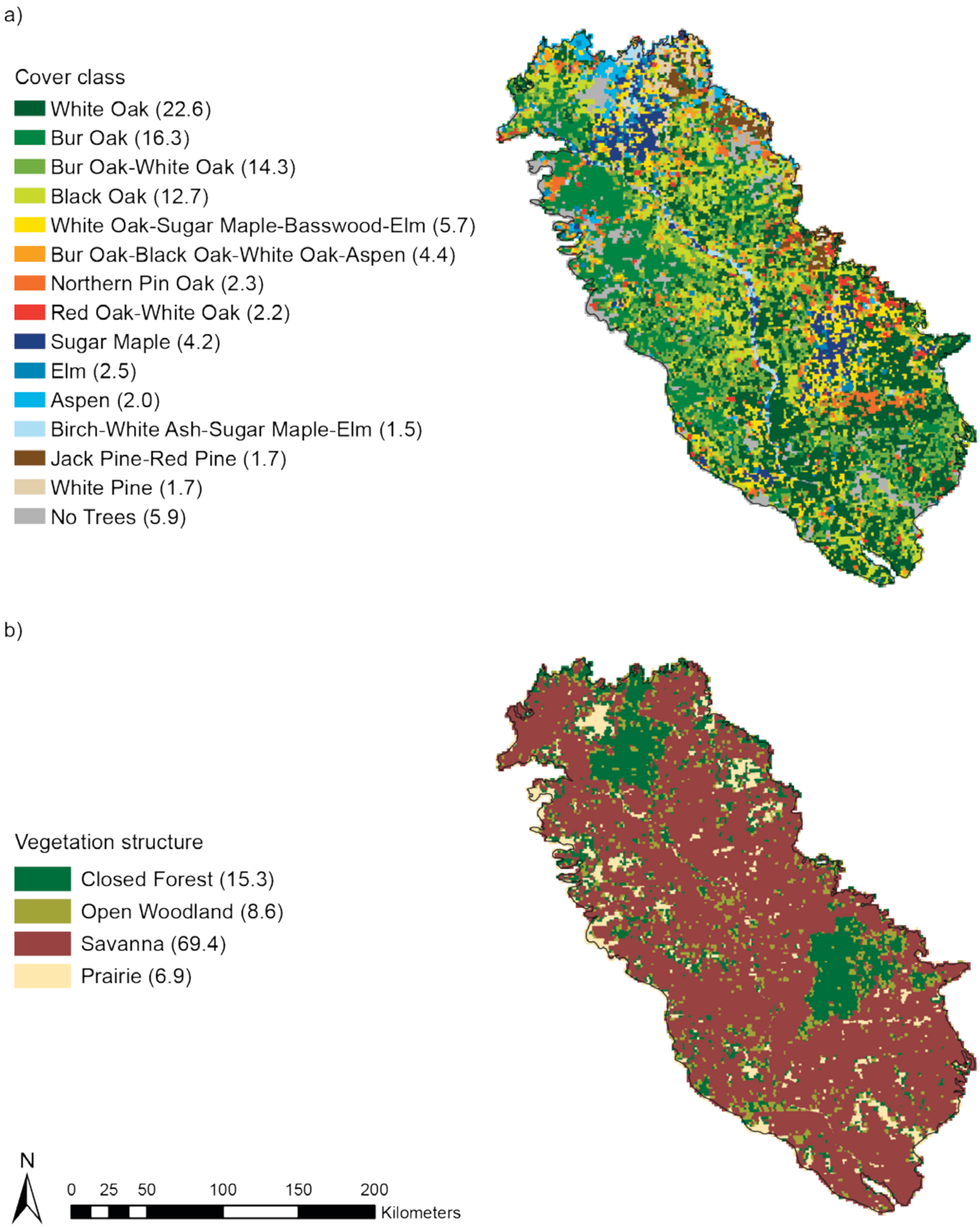

Figure 6. Pre-Euro-American settlement a) tree species cover classes and b) vegetation structure for the U.S. Midwest Driftless Area. Numbers in legend indicate percent of total sections. Each cell represents a Public Land Survey-designated section.

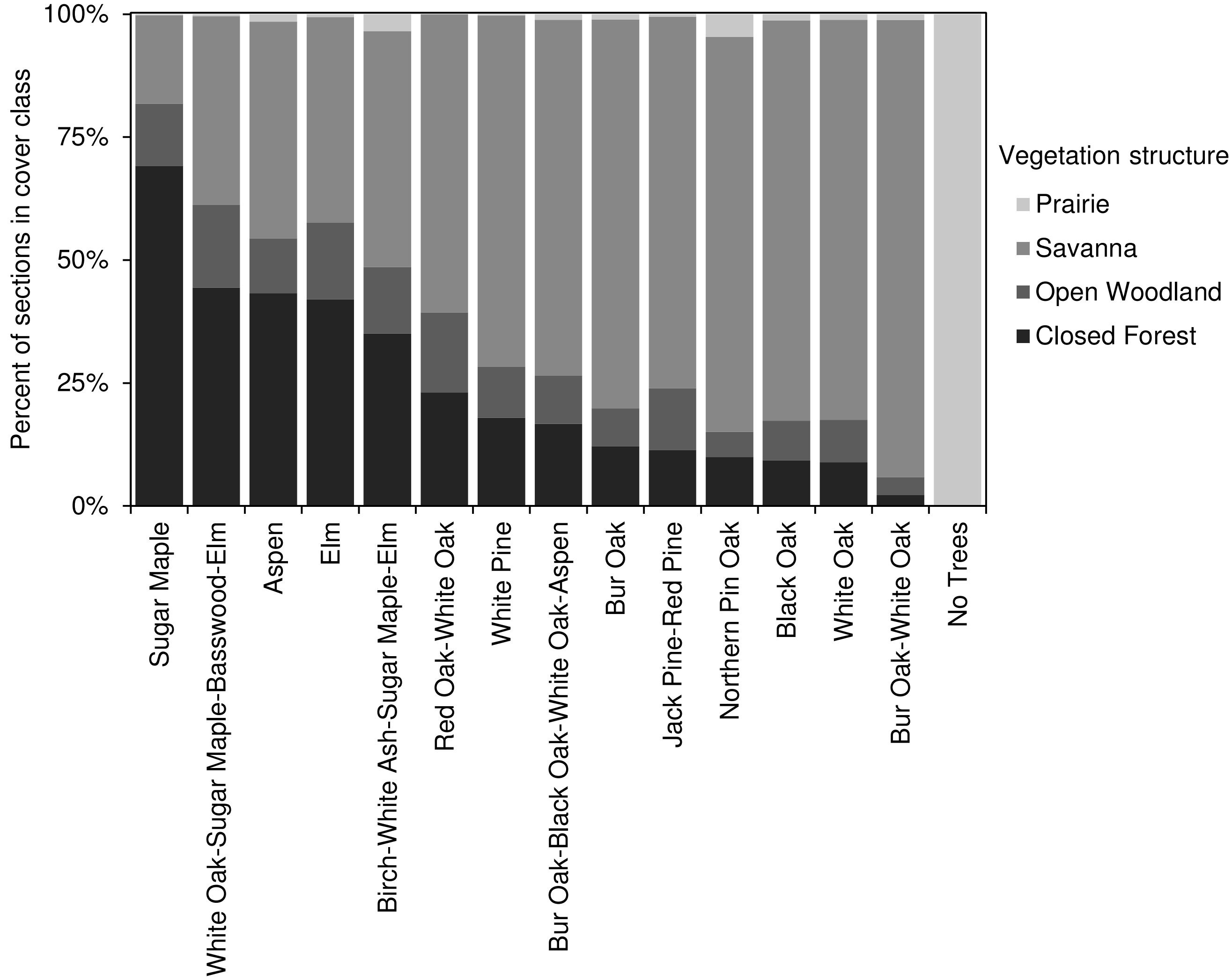

Figure 7. Relationship between pre-Euro-American tree species cover class and vegetation structure types for the U.S. Midwest Driftless Area. Shown here is the percent of the total number of sections in each cover class that is attributed to each of the vegetation structure types.

Table 2. Results of contingency table analyses of the relationships between tree species cover classes and environmental factors.

	Soil texture			Topographic roughness			Distance from waterway		
Cover class	*G*	DF	*p*	*G*	DF	*p*	*G*	DF	*p*
White Oak	144.82	3	< 0.0001	1640.71	3	< 0.0001	145.41	3	< 0.0001
Bur Oak	9.07	3	0.0284	1481.19	3	< 0.0001	12.58	3	0.0056
Bur Oak-White Oak	14.75	3	0.0020	375.14	3	< 0.0001	15.63	3	0.0014
Black Oak	53.64	3	< 0.0001	254.96	3	< 0.0001	51.57	3	< 0.0001
White Oak-Sugar Maple-Basswood-Elm	36.68	3	< 0.0001	323.81	3	< 0.0001	27.72	3	< 0.0001
Bur Oak-Black Oak-White Oak-Aspen	149.26	3	< 0.0001	21.32	3	< 0.0001	158.26	3	< 0.0001
Northern Pin Oak	12.68	3	0.0054	37.78	3	< 0.0001	11.12	3	0.0111
Red Oak-White Oak	24.24	3	< 0.0001	40.25	3	< 0.0001	34.76	3	< 0.0001
Sugar Maple	17.74	3	0.0005	48.05	3	< 0.0001	14.40	3	0.0024
Elm	380.96	3	< 0.0001	17.13	3	0.0007	361.17	3	< 0.0001
Aspen	7.93	3	0.0475	341.12	3	< 0.0001	10.41	3	0.0154
Birch-White Ash-Sugar Maple-Elm	297.49	3	< 0.0001	405.61	3	< 0.0001	261.89	3	< 0.0001
Jack Pine-Red Pine	35.85	3	< 0.0001	207.10	3	< 0.0001	38.01	3	< 0.0001
White Pine	97.94	3	< 0.0001	118.33	3	< 0.0001	91.26	3	< 0.0001
No Trees	64.55	3	< 0.0001	1570.79	3	< 0.0001	59.04	3	< 0.0001

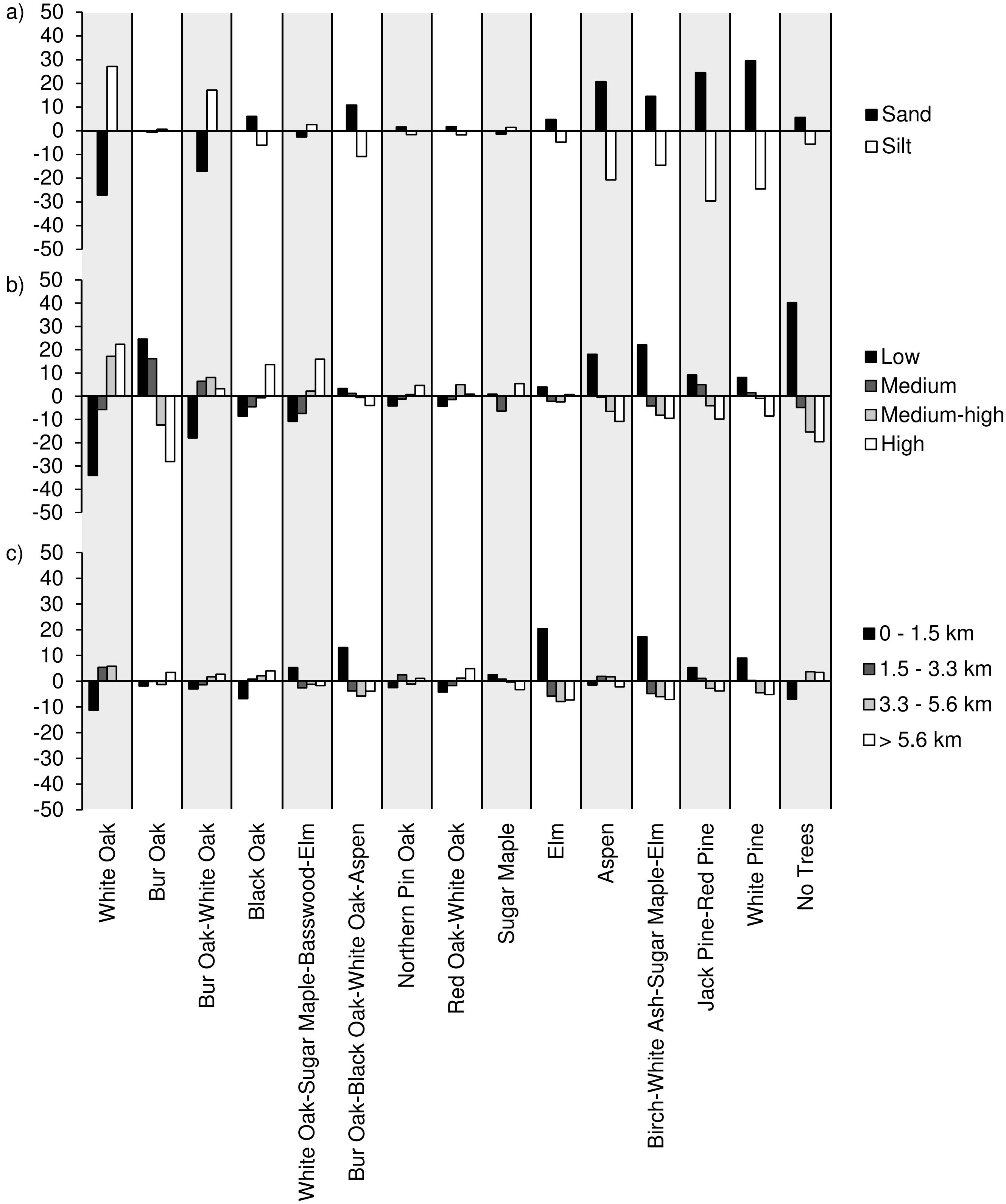

Figure 8. Standardized residuals for all cover classes significantly related to: a) soil type, b) topographic roughness, and c) distance from waterway. Bars with positive values indicate a positive relationship between the cover class and respective environmental factor category, and vice versa. Larger residual values indicate stronger associations.

soil and moisture conditions and white oak is also somewhat tolerant of shade (Curtis and McIntosh 1951, Burns and Honkala 1990). Versatility may be the reason these two species were a major part of multiple cover classes, each exhibiting an array of environmental associations. These two species' environmental associations sometimes overlapped: bur oak and white oak often occurred together, and they co-dominated the Bur Oak-White Oak cover class. Bur oak and white oak also dominated their own single-species cover classes, differing from one another in part by the Bur Oak cover class's strong association with low topographic roughness. This may be due to increased fire frequency in areas with more gentle topography (Stambaugh and Guyette 2008); bur oak has extremely thick bark is thought to be one of the most fire-resistant oak species in North America (Peterson and Reich 2001).

While frequent low-intensity fires likely maintained savanna over much of the Driftless Area, variation in fire intensity and frequency would have contributed to the patterning of prairie, open woodland, and closed forest ecosystems (Leitner et al. 1991). Variation in fire history can also affect tree species composition. For example, if fire is absent, an oak savanna is likely to develop into closed forest and may eventually become dominated by mesic species, a process known as mesophication (Nowacki and Abrams 2008). In the Driftless Area, it is possible that the White Oak-Sugar Maple-Basswood-Elm and Sugar Maple cover classes originated from White Oak communities that were in various stages of mesophication, depending on time since fire disturbance. Similarly, less fire-tolerant northern red oak could have invaded White Oak savannas in the absence of fire, forming the Red Oak-White Oak cover class (e.g., Abrams 2003). Red Oak-White Oak may have also arisen in places that experienced intense fire followed by a prolonged period without fire (Crow 1988, Abrams 2003). In either case, fire may have occurred relatively recently prior to the time of the survey; this is because there were very few shade-tolerant mesic hardwoods recorded in the canopy of Red Oak-White Oak communities, despite the fact that mesic hardwoods readily establish in forests dominated by northern red oak (Curtis and McIntosh 1951). Small-diameter mesic hardwoods may have been present in these communities, but often were not recorded because surveyors favored medium-sized witness trees where they were available (Bourdo 1956, Liu et al. 2011).

In addition to Sugar Maple, several non-oak cover classes were present in smaller portions of the Driftless Area. Elm and Birch-White Ash-Sugar Maple-Elm were both strongly associated with short distance from waterways and, given the species composition, probably comprised lowland forest communities (Curtis 1971, Burns and Honkala 1990). The Jack Pine-Red Pine and White Pine cover classes, which were mainly clustered in sections located on the northeastern edge of the Driftless Area, were strongly associated with sandy soils; these species are known to dominate Wisconsin forests in areas of sandy glacial outwash, which extends into the northeast margin of the Driftless Area (Curtis 1971, Bollinger et al. 2004). Elsewhere, isolated patches of the pine cover classes may be associated with relict pine communities, which occurred throughout the region on rocky cliffs (Curtis 1971, Ziegler 1995). Both pine cover classes had greater than 70% of their sections occurring in savanna, suggesting that frequent fires maintained pine barrens in an open landscape (Curtis 1971, Radeloff et al. 1999). Aspen occurred throughout the Driftless Area, but was only dominant in the northern part of the region. Clonal reproduction allows aspen to rapidly establish in recently disturbed or open spaces like prairies, particularly in areas with flat to moderate topography (Burns and Honkala 1990). The dominance of aspen in the north may be due to lower topographic roughness combined with proximity to prairies.

Historical Range of Variability and Modern Changes

The dominance of savannas and oak communities, and the presence of other fire-dependent communities, such as those dominated by aspen or pine species, indicates that fire played a key role in mediating HRV in the Driftless Area prior to Euro-American settlement (Abrams 1992). In the absence of fire, the region's annual rainfall is more than adequate for supporting closed forests composed of mesic species (Curtis 1971, Nowacki and Abrams 2008), as is the case today (Rogers et al. 2008, Rhemtulla et al. 2009, Schulte et al. 2011). While browsing by elk and deer, and potentially bison, may have also had an impact on vegetation dynamics (Anderson 2006), fire with a frequent return interval (1–15 years) would have been required to maintain open vegetation types over such large extents (Dickmann and Cleland 2002, Nowacki and Abrams 2008). Fire likely was a major determinant of the Driftless Area's HRV for several thousand years; indeed, paleoecological investigations at locations within or near the Driftless Area revealed that oak ecosystems were the dominant during the late Holocene leading up to Euro-American settlement (Davis 1977, Winkler et al. 1986, Baker et al. 1996, Bogen and Hotchkiss 2007).

Today, about 47% of the Driftless Area is used for agriculture, 13% is developed, and 34% is forested, mainly in fragmented closed forest patches (LANDFIRE 2013). Very little savanna remains, having been converted into pasture and crop fields or developed into closed forest with fire exclusion (Curtis 1971, Rhemtulla et al. 2009). While oak species sometimes dominate these forests, they are being replaced by more shade-tolerant and mesic species, such as maple, ash, and elm (Rogers et al. 2008, Knoot et al. 2010, Schulte et al. 2011). This mesophication of the forests is due in part to a sustained lack of fire disturbance since Euro-American settlement, a phenomenon that is occurring throughout much of the eastern U.S. (Nowacki and Abrams 2008). As oak savannas gave way to oak forests, which are now giving way to mesic hardwood forests, it is likely that much of the compositional diversity found in the pre-Euro-American vegetation, as detailed here, is being lost. These declines may be further compounded with climate change: current projections for tree species habitat response to climate change predict substantial reductions in importance values for currently prominent oak species, white oak and northern red oak, in the Driftless Area ecoregion (Prasad et al. 2007). These potential declines may be compensated by increasing importance of other oak species, black oak, post oak (*Quercus stellata*), and chinkapin oak (*Q. muehlenbergii*). Additionally, several non-oak species, including hackberry, boxelder, and honeylocust (*Gleditsia triacanthos*), are also projected to increase in dominance (Prasad et al. 2007).

Given the prevalence and diversity of oak communities prior to Euro-American settlement, we consider restoring oak ecosystems an urgent restoration goal for the Driftless Area. Oaks are often foundational species where they occur (Ellison et al. 2005), supporting a diverse array of plant and animal species (Fralish 2004). We expect declines in oak dominance and loss of oak communities to be indicative of substantial changes in ecosystem structure and function across the Driftless Area (Fralish 2004, USFWS 2006, NRCS 2013). To ameliorate oak declines due to mesophication, and to inhibit the potential negative impacts of climate change on oak ecosystems in the Driftless Area, it is important to restore a diverse array of oak communities and for them to be present in their appropriate structural condition (i.e. savanna, closed forest) to provide a broad template on which climate change will act.

Restoration in the Driftless Area

Our historical vegetation maps are the first of their kind to be constructed for the entire Driftless Area, and can be of great use to restorationists. These maps, coupled with our findings on cover class associations with environmental factors, can be used to inform development of regional, cross-boundary management and restoration plans for the Driftless Area. Our reconstructions can serve as a template to determine a range of possible target communities, including understanding what communities have historical precedence and what may be novel. The maps can also be used in combination with modern resource maps to help prioritize areas for restoration so that limited funding can be most effectively used (Palik et al. 2000, Brudvig et al. 2014). Furthermore, our findings can be used to help parameterize simulation models that can assist in regional restoration planning by being used to predict future outcomes from different management plans (Keane et al. 2009, Ravenscroft et al. 2010).

Our findings can also inform site-specific restoration planning, although caution should be used when doing this since we summarized vegetation and environmental factors over 2.54 km² units rather than at the site level. In this context, the maps can be used to help determine overall target vegetation communities. We suggest that the practitioner examine tree communities historically present at the specific restoration site and, to allow for a range of possibilities under HRV, also consider tree communities that were historically present in nearby areas with similar environmental characteristics. For example, a restoration site in the west-central Driftless Area, having silt-dominated soils, medium-high topographic roughness, and medium distance from a major waterway, that we categorized as Bur Oak-White Oak savanna could also have target communities composed of species prevalent in Black Oak, White Oak, Northern Pin Oak, and Sugar Maple cover classes. Consulting the relative dominance maps can also help planners determine what species were historically prevalent in the area surrounding the restoration site. While using this information to identify a range of possible target communities, specific restoration targets should be chosen based on current vegetation and environmental conditions, knowledge of species-specific associations with fine-scale environmental factors (e.g., black oak is known to grow on hilltops and south and west-facing slopes; Burns and Honkala 1990) and habitat type as determined by the understory plant community (Kotar 1986), additional restoration goals (e.g., Karner blue butterfly [*Lycaeides melissa samuelis*] restoration; Kleintjes et al. 2003), and other planning considerations (DellaSala et al. 2003).

Modern restoration efforts are faced with multiple challenges that can make historical conditions an infeasible restoration target in some areas (Jackson and Hobbs 2009). Nevertheless, these reconstructions can greatly benefit ecological restoration efforts in the region. Understanding a region's HRV can shed light on drivers of historical vegetation patterns and help planners recognize what processes to reinforce and sustain, as well as recognize those they cannot recreate (Swetnam et al. 1999, Jackson and Hobbs 2009, Keane et al. 2009). Where possible, restoring communities based on HRV can increase the ecological resilience of the region (Millar et al. 2007, Keane et. al 2009, Churchill et al. 2013). In light of the well-documented challenges to oak restoration and management posed by the current social-ecological system of the Driftless Area (Knoot et al. 2010), our findings can help restorationists develop targeted strategies designed to direct vegetation toward its HRV and to maintain oak ecosystems into the future.

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