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Historical range of variability for restoration and management in Wisconsin

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Abstract
In Wisconsin, as in other states, management goals sometimes include restoration of historical forest conditions, which may prepare forests to be more compatible with future climates, disturbances such as drought and fire, and forest health threats. We quantified historical (1830–1866) composition and structure to develop historical reference conditions for restoration and documented changes based on current (2005–2009) forest surveys in Wisconsin. We provided structural metrics, functional group composition, and forest types for 186 ecological land types, and we also summarized trends in composition and structure. Wisconsin forests historically were comprised of 46% oak or pine savanna or woodland, 6% pine forest, and 48% forests primarily consisting of late-successional eastern broadleaf forest species and early-successional northern mixed forest species; densities of these forest types ranged from 60 to 460 trees/ha. In the Eastern Broadleaf Forest ecological division, increased composition of the early-successional and mid-successional eastern broadleaf forest groups (from 10 to 40%) and (planted) pine group (8–23%) occurred along with decreased fire-tolerant oak composition (from 65 to 23%). Density increased in current forests compared to historical forests by a factor of 2.2; despite increased density, basal area increased only slightly due to the presence of larger diameter trees in historical tree surveys. In the Northern Mixed Forest ecological division, increased composition of the mid-successional eastern broadleaf forest group (from 12 to 24%) and late-successional northern mixed forest group (from 10 to 17%) occurred due to decreased composition of the fire-tolerant pine group (from 17 to 9%) and late-successional eastern broadleaf forest group (from 30 to 20%). Density remained similar in current forests compared to historical forests but current basal area was 50% of historical basal area. The transition from open fire-tolerant oak and pine forests, with rarity of early-successional tree species, to closed forests composed of a variety of early- and mid-successional tree species parallels results from other research. Replacement of open oak or pine forest ecosystems by dense forests

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has moved Wisconsin outside of the historical range of variability, likely reducing plant and wildlife species associated with open oak and pine ecosystems.

Keywords Disturbance · Fire · Historical · Oak · Pine · Regime shift · State transition

Introduction

Historic conditions and change in Wisconsin forests represent a microcosm of historical and current forests in the central eastern US, Northeast, and Great Lakes states. Open oak forest ecosystems historically dominated the Eastern Broadleaf Forest ecological division (Fig. 1) in southern Wisconsin, with some presence of sugar maple (*Acer saccharum*) and other shade-tolerant, late-successional 'northern hardwood' species, although the distribution of American beech (*Fagus grandifolia*) did not extend across Wisconsin (Bolliger et al. 2004; Schulte et al. 2007; Rhemtulla et al. 2007, 2009). Frequent low severity and infrequent moderate to high severity fires were important drivers controlling forest composition and structure in this region (Frelich and Lorimer 1991; Lorimer and White 2003). Many of these forests were converted to agriculture by the 1930s to 1940s, and the remainder became closed forests with increasing dominance by red maple (*Acer rubrum*) and other historically rare eastern broadleaf forest species following Euro-American settlement, logging, and fire exclusion (Rhemtulla et al. 2007; Goring et al. 2016).

In the Northern Mixed Forest division of northern Wisconsin (Fig. 1), characteristic species of tamarack (*Larix laricina* (Du Roi) K. Koch), spruce (*Picea* sp.), fir (*Abies* sp.), northern white-cedar (*Thuja occidentalis*), birch (*Betula* sp.), and aspen (*Populus* sp.) occupied wetlands and lowlands, mixed conifer-northern hardwood forests were present on better sites in the upland moraines and till plains, and pine barrens and savannas dominated sandy outwash plains (Radeloff et al. 1999; He et al. 2000; Schulte et al. 2002; Bolliger et al. 2004; Schulte et al. 2007; Rhemtulla et al. 2007, 2009). Northern mixed forests typically were maintained by mixed severity fire and wind regimes at 70 to > 1000 year intervals (Frelich and Lorimer 1991; Lorimer and White 2003; Schulte and Mladenoff 2005). Conifer-northern hardwood forests tended to be dense, closed forests, particularly on more productive sites where wind and fire disturbance on long return intervals drove stand regeneration and development (Canham and Loucks 1984; Frelich and Lorimer 1991; Schulte and Mladenoff 2005). From 1850s to 1930s, northern Wisconsin was logged in an exploitative and widespread manner, followed by frequent and often catastrophic fires that burned through the logging slash (Pyne 1982; Williams 1989; Whitney 1994). Since the 1930s, forest development toward late-successional forest composition (i.e., eastern hemlock, *Tsuga canadensis* Carrière; sugar maple; and American beech) has been impeded primarily by repeated selective cutting.

Quantification of reference conditions and examination of historical forest ecosystems compared to current forest ecosystems are important to guide restoration and provide baseline information for research and management. Even though studies of Wisconsin's forests are rich and varied, including changing composition, density, biomass, and early-successional species (e.g., Radeloff et al. 1999; He et al. 2000; Schulte et al. 2002, 2007; Bolliger et al. 2004; Rhemtulla et al. 2007, 2009; Fahey et al. 2012; Goring et al. 2016), we were not able to locate studies that provided tables of quantified density and other derived structural metrics or maps at scales to guide local efforts. Therefore, we used historical surveys conducted during 1830–1866 to reconstruct historical forests at the more general ecological division and section scales (section mean area of 4 million ha ranging from 0.55 to 16

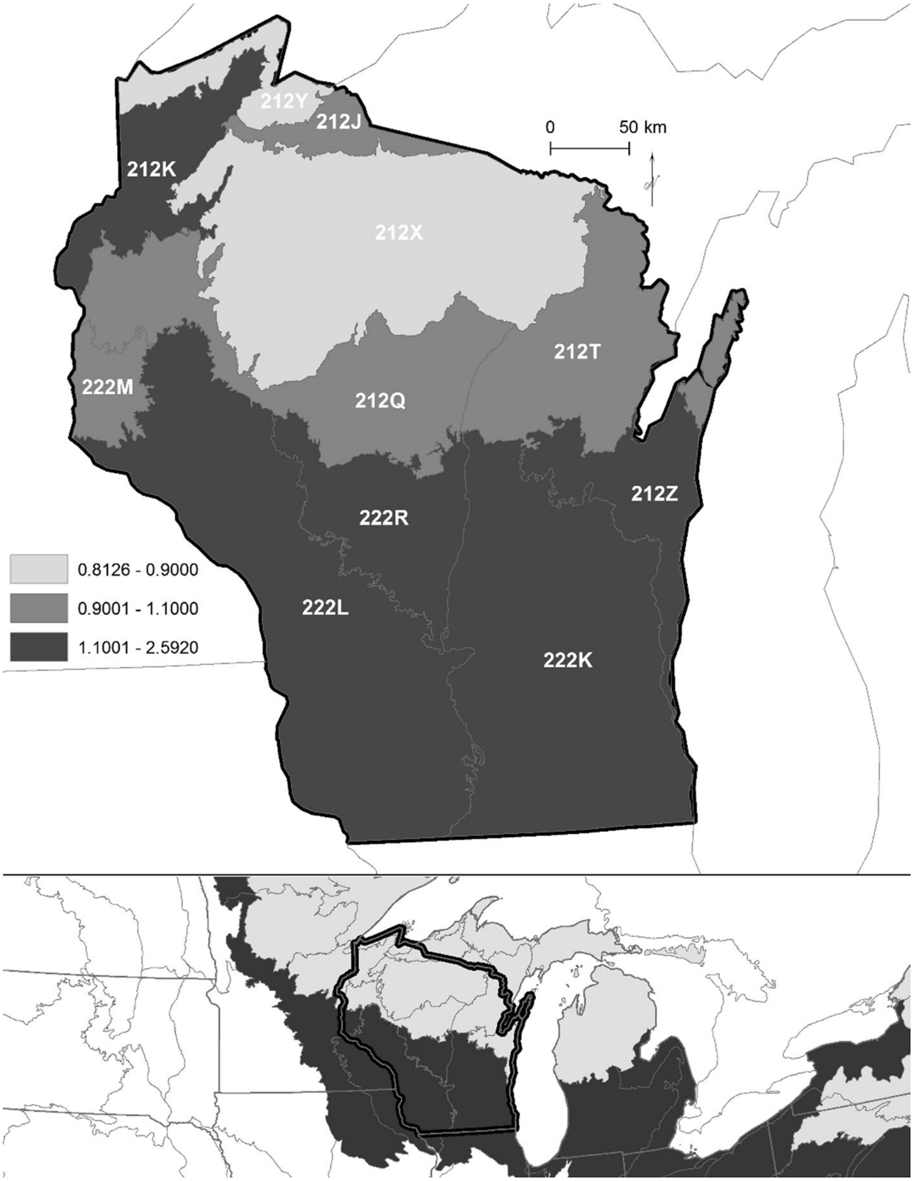

Fig. 1 Ecological sections in the Northern Mixed Forest division (prefixes of '212', shaded in lower panel) and the Eastern Broadleaf Forest division (prefixes of '222', shaded in lower panel) in Wisconsin. Change in density (current density/historical density) are displayed in ecological sections within Wisconsin

million ha; Fig. 1; Ecomap 2007) and supplied detailed structure suitable for local restoration projects at the land type association scale (mean area of 49,000 ha ranging from 1215 to 385,000 ha).

Historical forest composition may have differed from historical tree surveys, which were not random or complete records of species. Surveyors selected tree species at survey points, based on for example, moderate size with potential for long life and ease of blazing (i.e., smooth bark and lack of lower limbs; White 1983). Historical surveys may have bias due to surveyor selection of trees, resulting in inaccurate representation of tree species, size, and distance (e.g., Bourdo 1956; Kronenfeld and Wang 2007; Bouldin 2008; Hanberry et al. 2011, 2012a; Liu et al. 2011). However, surveyors were simultaneously recording two samples, one of selected trees at survey points (i.e., bearing trees) and one of encountered trees along survey transects (i.e., line trees), and comparison provides an indication of bias, albeit line trees were not always recorded, particularly in parts of northwestern and western Wisconsin. Additionally, some density equations may produce bias (Bouldin 2008; Hanberry et al. 2011; Cogbill et al. 2018); for example, Pollard (1971), Bouldin (2008), and Cogbill et al. (2018) showed that the most commonly used Cottam and Curtis estimator (1956) is biased. To our knowledge, we uniquely used the Morista estimator (Morisita 1957) and made adjustments for surveyor bias and potential tree spatial patterns (e.g., clustering) to quantify density for Wisconsin (Hanberry et al. 2011, 2012a).

Methods

Tree surveys

The United States General Land Office (GLO), established in 1812, administered the surveying and selling of public lands using a systematic method, the Public Land Survey System. Land was divided into square townships measuring 9.6 km per side and townships were subdivided further into 1.6 × 1.6 km sections. At survey points at the corners and middle of each section line (i.e., every 0.8 km), surveyors selected two to four bearing trees. Surveyors recorded tree species, diameter, and distance and bearing from survey points and surveyors also recorded trees encountered along section lines. In Wisconsin, surveys during primarily 1830–1866 contained about 138,000 (Eastern Broadleaf Forest division) to 184,000 (Northern Mixed Forest division) bearing trees and 43,000 line trees in the Eastern Broadleaf Forest and Northern Mixed Forest ecological divisions (Sickley et al. 2001). Line tree information was not recorded continuously, particularly in parts of northwestern and western Wisconsin.

The USDA Forest Service Forest Inventory and Analysis (FIA) established long term plots that occur about every 2500 ha. The FIA surveys each plot on a 5 years cycle. We used available plots (FIA DataMart, www.fia.fs.fed.us/tools-data; Bechtold and Patterson 2005) from the latest complete cycle during 2005–2009. Surveys contained about 40,000 trees in the Eastern Broadleaf Forest division and 110,000 trees in the Northern Mixed Forest division (Fig. 1).

Species trends

To identify species change at the ecological division scale, we determined percent composition of species for GLO line trees, which surveyors encountered along the section lines, and bearing trees, which surveyors selected at survey points, compared to trees in current FIA surveys at the division scale. Despite incomplete sampling throughout Wisconsin, the line trees provide another sample and therefore, we compared percent composition between trees encountered along section lines and trees selected at survey points to provide a range of variation that can occur with different sampling methods. We selected live trees that were ≥ 12.7 cm in diameter because smaller trees rarely were recorded by surveyors in GLO surveys (White 1983) and survey area is smaller for trees < 12.7 cm in FIA surveys (Bechtold and Patterson 2005). We included all tree species with ≥ 1% composition in any of the GLO line tree surveys, GLO bearing tree surveys, and FIA surveys, which represented 94–99% of total composition; we removed rare trees because they are not representative of the forests. Due to limited identification in GLO surveys for some trees, we matched GLO and FIA trees by species if possible and genera if necessary, for pine, maple, aspen, ash, and spruce in particular.

Functional groups for forest types

At the division, section, and land type association scales, we classified seven functional groups based on functional traits: (1) oaks (*Quercus*), (2) pines (*Pinus*), (3) early-successional northern mixed forest species of tamarack, birch, and aspen, (4) late-successional northern mixed forest species of northern white-cedar, spruce, and fir, (5) late-successional eastern broadleaf forest species (i.e., shade tolerance ≥ 3.98 for sugar maple, beech, eastern hemlock, and American basswood, *Tilia americana*; Niinemets and Valladares 2006), (6) early-successional eastern broadleaf species (shade tolerance < 2.5, e.g., black cherry, *Prunus serotina*), and (7) mid-successional eastern broadleaf species (shade tolerance ≥ 2.5 and < 3.98 such as red maple). Shade tolerance was measured on a continuous scale of increasing tolerance from < 1 to 5 (Niinemets and Valladares 2006) and we applied thresholds of shade tolerance classes based on placing shade-intolerant black cherry (shade tolerance = 2.46) in the early-successional class and shade-tolerant American basswood (shade tolerance = 3.98) in the late-successional class. Some species that we classed as eastern broadleaf forest species, particularly late-successional species or 'northern hardwoods', overlapped both regions. We used bearing trees from GLO surveys, which had a greater sample size; grouping by traits reduced biases in species selection.

Structure

Density and basal area

We calculated density and basal area at the division and section scales for historical and current forests, and also at the smaller land type association scale for historical forests only due to small sample sizes for FIA data. We applied the Morista estimator (Morisita 1957) for (1) survey points with two trees and (2) survey points with three trees and the nearest three trees for survey points with four trees (diameters ≥ 12.7 cm; surveyors selected two to four bearing trees at survey points at the corners and middle of each section line, or every 0.8 km). To provide a reliable density estimate for each ecological unit, we set the minimum number of points at 200 for points with two trees and at 50 for points with three trees (for land types, mean sample size = 702). We then produced a low and high value based on adjustment for potential spatial patterning (clustered or regular patterns), which we carried into the low and high corrections for surveyor bias (Hanberry et al. 2011). Surveyors potentially did not select the nearest two to four trees at each survey point and selection of more distant trees will result in underestimated densities. We adjusted density estimates using a rank-based method of correction to estimate a low value and a mean value (Hanberry et al. 2012a). Using a complementary method to correct for non-random ratios of quadrants and azimuth and differences between frequencies of species and diameter in bearing and line tree samples, we produced density estimates for an alternative mean value and a high value (Hanberry et al. 2012a). We then determined a weighted average of the two mean values from the two complementary methods and retained the low value from the rank-based method and high value from the bias method. For basal area estimates, we used the quadratic mean diameter (square root of the mean diameter^2) to calculate mean tree basal area and multiplied this by the number of trees per ha for each scale (e.g., all trees in a section).

For current forest density, we used FIA data to calculate trees per acre using the expansion factor of 6.02, based on one tree representing the inverse of the plot area in acres (i.e., 1/(4*0.042)), and summed the values for each plot (tree diameters ≥ 12.7 cm). We selected plots that contained at least two trees and were 100% forestland, which FIA defines as land at least 0.4 ha in size and 37 m wide with at least 10% cover by live trees of any size, "including land that formerly had such tree cover and that will continue to have forest use". For basal area estimates, we used the quadratic mean diameter (square root of the mean diameter^2) to calculate mean tree basal area and multiplied this by the number of trees per ha for each scale (e.g., all trees in a section).

Stocking and forest types—historical forests

We calculated stocking and forest types at the land type association scale for historical forests. A stocking percent of 100 represents full use of growing space; sites only can hold a certain number of trees of a certain diameter and thus, increases in site quality lead to increased tree height and faster diameter growth. We used stocking equations and coefficients developed by FIA (Arner et al. 2003).

We then applied thresholds developed in Hanberry et al. (2014b; based on quantifications of expert designations) to classify tree density and stocking into the following forest types: oaks or pine prairie/savanna, oak or pine woodland, pine forest, forest of late-successional eastern broadleaf species, forest, and forest of low stocking. For thresholds, we set the boundary between savanna and woodlands at 30% stocking, taking into account that we only used trees ≥ 12.7 cm diameter and therefore, there was a missing component to percent stocking (Hanberry et al. 2014b). We used the boundary between woodlands and closed forests of 75% stocking, and added a functional group if group composition commonly was ≥ 40% (i.e., for oak, pine, and late-successional eastern broadleaf species). If tree densities were ≥ 250 trees/ha and stocking was < 75%, we classed this forest type as 'forests of low stocking'.

Results

Species trends at the division scale

In the Eastern Broadleaf Forest division, there was a large difference (≥ 4.5%) between line and bearing tree data for bur oak, sugar maple, and American basswood (Table 1). Nevertheless, and despite gaps in sampling of line trees, mean absolute difference between line and bearing tree data was 1.3%. In contrast, mean absolute difference between current tree data and either line or bearing tree data was 4.1–4.2%. Species that increased in percent composition were red pine (i.e., *Pinus resinosa* Aiton increased by approximately 8.5% in composition from about 1% in both line and bearing tree surveys to 9.5% in current

Table 1 Percent composition of historical trees encountered by surveyors along survey lines (historical line), historical trees selected by surveyors (historical bearing), or current trees (≥ 1% composition in one of the datasets; ≥ 12.7 cm in diameter) in the Eastern Broadleaf Forest and Northern Mixed Forest Division of Wisconsin

Eastern Broadleaf Forest division							Northern Mixed Forest division						
Species	Historical line		Historical bearing		Current		Species	Historical line		Historical bearing		Current	
	Count	%	Count	%	Count	%		Count	%	Count	%	Count	%
White oak, *Quercus alba*	8945	21.40	30467	21.83	2152	6.11	Eastern hemlock, *Tsuga canadensis*	7073	16.00	26068	14.08	1976	2.09
Black oak, *Q. velutina*	6400	15.31	22832	16.36	1833	5.20	Sugar maple	4222	9.55	17842	9.64	12567	13.27
Bur oak, *Q. macrocarpa*	5100	12.20	31789	22.77	898	2.55	Pine	3233	7.31	4365	2.36		
Sugar maple, *Acer saccharum*	3842	9.19	6570	4.71	1043	2.96	Eastern white pine	4215	9.54	13125	7.09	2113	2.23
American basswood, *Tilia americana*	3051	7.30	3253	2.33	1394	3.96	Red pine	1061	2.40	7041	3.80	5129	5.42
American elm, *Ulmus americana*	2178	5.21	4648	3.33	1924	5.46	Jack pine	457	1.03	6536	3.53	1598	1.69
Northern red and pin oaks, *Q. rubra, ellipsoidalis*	1690	4.04	5612	4.02	1950	5.53	Paper birch	3199	7.24	26678	14.41	3921	4.14
Aspen	1424	3.41	4622	3.31	2499	7.09	American beech	2555	5.78	6171	3.33	141	0.15
Quaking aspen, *Populus tremuloides*					1410	4.00	American basswood	2443	5.53	3983	2.15	3778	3.99
Bigtooth aspen, *P. grandidentata*					1089	3.09	Tamarack	2126	4.81	14737	7.96	2524	2.67
Tamarack, *Larix laricina*	1267	3.03	4523	3.24	300	0.85	American elm	2044	4.62	6221	3.36	0	0.00
American beech, *Fagus grandifolia*	967	2.31	1260	0.90	30	0.09	Northern white-cedar, *Thuja occidentalis*	1994	4.51	8025	4.33	6895	7.28
Eastern hophornbeam, *Ostrya virginiana*	904	2.16	1770	1.27	395	1.12	Maple	1893	4.28	7558	4.08		
Pine	778	1.86	2229	1.60			Red maple					13274	14.02
Eastern white pine, *Pinus strobus*	853	2.04	3645	2.61	2161	6.13	Aspen	1541	3.49	7134	3.85	13489	14.25
Jack pine, *P. banksiana*	325	0.78	3549	2.54	1208	3.43	Quaking aspen					11160	11.79
Red pine, *P. resinosa*	267	0.64	1896	1.36	3376	9.58	Bigtooth aspen					2329	2.46
Ash	122	0.29	545	0.39			Ash	59	0.13	1190	0.64		
Black ash, *Fraxinus nigra*	763	1.83	1367	0.98	488	1.38	Black ash	1165	2.64	3195	1.73	4932	5.21
White ash, *F. americana*	445	1.06	956	0.68	603	1.71	White ash	367	0.83	761	0.41	1206	1.27

Table 1 (continued)

Eastern Broadleaf Forest division							Northern Mixed Forest division						
Species	Historical line		Historical bearing		Current		Species	Historical line		Historical bearing		Current	
	Count	%	Count	%	Count	%		Count	%	Count	%	Count	%
Green ash, *F. pennsylvanica*					852	2.42	Green ash					1548	1.64
Maple	731	1.75	2722	1.95	1820	5.16	White oak	964	2.18	2760	1.49	522	0.55
Boxelder, *A.negundo*					1268	3.60	Yellow birch, *B. alleghaniensis*	889	2.01	4642	2.51	2080	2.20
Silver maple, *A. saccharinum*					552	1.57	Black oak	822	1.86	2227	1.20	35	0.04
Red maple, *A. rubrum*	10	0.02	4	0.00	3057	8.67	Eastern hophornbeam	460	1.04	2188	1.18	495	0.52
Hickory	443	1.06	1036	0.74	1785	5.07	Balsam fir, *Abies balsamea*	422	0.95	4362	2.36	5433	5.74
Shagbark hickory, *Carya ovata*					1080	3.06	Spruce	415	0.94	5550	3.00	4000	4.23
Bitternut hickory, *C. cordiformis*					705	2.00	Black spruce, *Picea mariana*					2514	2.66
Paper birch, *Betula papyrifera*	377	0.90	2078	1.49	1085	3.08	White spruce, *P. glauca*					1486	1.57
Black cherry, *Prunus serotina*	170	0.41	314	0.22	1528	4.34	Northern red oak	143	0.32	898	0.48	3199	3.38
Slippery elm, *U. rubra*	116	0.28	201	0.14	452	1.28							
Black walnut, *Juglans nigra*	27	0.06	93	0.07	429	1.22							

surveys), red maple (+9%), and eastern white pine (*Pinus strobus*; +4%) and black cherry (+4%). Species that decreased in percent composition were white oak (*Quercus alba*; −15%), black oak (*Q. velutina*; −10%), and bur oak (*Q. macrocarpa*; −10% based on line trees to −20% based on bearing trees).

In the Northern Mixed Forest, there was a large difference (≥4.5%) between line and bearing tree data for paper birch (*Betula papyrifera*) and undifferentiated pine. Nonetheless, and including incomplete line tree sampling, mean absolute difference between line and bearing tree data was 1.4% and mean absolute difference between current tree data and either line or bearing tree data was 3.8–3.9%. Species that increased in percent composition were quaking aspen (*Populus tremuloides*) of the aspen group (+8%), red maple (+10% to 14%, depending on comparison to line or bearing trees), and balsam fir (*Abies balsamea*; +4%). Northern white-cedar, black ash (*Fraxinus nigra*), and northern red oak (*Q. rubra*) also increased (approximately +3% each). Species that decreased in percent composition were eastern hemlock (−13%), eastern white pine (*Pinus strobus* −6%), paper birch (−3% to −10%, depending on comparison to line or bearing trees), American beech (−3% to −6% depending on comparison to line or bearing trees), American elm (*Ulmus americana*; −4%), and tamarack (−2% to −5% depending on comparison to line or bearing trees).

Functional groups and structure at the section scale

Overall, in Eastern Broadleaf Forest sections, increased composition of the early-successional eastern broadleaf forest group (from 2 to 13%), mid-successional eastern broadleaf forest group (from 8 to 27%), and pine group (8 to 23%) occurred with decreased oak composition (from 65 to 23%; Table 2; Fig. 2). In Northern Mixed Forest sections, increased composition of the mid-successional eastern broadleaf forest group (from 12 to 24%) and late-successional northern mixed forest group (from 10 to 17%) occurred with decreased composition of the late-successional eastern broadleaf forest group (from 30 to 20%), pine group (from 17 to 9%), and early-successional northern mixed forest group (from 26 to 21%).

In the Eastern Broadleaf Forest division, density increased by a factor of 2.2 to about 274 trees/ha in current forests from 124 trees/ha in historical forests, particularly due to low densities of 110 trees/ha in open oak ecosystems (73% oak) in two sections (Table 2; Fig. 3). Despite increased density, basal area increased only slightly (from 11 to 14 m^2/ha) due to effects of larger diameter trees in historical tree surveys. In the Northern Mixed Forest division, density in current forests (374 trees/ha) was similar to that in historical forests (387 trees/ha) but current basal area (16 m^2/ha) was 50% of historical basal area (32 m^2/ha) due to the higher density of large diameter trees in historical tree surveys. Mean diameters were about 30.5 cm in historical tree surveys and 22 cm in current surveys.

Historical reference conditions

At the land type association scale, the percent area of historical reference conditions was 46% oak savanna (comprised of 88% oak) and oak or pine woodland (46% oak and 16% pine) at about 6 million ha, 6% pine forest (56% pine), 16% primarily (50% of all species) late-successional eastern broadleaf forest, and 33% a combination of late-successional eastern broadleaf forests and early-successional northern mixed forests (combined > 50% of all species; Table 3; Fig. 4). In Wisconsin, about 6% of the area, or 11 land types, had a structure of lower stocking that matched woodlands, yet tree densities of ≥250/ha that exceeded

Table 2 Percent composition by functional group (*eebf* early-successional eastern broadleaf species, *mebf* mid-successional eastern broadleaf species, *lebf* late-successional eastern broadleaf species, *enmf* early-successional northern mixed forest species, *lnmf* late-successional northern mixed species), density (trees/ha), and basal area (BA; m^2/ha) for historical bearing trees selected by surveyors and current trees (≥ 12.7 cm in diameter) by ecological sections and two ecological divisions (area-weighted mean of ecological subsection values) in Wisconsin

Section	Historical							Current							Historical		Current	
	eebf	mebf	lebf	enmf	lnmf	Oak	Pine	eebf	mebf	lebf	enmf	lnmf	Oak	Pine	Density	BA	Density	BA
222K	1.93	7.65	11.31	5.80	0.37	72.09	0.85	16.15	28.52	6.69	8.62	3.74	17.04	19.24	109	11	283	14
222L	1.48	7.31	8.49	5.15	0.00	73.73	3.85	15.26	29.97	11.21	10.42	0.27	24.57	8.30	110	10	261	14
222M	1.36	17.73	23.28	22.13	0.00	33.55	1.95	14.92	25.10	12.50	15.89	2.62	16.28	12.69	239	20	255	13
222R	0.39	6.71	2.82	19.46	0.64	30.85	39.14	2.22	18.44	1.07	12.27	0.23	25.15	40.62	186	15	295	13
Eastern Broadleaf division	1.50	7.72	9.32	8.09	0.24	65.41	7.72	12.54	26.86	7.80	10.53	1.21	22.54	18.51	124	11	274	14
212J	0.11	5.08	44.20	28.59	19.48	0.21	2.34	1.77	25.14	36.74	12.29	20.66	0.83	2.57	481	38	453	19
212K	0.18	5.22	2.62	22.38	6.80	5.87	56.93	0.48	20.34	3.97	24.75	8.55	15.41	26.50	310	22	352	14
212Q	1.06	17.56	33.44	27.80	2.16	7.88	10.10	5.79	34.30	17.72	17.94	5.45	11.35	7.44	330	31	315	14
212T	0.70	12.66	34.10	21.55	10.74	2.12	18.14	3.01	21.17	15.07	17.38	25.73	6.04	11.60	431	38	425	18
212X	0.27	10.22	31.35	31.16	12.19	1.37	13.44	2.43	22.35	24.75	22.43	17.41	3.99	6.64	433	35	369	16
212Y	0.21	8.80	15.36	29.56	24.95	1.19	19.93	0.59	27.17	10.73	35.39	16.70	4.50	4.92	441	34	358	14
212Z	2.50	22.53	45.57	10.84	4.96	8.90	4.71	9.09	42.18	11.44	13.32	15.18	6.27	2.52	330	28	391	18
Northern Mixed division	0.66	12.43	30.38	26.25	9.69	3.81	16.77	2.82	24.27	19.65	20.86	16.92	6.25	9.23	387	32	374	16

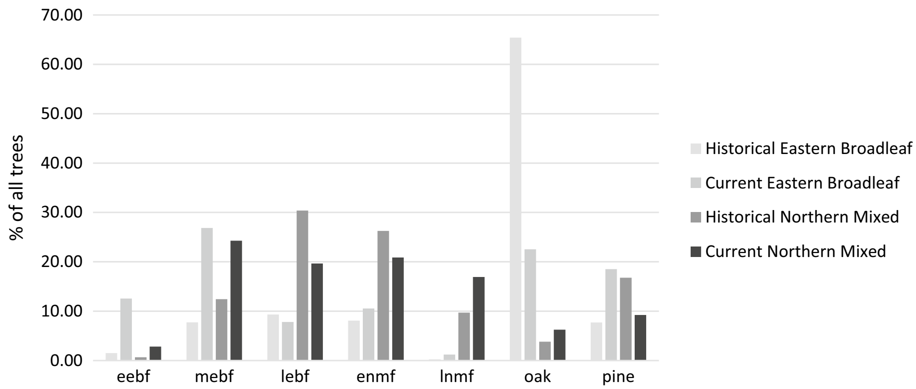

Fig. 2 Percent of each functional group (*eebf* early-successional eastern broadleaf species, *mebf* mid-successional eastern broadleaf species, *lebf* late-successional eastern broadleaf species, *enmf* early-successional northern mixed forest species, *lnmf* late-successional northern mixed species) for historical and current forests of the Eastern Broadleaf Forest and Northern Mixed Forest divisions

woodlands, and 13% oak and 13% pine composition. We called the characteristics of lower yet generally fully stocked forest (i.e., percent stocking ≥ 60) and closed forest densities as 'forests of low stocking', which may be due to the presence of pines and oaks.

Discussion

We used historical composition by functional groups and structure to reconstruct historically common forest types (Table 3; Fig. 4). We also provided historical functional groups, structure, and forest types for 186 land types to provide reference conditions at a scale that matches local restoration (Online Appendix A; Fig. 3). The forest types represent a gradient in density from prairie/savanna to open/closed woodland to closed forest. This canopy spectrum of forest structure is no longer present at landscape scales (Hanberry et al. 2014b; Hanberry and Abrams 2018). In the Eastern Broadleaf Forest division, density increased in current forests compared to historical forests by a factor of 2.2 (Table 2). Even current forests with low tree densities and stocking (e.g., < 75%) typically are comprised of many small diameter trees that fill in the vertical profile and inhibit herbaceous growth due to low levels of available light and occupation of physical space (Hanberry et al. 2018). In general, trees are smaller (e.g., < 25 cm in diameter) now than before Euro-American influence. Others have observed the conversion of open oak and pine savannas and woodlands to closed, dense forests following fire suppression, and the loss of large diameter trees in Wisconsin forests (Schulte et al. 2007; Rhemtulla et al. 2009).

Vegetation phases of savanna, open woodland, and closed woodland are continuous in structure, with spatial variation in tree densities. Indeed, we did not differentiate prairies from savannas, because eastern prairies contain trees along riparian corridors and other wetlands as well as steeper topographies, but a general threshold may be around 10% stocking and 50 trees/ha. About 5 land types of the 222L ecological section and 8 land types of the 222 K ecological section had 6–15% stocking and < 50 trees/ha. Although this area of Wisconsin has been described as oak-brushlands and scrub (Cottam 1949), tree diameters were equivalent to other areas and forest types (Table 3; Online Appendix A).

Fig. 3 Historical density estimates ranging from 26 to 800 trees/ha (shaded light to dark gray; see Online Appendix A) by land type association within Wisconsin

Table 3 Mean quantified structure (density in trees/ha, stock = percent stocking, DBH = diameter in cm, BA = basal area in m^2/ha) and functional group composition (*mebf* mid-successional eastern broadleaf species, *lebf* late-successional eastern broadleaf species, *enmf* early-successional northern mixed forest species, *lnmf* late-successional northern mixed species) by forest type

Forest type	Count	Density	Stock	DBH	BA	Oak	Pine	mebf	lebf	enmf	llmf
Oak or pine prairie/savanna	40	59.5	17.7	31.2	5.3	88.4	4.1	2.5	1.1	3.5	0.1
Oak or pine woodland	35	156.7	42.9	30.5	13.9	46.4	16.1	11.0	11.4	12.9	1.2
Forest of low stocking	11	274.0	67.3	30.2	23.2	12.6	12.6	15.9	25.3	26.1	8.2
Pine forest	16	361.7	68.4	28.6	28.3	4.7	56.1	4.6	5.7	24.1	5.4
Late forest	36	399.7	119.0	31.4	36.2	4.7	4.5	14.0	50.2	19.2	6.7
Forest	48	458.1	107.6	29.5	36.1	4.0	11.5	14.0	28.5	29.2	12.9

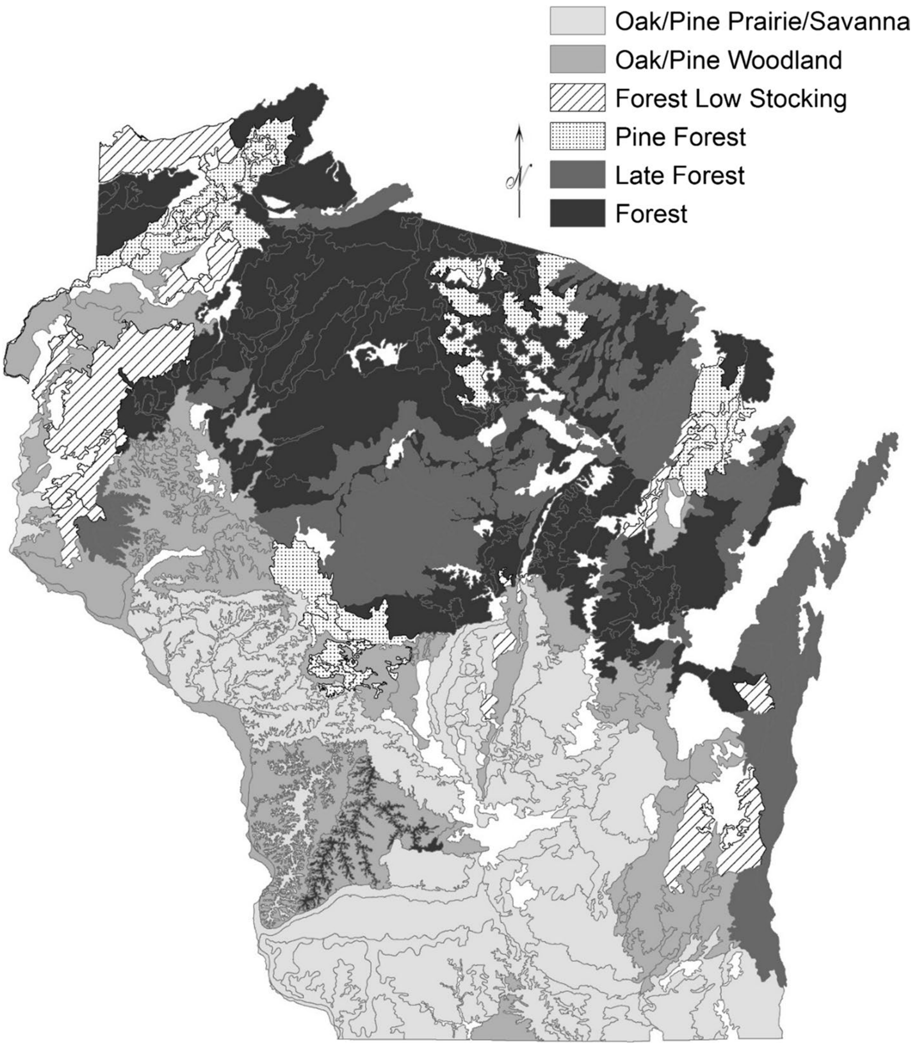

Fig. 4 Historical forest types in Wisconsin. Late-successional forest consists primarily of late-successional eastern broadleaf species while 'forest' contains both late-successional eastern broadleaf species and early-successional northern mixed forest species

It is important to recognize that a state transition or regime shift occurs when open-structured ecosystems such as savannas and woodlands become closed forests as mid-and understory tree layers develop after fire exclusion (Zenner et al. 2006; Peterson and Reich 2008; Waldrop et al. 2008; Ratajczak et al. 2012; Hanberry et al. 2014a; Kinkead et al. 2017; Vander Yacht et al. 2017; Hanberry et al. 2018). The initial response to fire exclusion is for oak and pine species to increase as savannas and woodlands transition to forests. As Rogers et al. (2008) noted, without fire, forests will be dominated by oaks for a single generation, albeit an oak generation may last for hundreds of years without overstory disturbance. Overstory tree removal of oaks by cutting accelerates the transition to fire-sensitive tree species such as maples and black cherry, which increasingly establish and out-compete oak and pine species without fire. Reversal of the transition from closed forest to open forest is difficult because of conditions that increasingly become less flammable, without the fine fuels from the herbaceous layer and fire-tolerant tree litter that spread fire, and due to increased fire resistance by fire-sensitive species that is gained by thicker bark on larger diameter trees (i.e., the mesophication process, Nowacki and Abrams 2008; Hanberry et al. 2014a).

Nonetheless, in the historical forest types, we identified pine forests that perhaps may represent a stable state in the transition from open to closed forests. We suggest that lower stocking, high tree densities, and slightly smaller diameters represent dense regeneration after relatively recent high severity disturbances. Pines tolerate a more variable fire regime and may produce dense regeneration after severe fires. The forest type identified as forests of low stocking had a greater percent of pine and oak (25% combined), which may produce similar characteristics. However, local variation in density changes occurred, primarily in pine barrens and savannas where density increased in modern times as trees established and developed following fire suppression to form closed forests. Generally, in the Northern Mixed Forest division, density remained similar in current forests compared to historical forests overall, but basal area decreased due to the loss of larger diameter trees in modern forests. These results were similar to structural changes that occurred in Minnesota (Hanberry et al. 2012b).

We also chronicled changes in composition and the major functional groups from historical to current forests in Wisconsin, similar to previous reports (Radeloff et al. 1999; Bolliger et al. 2004; Schulte et al. 2007; Rhemtulla et al. 2009), which paralleled changes in functional groups of the eastern United States (e.g., Hanberry 2019). The concept of mesophication (Nowacki and Abrams 2008) expresses the transition from open fire-tolerant oak and pine forests due to fire exclusion to closed forests that are more resistant to surface fires, and likely at more risk for severe fires as woody biomass develops throughout the vertical profile, providing ladder fuels to the canopy. The process of succession, to mesic species of increased shade tolerance, may co-occur but is not necessary. Generally in eastern broadleaf forests, as is the case of Wisconsin, a variety of early- and mid-successional species increase but late-successional species decrease, due to factors such as disease and land use that remove long-lived shade-tolerant species (e.g., Hanberry 2019). Oak composition showed the greatest decrease from 65 to 23% in the Eastern Broadleaf Forest division of Wisconsin and historically dominant oaks continue to decrease throughout the eastern United States (Rhemtulla et al. 2009; Hanberry and Abrams 2018). In the absence of fire since the 1930s, fire-sensitive early- and mid-successional eastern broadleaf species, such as black cherry and red maple have established and out-competed the fire-adapted oaks in Wisconsin and the eastern United States (Johnson et al. 2019). In addition, red pine plantations have increased composition of the pine group in southern Wisconsin (Rhemtulla et al. 2009), as occurred in Minnesota (Hanberry et al. 2012a, b). In the Northern Mixed Forest division, land use history reduced late-successional eastern hemlock and American beech from 30 to 20% composition, as reported for northern Wisconsin (Rhemtulla et al. 2009), and elsewhere (Whitney and Decant 2003; Thompson et al. 2013; Hanberry 2019). Aspen has increased throughout the state by establishment of the pulp and paper industry (Bolliger et al. 2004; Schulte et al. 2007; Rhemtulla et al. 2009). Pines also decreased in composition overall, while the mid-successional eastern broadleaf forest group and late-successional northern mixed forest group increased (Bolliger et al. 2004; Schulte et al. 2007; Rhemtulla et al. 2009). Red pine has remained stable in dominance due largely to establishment of plantations.

The functional groups establish the rarity of early-successional species in historical forests. Early-successional tree species typically were about 0.5–1.5% of species, excluding characteristic northern mixed forest species of tamarack, birch, and aspen, because succession due to disturbance that removed overstory trees was rare in eastern broadleaf forests (Canham and Loucks 1984; Frelich and Lorimer 1991; Schulte and Mladenoff 2005; Hanberry et al. 2018). Infrequent overstory tree disturbance allowed continuity of oak and late-successional forests (Hanberry et al. 2018; Hanberry 2019). Conversely in northern mixed forests, early-successional species of tamarack, birch, and aspen were abundant because tree species in replacement stands, after relatively frequent overstory tree removal (around 100 years), were identical to the previous generation, although shorter fire return intervals and greater severity fires may favor birch and aspen (Johnstone and Chapin 2006; Johnstone et al. 2010). Thus, these forests were maintained by severe fire regimes as successional forests that had time to develop in structure but not progress in composition to more shade-tolerant species, somewhat similar to current forests with frequent overstory tree removal.

Using historical reference conditions as a restoration guide for the future

Historical reference conditions provide perspective on (1) the range of variability that can develop over time, (2) conditions that supported native species, and (3) changes that have occurred in composition and structure to prioritize now underrepresented ecosystems (Moore et al. 1999; Thompson et al. 2009). Historical reference conditions help impart an ecological context for determining desired future conditions at community and landscape scales. They also supply guidance for silvicultural prescriptions that can mimic natural disturbance regimes into the sequence of practices while taking into account socioeconomic constraints. Historical reference conditions can inform silvicultural systems, harvest frequency, harvest size and shapes, tree retention, and spatial distribution of tree removals. For example, reference conditions help explain why simply burning as a treatment may have unexpected results due to widespread structural and compositional differences in current forests (Moore et al. 1999) that make them resistant to management by fire alone, i.e., mesophication. In addition, deviation from reference conditions suggests that ongoing human interaction through management and restoration are both necessary and probably desirable.

Lack of variability in density and structure typifies current forests compared to historical forests (Hanberry et al. 2018). We note that variability in tree species is not necessarily desirable in open oak and pine forests, where tree species richness was limited to species tolerant of frequent fire, but provision of open forest structure will increase native diversity of herbaceous and wildlife species (Leach and Givnish 1999; Peterson and Reich 2008; Hunter and Schmiegelow 2011; Hanberry and Thompson 2019). Variability is a hallmark of ecology and evolution, and will make future desired conditions and management for those conditions more relevant and more viable. Incorporation of variability into management plans will reduce deterministic and uniform management actions (Landres et al. 1999). Indeed, we previously have recommended that the restoration or management objective should be to control tree regeneration and remove tree growth in the midstory, without inflexibly focusing on achieving specific structural measurements of a particular phase of savanna, open woodland, or closed woodland, given the difficulty of restoration and the value in spatial variability in tree structures (Hanberry et al. 2014b).

Historical references used to define objectives and targets for restoration may be considered to be of limited relevance and too static under climate change and other anthropogenic land uses (Millar and Woolfenden 1999; focus groups in Mitchell and Duncan 2009;

Thompson et al. 2009). However, the inertia that results from trees that can live for centuries means that a 'snapshot in time' (i.e., General Land Office surveys) represents the legacy of thousands of years of limited tree generations under dynamic interactions and processes that produced the historic state over several climate warming and cooling periods, including megadroughts, which current novel forests have yet to experience. The prospect for the future is expansion of trees in a poleward direction, as has happened in the past and is simulated in statistical or process-based models, based on climate envelopes. The northern range of open oak forests occurs in southern Wisconsin, and the oak range extends south for another 1000 km to the north range of Coastal Plain pine forests, supplying an appropriate ecosystem match to climate. Indeed, if not for sandy soils of the southernmost US, oaks likely would have dominated forests to the Gulf of Mexico. Therefore, management of open oak forests is compatible with expected climate change in Wisconsin (McKenney et al. 2007; Iverson et al. 2008; Brandt et al. Brandt et al. 2014). Moreover, open oak and pine forests provide resistance to increased frequency of severe fires and drought, which may occur in the future (Allen et al. 2010; Guyette et al. 2014; IPCC 2014).

Because of increases in tree density, loss of oak, and conversion to agriculture in the Eastern Broadleaf Forest division, savannas and woodlands that once covered almost half of Wisconsin are no longer present at a landscape scale (e.g., Hanberry and Abrams 2018). A substantial extinction debt likely has accrued, exhibited by a slow decrease in abundance and number of species due to reduced survival and reproduction in degraded or alternative habitat (Tilman et al. 1994; e.g., the 'insect apocalypse'). Localized remnants support the now rare herbaceous species associated with open oak forest ecosystems (Leach and Givnish 1999; Peterson and Reich 2008; Rogers et al. 2008, 2009; Foltz et al. 2013). Likewise, species that are dependent on complex structure that develops over time in late-successional eastern hemlock and American beech forests also are declining (Rooney et al. 2004; Amatangelo et al. 2011).

Critically, the species of these now rare historical reference conditions are not irrelevant, as long as they persist (Rooney et al. 2004; Rogers et al. 2008; Hanberry and Thompson 2019). Despite the almost complete loss of the historically dominant open oak forest ecosystems in the Eastern Broadleaf Forest division and loss of the archetypical old growth forests of late-successional species in the Northern Mixed Forest division, there still is time to support species using restoration rather than dismiss species associated with these open or structurally complex systems as impossible to support under current and future conditions. Indeed, there are socioeconomic resources available for restoration, and restoration principles align with forest management for the future, rather than undermining preparation for future forests (Hanberry et al. 2015).

Restoration ecology is not limited to the goal of returning an ecosystem to a prior condition. Instead, restoration and management objectives include meeting societal demands for ecosystem goods and services and producing ecosystems that are well-adapted to environmental stresses and biotic threats, to prepare ecosystems for an uncertain future (Hanberry et al. 2015). Assisting recovery of an ecosystem to a state (historically faithful or not) with species composition, structure, and function (i.e., natural processes) operating within the range of variation experienced by those species over evolutionary time may make the ecosystem more resilient to future change, because these ecosystems have withstood the test of varying climates (e.g., the Medieval Warm Period, Little Ice Age, megadroughts) compared to current novel forests (Hanberry et al. 2015). Nonetheless, restoration goals for functioning ecosystems may rely more heavily on supporting historically common conditions, eventually resulting in management of achieved desired conditions, whereas goals for severely degraded or novel ecosystems may be based on maximizing ecosystem functions or services (Hanberry et al. 2015).

Conclusion

Open oak ecosystems dominated the Eastern Broadleaf Forest division in Wisconsin historically, while open pine ecosystems were present in the Northern Mixed Forest division. Replacement by dense forests has reduced plant and wildlife species associated with more open oak and pine ecosystems (Rooney et al. 2004; Rogers et al. 2009). Restoration of open oak forest ecosystems or pine forest ecosystems would fulfill multiple objectives and correspond with regional interests. Historical ecosystems have been tested by previous climate change, unlike current forests, and the northern front of historical open oak ecosystems occurred in Wisconsin and extended 1000 km to the south, providing appropriate ecosystems under future expected climates. There is no compelling incompatibility between restoration and forest management for current and future conditions. These reference conditions provide a provisional starting point for management, although management is an adaptive process that will vary by ecological context, weather, and climate.

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