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Baseline to novel ecosystems in Michigan, USA, with a quantitative and qualitative assessment

Brice B. Hanberry

Grassland, Shrubland, and Desert Ecosystem, USDA Forest Service, Rapid City, SD, USA

ABSTRACT

Pre-Euro-American settlement vegetation provides information about historical ecology. I evaluated baseline conditions and novel status of current forests in Michigan using historical (1836 to 1858) and current (2010–2015) surveys and assessed quantitative and qualitative measures of novel status. Aspen (increased from 2% to 11% of all trees) and red maple (<2% to 12.5%) replaced eastern hemlock (15% to 2%) and American beech (8% to <1%) as most abundant species. Density was similar between surveys but mean diameter (trees ≥12.7 cm) decreased from 39 to 22 cm. The emerging forest type is a mix of early- to mid-successional species, particularly red maple, from eastern broadleaf forests of the central-eastern US.Openlands in southern Michigan have been replaced by agriculture and closed forests. Historical forests dominated by few tree species have transitioned to diverse eastern broadleaf forests throughout the eastern US, conforming to quantitative and qualitative measures of novel ecosystem status. Besides exceeding a quantitative threshold (e.g., squared chord distance), current forests meet novel status because they are ubiquitous, constitute a new normal, arise predictably, and unavoidably in response to disturbance or land-use change, auto-organize, and retain novelty after crossing thresholds challenging to reverse.

RÉSUMÉ

La végétation d'avant la colonisation euro-américaine informe sur l'écologie historique. J'ai évalué les conditions de base et le statut nouveau des forêts actuelles au Michigan en utilisant des recensements historiques (1836 à 1858) et récents (2010-2015) afin d'obtenir des mesures quantitatives et qualitatives de statut nouveau. Les peupliers (qui ont augmenté de 2% à 11% de tous les arbres) et l'érable rouge (<2% à 12,5%) ont remplacé la pruche du Canada (15% à 2%) et le hêtre à grandes feuilles (8% à <1%) comme espèces les plus abondantes. La densité était similaire entre les recensements, mais le diamètre moyen (arbres ≥12,7 cm) a diminué de 39 à 22 cm. Le type de forêt émergent est un mélange d'espèces de début et de milieu de succession, particulièrement l'érable rouge, des forêts feuillues orientales du centre-est des États-Unis.Les milieux ouverts du sud du Michigan ont été remplacés par des milieux agricoles et des forêts fermées. Les forêts historiques dominées par peu d'espèces arborescentes se sont transformées en forêts feuillues orientales diversifiées dans l'est des États-Unis, en conformité avec les mesures quantitatives et qualitatives de statut de nouvel écosystème. En plus de dépasser un seuil quantitatif (p. ex.: mesure de corde au carré), les forêts actuelles ont le statut nouveau parce qu'elles sont omniprésentes, constituent une nouvelle normalité, apparaissent inévitablement après une perturbation ou un changement d'utilisation du territoire, s'auto-organisent, et conservent leur état nouveau après avoir passé des seuils de risque de réversion.

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Introduction

Reconstruction of vegetation during pre-Euro-American settlement delivers information about historical ecology and gives context about the magnitude and trajectory of change in current ecosystems for research and resource management. Without knowledge of historical vegetation, ecology and management are based on vegetation during post-Euro-American settlement as the baseline condition, which may represent novel ecosystems that have been greatly influenced by human land use (Murcia et al. 2014). Thus, current forests may not characterize desired conditions ecologically and for management across the landscape. In addition, application of historical ecology is relevant in understanding species response under climate change. Indeed, documentation of historical species distributions after glaciation imparts a foundation for projections of future distributions and ecosystem disassemblies, whereas reconstructed climate conveys perspective for future climate models. The past helps inform the future.

CONTACT Brice B. Hanberry brice.hanberry@usda.gov

Historical forest types in the Great Lakes states spanned a wide range of disturbance gradients, from open oak and pine forests primarily under a frequent low severity fire (e.g., understory disturbance) regime, to late-successional forests of *Acer saccharum* (sugar maple), *Fagus grandifolia* (American beech), and *Tsuga canadensis* (eastern hemlock) that experienced rare understory or overstory disturbance (70 years for ≥10% canopy removal to 1920 years for ≥60% canopy removal, Frelich and Lorimer 1991; Leahy and Pregitzer 2003), to perpetually successional boreal forests under frequent high severity fire regimes that replaced the overstory every 50 to 150 years (Heinselman 1973; Cleland et al. 2004). Despite rapid succession in structure, boreal forests tended to auto-replace with the species that were present before high severity disturbance, resulting in relatively stable composition, of either shade-sensitive *Larix laricina* (tamarack), *Betula papyrifera* (paper birch), and aspen [*Populus tremuloides* (quaking aspen) and *Populus grandidentata* (bigtooth aspen)] or shade-tolerant *Thuja occidentalis* (northern white-cedar), *Picea glauca* and *mariana* (white and black spruce), and *Abies balsamea* (balsam fir; Heinselman 1973). Trees of any species established within 5 years of fire and forests often contained an understory of suppressed trees (Heinselman 1973).

After the turn of the twentieth-century logging in most of Michigan, with associated very frequent slash fires, and mid-1800s land cultivation in southern Michigan, little of the original ecosystems remained (Whitney 1987; Frelich and Lorimer 1991; Chapman and Brewer 2008). Regional differences in land use developed based on forestry in forestlands of the Upper and northern Lower Peninsula and agriculture in the open forests, grasslands, and wetlands of southern Lower Peninsula (50% to 80% of land in agriculture by 1910, Figure 1). Fire is suppressed throughout Michigan (Heinselman 1973; Cleland et al. 2001, 2004; Leahy and Pregitzer 2003). In southern Michigan, land outside of agriculture transitioned to closed forests in the absence of (low severity) fire (Chapman and Brewer 2008). In northern forestlands of Michigan, deciduous trees that reproduce vegetatively, particularly aspen, increased in the absence of coniferous seed sources (Whitney 1987; Cleland et al. 2001). Slash fires in the early 1900s also exposed mineral soil for aspen establishment and stimulated root suckering and aspen became a staple of the pulpwood industry (Whitney 1987). However, aspen stands start to decline after 35 to 60 years (Whitney 1987). Aspen-birch forest area peaked in abundance during the 1930s, followed by slight declines (0.2% per year) until the 1960s and strong declines (≥1% per year) through at least the 1980s (Cleland et al. 2001). Aspen declines suggest a new wave of species competitive under current land use, excluding areas intensively managed for aspen pulpwood. Goring et al. (2016) examined all of the Great Lake states

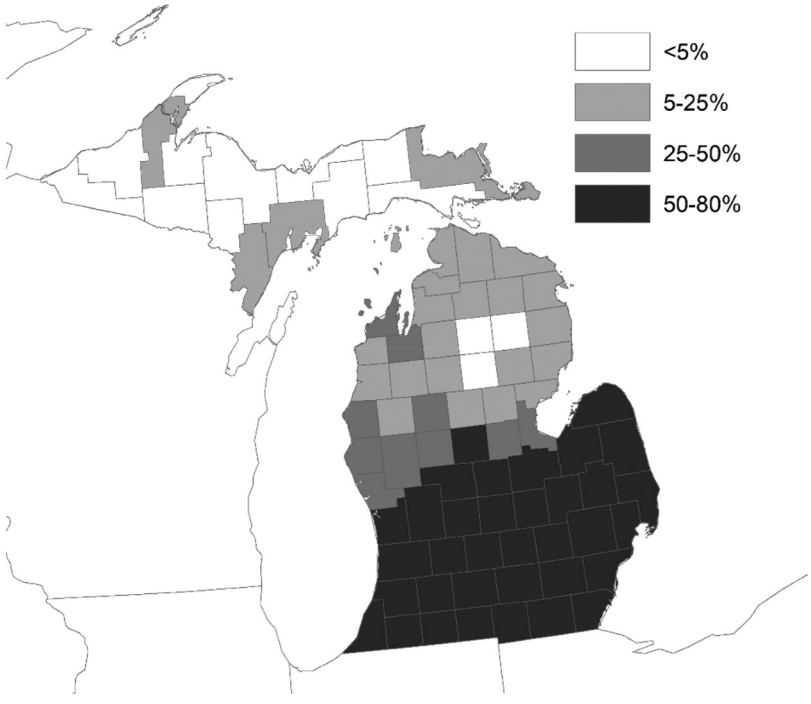

Figure 1. Percent of land in farms by county, 1910 (modified from Maizel et al. 1998).

(excluding southern Michigan) for lost and novel forests and determined lost forests included tamarack-pine-birch-spruce-poplar, cedar/juniper-pine-maple-hemlock, and beech-hemlock-maple in Michigan and novel forests were ash-maple-cedar/juniper-birch, maple-poplar-spruce, and poplar-maple-ash across the Great Lakes region.

In addition to disturbance as a driver of change, soils, climate (including the lake effect from the Great Lakes), and invasive insects and disease are important determinants of tree distributions by filtering traits related to flood, freeze, and infection tolerance. However, given that only modern soil surveys are available and some factors of soil formation are very stable (e.g., parent material, topography) despite disturbance by land use (e.g., drainage, tillage), studies that use edaphic factors necessarily hold soil constant while tree species have rearranged, resulting in weak apparent influence by soils on vegetation (i.e., Whitney 1999; Hanberry et al. 2013; Goring et al. 2016; Hanberry 2018). Historical disturbances interacted with soils, topography, and microclimate to amplify and differentiate tree distributions, while current land use may reduce environmental gradients by allowing expansion by many tree species or increase gradients by restricting competitiveness of some tree species (Whitney 1987; Palik and Pregitzer 1992; Barrett et al. 1995; Leahy and Pregitzer 2003; Hanberry et al. 2013; Goring and Williams 2017). Although temperature has warmed since the 1800s in Michigan (Bernabo 1981), cool anomalies particularly since the 1950s (Partridge et al. 2018) and the slow response of tree dynamics to climate change (Webb 1986; Davis and Shaw 2001) are among reasons that climate may not be very strong in influencing current tree distributions relative to land use or at minimum climate is interactive with land use (Zhang et al. 2014; Goring et al. 2016, 2017; Danneyrolles et al. 2019; Hanberry et al. 2019). There is no systematic evidence of northern latitudinal range shifts by eastern tree species (Hanberry and Hansen 2015; Woodall et al. 2018). Invasive species are issues for hemlock and beech, which are confronting either *Adelges tsugae* (hemlock wooly adelgid) and beech bark disease (beech scale insect, *Cryptococcus fagisuga*, with lethal fungal infections by *Neonectria* spp.; Lovett et al. 2006). Nonetheless, hemlock wooly adelgid is not a widespread problem yet in Michigan and while beech bark disease has killed a large number of beech trees in Michigan, beech bark disease was first detected during 2000, so these losses have been recent (McCullough 2016). As for white-tailed deer (*Odocoileus virginianus*) as a potential driver of forest changes, trends in tree species abundance and deer browse preference do not correspond (Hanberry and Abrams 2019). Additionally, high deer densities are not a new disturbance, given that there are an estimated 30 million deer currently in the US and estimates for historical deer populations generally ranged from 3 to 8 deer per km^2 or 24 million to 62 million animals (McCabe and McCabe 1984; Miller et al. 2003).

Using species groupings by disturbance gradients, I provide detailed information about historical forest composition and structure in Michigan and compare historical forests to current forests for restoration and management, with a discussion of novel ecosystem status. I evaluated General Land Office (GLO; 1836 to 1858) and USDA Forest Service Forest Inventory and Analysis (FIA; FIA DataMart, www.fia.fs.fed.us/tools-data, 2010 to 2015) surveys in the Upper Peninsula and northern Lower Peninsula (Figures 2 and 3; Cleland et al. 1997; Ecomap 2007) to provide tables of quantified density and other derived structural metrics at scales to guide local efforts. I also mapped historical and current ecosystems in Michigan, including a reconstruction of southern Michigan, where historical surveys were not available. Lastly, I assessed the novel status of Michigan's ecosystems using the squared chord distance metric (Overpeck et al. 1985) and conformation to Murcia et al. (2014) characteristics of novel ecosystems and placed Michigan's novel ecosystems in the context of novel ecosystems in the eastern US.

Methods

In the Upper Peninsula and northern Lower Peninsula of Michigan, the General Land Office conducted surveys from 1836 to 1858 following a systematic method in which undivided land was measured into 9.6 × 9.6 km townships that were subdivided further into 1.6 × 1.6 km sections. Surveyors selected two to four trees at survey points in the corners and middle of each section line (i.e., every 0.8 km). Surveyors recorded species, diameter, distance, and bearing of bearing trees from the survey points and also recorded line trees, or trees encountered along section lines for about 200,000 of both bearing and line trees (dataset from E. Schools, Michigan Natural Features Inventory). The southernmost portion of the northern Lower Peninsula of Michigan contained incomplete survey information in the database.

The GLO surveys contain bias because surveyors selected trees at survey points. The selection of trees resulted in trees that were not the nearest trees to

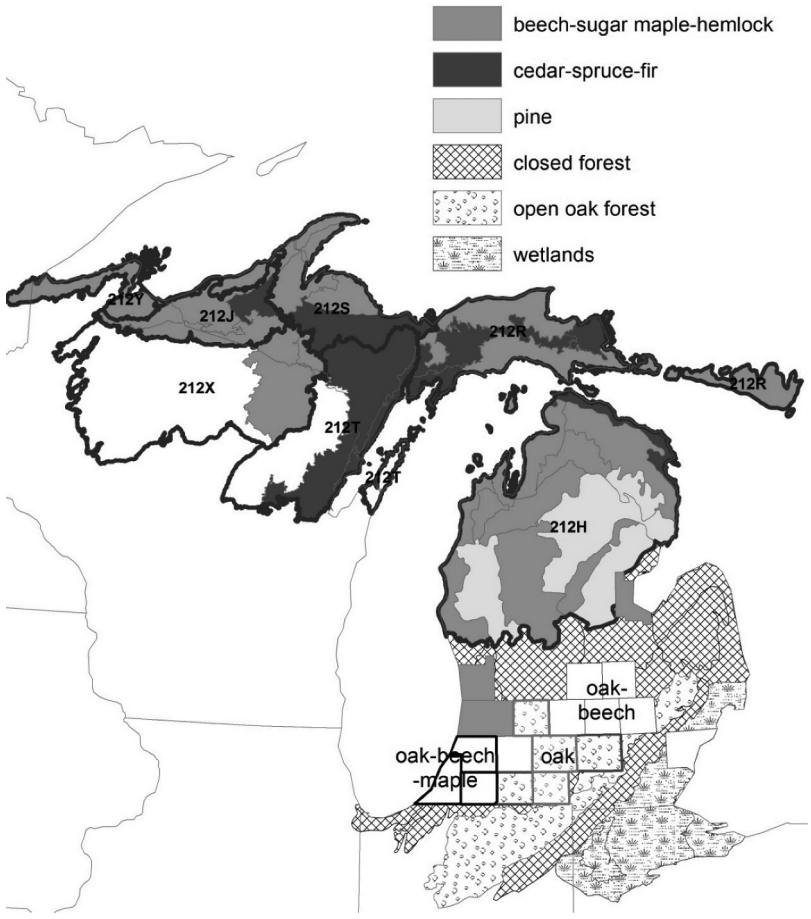

Figure 2. The Upper and northern Lower Peninsulas (outlined and labeled by ecological sections) of Michigan classified by the most abundant historical forest type by ecological subsection (light outline). The vegetation types for the southern Lower Peninsula (modified from the Michigan Presettlement Vegetation Cover, gis-michigan.opendata.arcgis.com/datasets; Hanberry and Abrams 2018) overlaid with forest types from counties with surveys. Three counties were beech-sugar maple-hemlock within the closed forests classification and one county was oak within the open oak forests classification. Seven counties were oak-beech (white shading) and three counties (white shading and dark outline) were oak-beech-sugar maple forests. Four counties were oak forests within closed forests.

survey points. In addition, selected trees were of moderate diameter in order to endure as markers. Due to line tree surveys that were comparable in number to bearing trees, I used line trees for determining composition. However, only the bearing trees provided the distance information necessary to determine the structure. I excluded any trees with diameters <12.7 cm to maintain a consistent diameter threshold.

The USDA Forest Service Forest Inventory and Analysis surveyed long-term plots from 2010 to 2015 in Michigan. The FIA surveys contained about 135,000 trees in the Upper Peninsula and northern Lower Peninsula of Michigan. I selected trees with diameters ≥12.7 cm to match GLO surveys and additionally because trees with diameters <12.7 cm are not surveyed as intensively as larger diameter trees in FIA surveys.

I presented percent composition of species for the entire extent and the most common species by ecological subsection. Due to imperfect identification by GLO surveyors for some trees, I matched GLO and FIA trees by genera or subgenus in some cases (i.e., pine, spruce, maple, aspen, the red oak group; see Table 1). I also quantified forest types based on response to disturbance for the entire extent and by ecological subsection. The five forest types were (1) late-successional sugar maple, American beech, and eastern hemlock, (2) pines, (3) shade-sensitive boreal forest species of tamarack, paper birch, and aspen, (4) shade-tolerant boreal forest species of northern white-cedar, spruce, and fir, (5) remaining species (i.e., eastern broadleaf forest species; see Table 1).

For the entire extent and by ecological subsection, I compared (dis)similarity of composition (percent of all trees as a ratio of 1 rather than 100, and grouped into 16

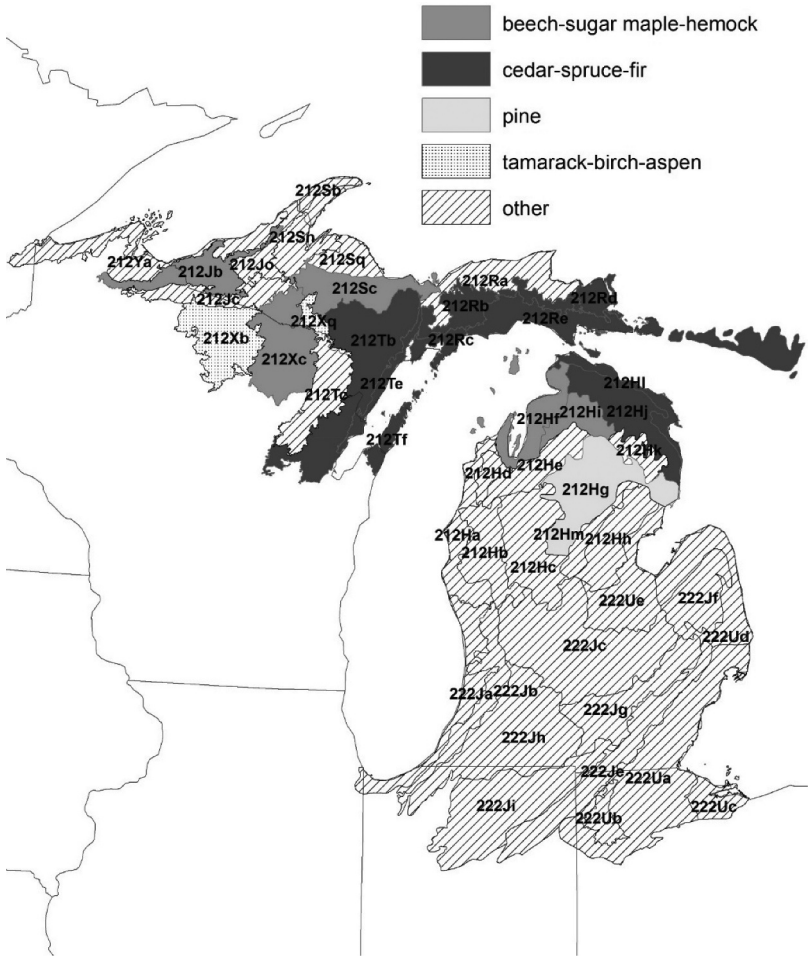

Figure 3. The Upper and northern Lower Peninsulas (labeled by ecological subsections) of Michigan classified by the most abundant current forest type by ecological subsection (light outline).

genera of *Abies, Acer, Betula, Carpinus-Ostrya, Fagus, Fraxinus, Larix, Picea, Pinus, Populus, Prunus, Quercus, Thuja, Tilia, Tsuga*, and *Ulmus*) between historical line trees and current trees using the squared chord, Jaccard, and Sørenson distance metrics (R Core Team package philentropy; Drost 2018). Numerous distance metrics are available with similar properties, at least after transformation (Legendre and De Cáceres 2013), but the squared chord distance metric is used for pollen samples of genera and additionally has a threshold for novel status (Overpeck et al. 1985). Modern pollen samples collected from historically different forest types tend to have squared chord distance ≥0.15, and given that thresholds divide continuous data, values between 0.12 and 0.15 indicate divergence (Overpeck et al. 1985).

I estimated historical density for each ecological subsection (Figure 2) with the Morisita estimator (Morisita 1957) for, p. 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; Hanberry et al. 2011). I then produced a low and high value based on adjustment for potential spatial patterning (clustered or regular patterns; Hanberry et al. 2011). I transferred values to corrections for surveyor bias. Surveyors potentially did not select the nearest trees to each survey point, which would produce a distance rank of 1. Selection of more distant trees will result in underestimated densities. I then determined a weighted average of mean values from two complementary methods, which also provided a low and high value. For a rank-based method, I adjusted density estimates to estimate a low value, based on selected trees having a mean rank of 1.4, and a mean value, assuming selected trees had a mean rank of 1.8 (ranks based on a tree selection dataset; Hanberry et al. 2012). Using a complementary method to correct for bias using equations (i.e., for non-random ratios of quadrants and azimuth and differences between frequencies of species and diameter of bearing and line trees), I calculated density estimates for another mean value and a high value (Hanberry et al. 2012).

For current tree surveys, summation of the number of trees per plot and expansion to a hectare results in

Table 1. Percent composition (≥1% of total stems; trees ≥12.7 cm in diameter) of historical trees encountered by surveyors along survey lines (historical line), historical trees selected by surveyors (historical bearing), or current trees, Upper Peninsula and Northern Lower Peninsula of Michigan.

Historical line				Historical bearing			Current		
Species		Count	%	Species	Count	%	Species	Count	%
Sugar maple	*Acer saccharum*	29,329	15.5	American beech	26,352	13.2	Sugar maple	18,924	13.6
Eastern hemlock	*Tsuga canadensis*	27,871	14.8	Sugar maple	25,134	12.6	Northern white-cedar	18,088	13.0
Northern white-cedar	*Thuja occidentalis*	18,590	9.9	Eastern hemlock	24,743	12.4	Red maple	17,486	12.6
American beech	*Fagus grandifolia*	14,913	7.9	Northern white-cedar	23,067	11.5	Red pine	11,140	8.0
Pine				Pine			Quaking aspen	10,466	7.5
Pine – unidentified		8223	4.4	Pine – unidentified	5153	2.6	Balsam fir	8496	6.1
Eastern white pine	*Pinus strobus*	12,826	6.8	Eastern white pine	11,816	5.9	Black spruce	4693	3.4
Red pine	*Pinus resinosa*	8258	4.4	Red pine	9210	4.6	Bigtooth aspen	4398	3.2
Jack pine	*Pinus banksiana*	6794	3.6	Jack pine	7375	3.7	Eastern white pine	4016	2.9
Balsam fir	*Abies balsamea*	10,205	5.4	Tamarack	11,146	5.6	Jack pine	3734	2.7
Tamarack	*Larix laricina*	9095	4.8	Spruce	9641	4.8	Black ash	3595	2.6
Spruce	*Picea glauca, mariana*	8863	4.7	Yellow birch	8243	4.1	Paper birch	3499	2.5
Yellow birch	*Betula alleghaniensis*	8176	4.3	Balsam fir	7996	4.0	Northern red oak	3190	2.3
Paper birch	*Betula papyrifera*	5647	3.0	Paper birch	7126	3.6	Eastern hemlock	3148	2.3
Maple (with sugar maple)	*Acer saccharum, rubrum, saccharinum*	5335	2.8	Maple	6325	3.2	White spruce	2819	2.0
							American basswood	2627	1.9
Aspen	*Populus tremuloides, grandidentata*	3473	1.8	Aspen	3689	1.8	Tamarack	2401	1.7
							Yellow birch	2352	1.7
American basswood	*Tilia americana*	2607	1.4	Black ash	3068	1.5	Black cherry	1928	1.4
American elm	*Ulmus americana*	2450	1.3	American elm	2214	1.1	White oak	1645	1.2
Black ash	*Fraxinus nigra*	2220	1.2	American basswood	2058	1.0	Green ash	1361	1.0
White oak	*Quercus alba*	1215	0.6	White oak	1978	1.0	Northern pin oak	1330	1.0
Red oak	*Quercus rubra, ellipsoidalis, velutina*	1070	0.6	Red oak	1384	0.7	American beech	1178	0.8

density estimates for each plot. I then determined mean density by ecological subsection. For basal area estimates, I used the quadratic mean diameter (square root of the mean diameter^2) to calculate the mean tree basal area.

Although historical surveys for southern Michigan are not available as a database, I pieced together the area using the Michigan Presettlement Vegetation Cover (gis-michigan.opendata.arcgis.com/datasets, Comer et al. 1995 although not attributed in the metadata) modified in Hanberry and Abrams (2018) to a larger resolution of ecological subsections. I used seven publications at small scales (one to five US counties) to determine historical forest types (Kenoyer 1930, 1934, 1939, 1942; Dick 1937; Hartesveldt 1951; Jones and Kapp 1972; Dodge 1987) in counties of the southern Lower Peninsula.

Results

Eastern hemlock (15% of all trees) and American beech (8% of all trees) decreased from among the most abundant species to uncommon species (2.3% and 0.8% of all trees, respectively; Table 1). Aspen and red maple increased from uncommon (2% of all trees) to among most abundant (11% and 13%, respectively). Pines decreased from 19% to 14% of all trees and tamarack decreased from 5% to 2% of all trees. Northern white-cedar increased from 10% to 13% of all trees.

Beech, sugar maple, and hemlock forest types were the most abundant historically (41% of all trees; Table 2). Currently, forests composed of early-mid eastern broadleaf species, primarily red maple, are the most common type (29% of all trees), increasing from 10% of all trees. The tamarack-birch-aspen group increased as well due to aspen increases (from 10% to 16% of all trees). Pines decreased (−5 percentage points) and cedar-spruce-fir increased (+5 percentage points). For distances between historical and current surveys, with grouped genera, the squared chord distance was 0.19, the Jaccard distance was 0.29, and the Sørenson distance was 0.31.

Table 2. Percent composition by forest type (BSH = beech, sugar maple, hemlock; CSF = cedar, fir, spruce; TBA = tamarack, birch, aspen; other = early- to mid-successional eastern broadleaf species) for historical and current surveys, Upper Peninsula and Northern Lower Peninsula of Michigan.

Historical	Count	%	Current	Count	%
BSH	77,448	41.1	Other	40,732	29.2
CSF	37,658	20.0	CSF	34,096	24.5
Pine	36,101	19.1	BSH	23,250	16.7
Other	19,152	10.2	TBA	21,798	15.6
TBA	18,275	9.7	Pine	19,439	14.0

Table 3. Percent composition by forest type (BSH = beech, sugar maple, hemlock; CSF = cedar, fir, spruce; TBA = tamarack, birch, aspen; other = early- to mid-successional eastern broadleaf species) and most abundant species by ecological subsection for historical and current surveys, Upper Peninsula and Northern Lower Peninsula of Michigan. Unidentified pine species and combined spruce genus in the historical line surveys are not equivalent to species.

	Historical							Current						
Subsection	BSH	CSF	TBA	Pine	Other	Species	%	BSH	CSF	TBA	Pine	Other	Species	%
212 Ha	63	4	3	15	15	American beech	24	12	2	11	30	45	Red pine	19
212Hb	27	5	3	53	12	Pine	34	3	3	8	39	48	Red pine	26
212Hc	59	3	3	25	9	Eastern hemlock	22	18	7	16	29	30	Red pine	22
212Hd	74	8	4	7	8	Sugar maple	31	19	12	7	27	34	Red pine	23
212He	68	5	3	17	8	Sugar maple	28	18	12	17	24	29	Sugar maple	16
212Hf	78	8	4	2	9	Sugar maple	33	37	20	15	8	20	Sugar maple	33
212Hg	14	9	11	62	4	Jack pine	26	1	14	16	42	26	Red pine	20
212Hh	35	10	7	41	6	Eastern white pine	27	0	6	25	17	52	Red maple	25
212Hi	72	9	4	7	8	Sugar maple	34	36	16	13	9	26	Sugar maple	32
212Hj	36	20	14	25	6	Northern white-cedar	15	6	35	22	15	22	Northern white-cedar	25
212Hk	25	6	10	55	4	Red pine	30	1	19	27	18	34	Red maple	15
212Hl	24	32	23	16	5	Northern white-cedar	25	2	47	17	9	25	Northern white-cedar	31
212Hm	57	7	8	19	8	Eastern hemlock	31	8	9	21	28	34	Red pine	25
212Jb	49	25	5	1	20	Sugar maple	28	36	19	9	1	35	Sugar maple	32
212Jc	42	27	8	5	17	Eastern hemlock	22	31	21	13	5	31	Sugar maple	26
212Jo	27	36	13	13	11	Northern white-cedar	15	16	27	22	7	28	Quaking aspen	18
212Ra	41	22	8	21	7	Sugar maple	15	24	21	7	21	27	Red maple	20
212Rb	16	36	27	18	3	Tamarack	20	7	47	12	19	16	Northern white-cedar	26
212Rc	27	31	24	15	4	Northern white-cedar	20	6	55	12	13	14	Northern white-cedar	38
212Rd	21	41	23	8	7	Spruce	19	3	48	23	2	25	Northern white-cedar	19
212Re	33	33	23	7	4	Northern white-cedar	18	11	55	16	5	12	Northern white-cedar	37
212Sb	62	18	4	2	14	Sugar maple	46	33	23	7	3	34	Sugar maple	29
212Sc	29	35	10	14	13	Sugar maple	16	30	29	11	5	24	Sugar maple	24
212Sn	48	23	6	7	15	Sugar maple	23	32	14	8	10	36	Sugar maple	25
212Sq	39	31	6	9	15	Sugar maple	22	29	24	7	5	36	Red maple	25
212Tb	31	38	13	5	13	Northern white-cedar	25	13	43	16	4	24	Northern white-cedar	30
212Te	19	42	23	12	5	Northern white-cedar	33	7	39	10	8	36	Northern white-cedar	25
212Xc	35	32	6	7	19	Sugar maple	25	30	24	18	5	23	Sugar maple	28
212Xq	29	26	7	23	15	Sugar maple	16	20	23	30	8	19	Sugar maple	20
212Ya	64	12	4	1	20	Eastern hemlock	35	16	15	30	3	36	Quaking aspen	21

At the smaller scale of ecological subsections, sugar maple and northern white-cedar were the most common species both historically and currently (>7 subsections each species; Table 3; Figures 2 and 3). Eastern hemlock was the most common species in four subsections historically but none currently, while aspen and red maple have become new most abundant species in two and four subsections, respectively. Red pine also appeared to increase from being the most common in one or perhaps two subsections to six subsections, although unidentified pine species adds uncertainty to pine trends. Two subsections had squared chord values <0.12, three subsections had squared chord values ranging from 0.12 to 0.15, and 24 subsections had values >0.15, up to 0.51 (Figure 4).

Density remained similar between surveys (Table 4). The historical mean density estimate, adjusted for surveyor bias, was 441 trees/ha (area-weighted) and the current mean density was 423 trees/ha. Current density ranged from 72% to 158% of historical density by subsection (Figure 5). Adjustments for surveyor bias are liberal, but a range between unadjusted and mean values conveys a measure of variability. Nevertheless, current mean diameter (for trees ≥12.7 cm in diameter) was 21.6 cm compared to 38.7 cm historically, and 63% to 81% of historical diameter by subsection. Thus, basal area decreased from 39 m^2/ha to 17.9 m^2/ha.

Southern Michigan consisted of oak and beech in various combinations, based on a modification of a historical map overlaid with counties that had historical tree composition (Figure 2). There was good agreement between the map and surveys for three counties that were beech-sugar maple-hemlock within the closed forests classification and one county was oak within the open oak forest classification. Hemlock became rare to the south. Seven counties were oak-beech and three counties were oak-beech-sugar maple forests with the closed forests classification, due to fine-scale intermixing of forest types (see map in Dick 1937). Four counties were primarily oak forests within closed forests. Currently, southern Michigan has become an assembly of early-mid successional species from the central-eastern US ('other species'; Figure 3).

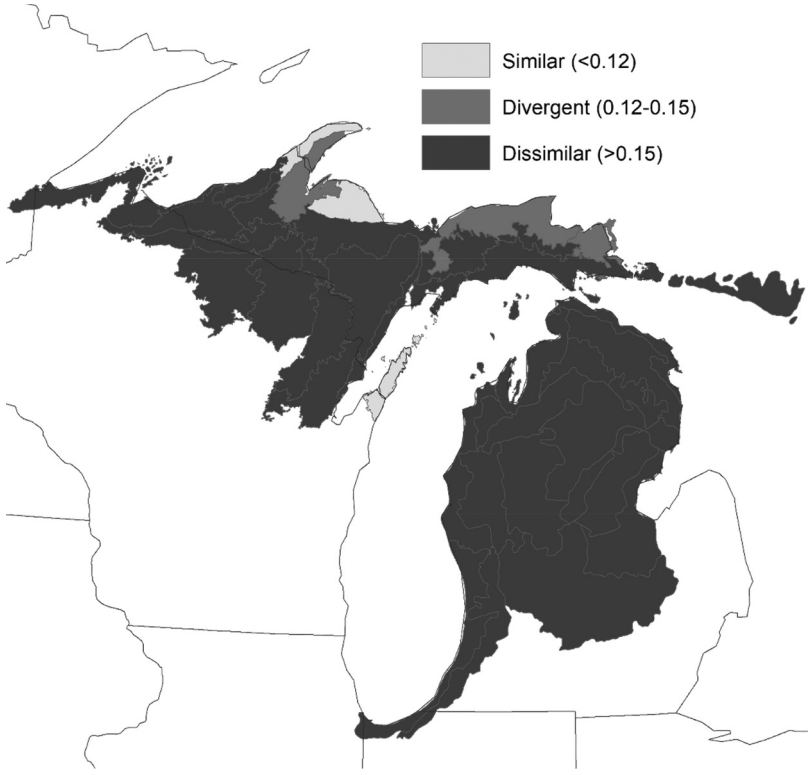

Figure 4. Squared chord distance by ecological subsection (light outline) in the Upper and northern Lower Peninsulas, Michigan.

Table 4. Structure (TPH = tree density in trees/ha, DBH = diameter in cm, BA = basal area in m2/ha) for historical and current surveys, Upper Peninsula and Northern Lower Peninsula of Michigan.

				Historical						Current	
Subsection	TPH (unadj)	TPH	Low	High	DBH	BA	Low	High	TPH	DBH	BA
212 Ha	201	342	176	452	31	32	16	42	418	23	21
212Hb	214	373	187	503	30	32	16	43	476	23	23
212Hc	237	403	207	534	31	37	19	49	441	23	21
212Hd	223	367	196	475	31	34	18	43	572	22	24
212He	212	346	186	445	31	32	17	42	393	23	18
212Hf	259	406	226	508	30	36	20	46	380	23	19
212Hg	237	358	208	435	29	30	17	36	416	21	17
212Hh	273	432	240	542	30	37	21	47	332	22	14
212Hi	261	429	229	554	32	42	22	54	506	23	23
212Hj	268	436	235	559	30	38	21	49	466	21	18
212Hk	188	362	164	518	36	49	22	69	515	22	23
212Hl	319	478	279	575	27	34	20	41	480	21	19
212Hm	241	423	207	576	32	40	20	55	450	22	19
212Jb	257	424	224	549	32	41	22	53	503	23	24
212Jc	256	458	224	625	33	47	23	65	453	23	22
212Jo	279	500	244	687	31	47	23	64	395	23	19
212Ra	197	326	172	424	30	28	15	37	452	23	21
212Rb	287	425	252	507	26	28	17	34	491	21	19
212Rc	380	583	332	716	27	43	24	53	581	20	21
212Rd	279	445	245	561	28	46	25	58	402	20	15
212Re	314	496	275	625	26	32	18	40	597	21	23
212Sb	249	470	218	664	29	37	17	52	387	24	20
212Sc	233	390	204	511	31	41	21	54	423	22	19
212Sn	252	429	220	569	30	37	19	50	434	24	24
212Sq	200	313	174	390	30	28	15	35	494	23	24
212Tb	262	494	230	697	32	47	22	66	474	21	18
212Te	357	618	313	822	29	47	24	63	445	21	18
212Xc	192	359	167	507	33	38	18	53	428	22	19
212Xq	183	366	157	536	32	34	15	50	364	22	15
212Ya	243	399	211	518	34	42	22	55	387	21	16

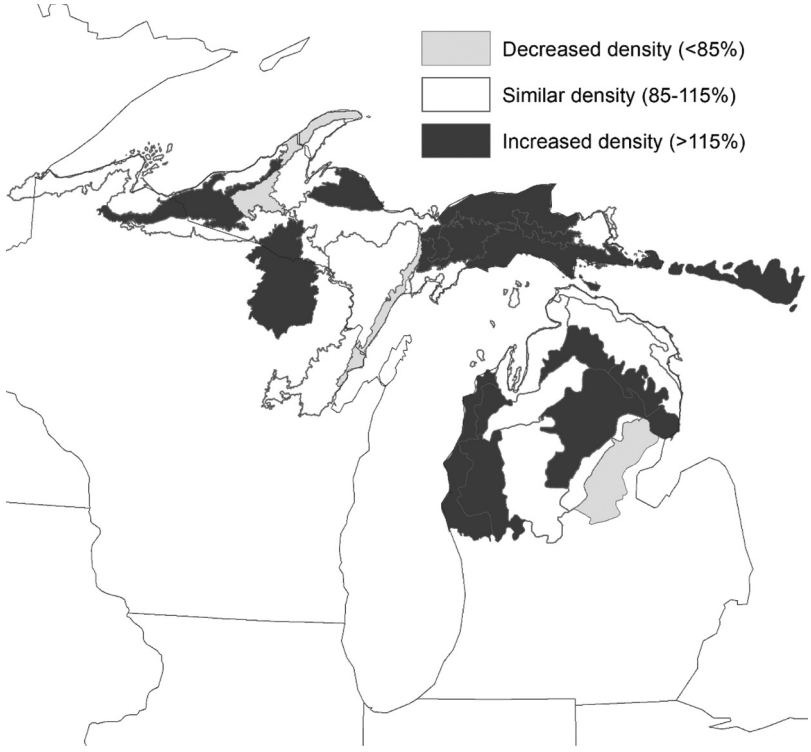

Figure 5. Change in density (current density/historical density) by ecological subsection (light outline) in the Upper and northern Lower Peninsulas, Michigan.

Discussion

In this study, I quantified composition and structure of Michigan's Upper and northern Lower Peninsula during the 1800s, for the whole extent and at the ecological subsection scale, to provide baseline conditions and determine the magnitude and trajectory of departure in current conditions for restoration and management (see Tables and Figures). Current forests with an abundance of aspen and maple are outside the range of forest types during this historical interval, using the squared chord distance metric. Nonetheless, some aspects of historical composition and structure remain. For example, the fine-scaled intermixing of forest ecosystem types within landscapes (i.e., subsections; Figure 2) and tree densities of around 430 trees/ha. The low to mean density values impart a range of target values that may vary depending on the ecological context. The three subsections dominated by pine had lower density values that were within the open forest range if not adjusted for surveyor bias, but due to presence of other species at greater densities, occurrence of high severity fire regimes, and dense establishment by pines ('dog-hair', jack pines, in particular, can produce 4 million seeds per ha; Thomas and McAlpine 2010), it seems likely that the subsections overall contained dense, closed forests, with some local areas of open pine forests with mixed fire severities.

Shade-tolerant boreal species also remained relatively stable. Despite concern for northern white-cedar due to deer herbivory, northern white-cedar increased in Michigan, similarly to increases in the other two Great Lakes states (Hanberry et al. 2013; Hanberry and Dey 2019). Although some areas of eastern Canada decreased in northern white-cedar, increases occurred perhaps due to incomplete disturbance, such as partial cutting, where advance regeneration was present (Danneyrolles et al. 2017). Balsam fir and spruce (*Picea glauca, mariana*) also increased slightly. These species increased or were stable in Wisconsin and Minnesota (Hanberry et al. 2013; Hanberry and Dey 2019). Fir increased and spruce declined in the northern parts of the Northeast (i.e., the northeastern US states of Maine, New Hampshire, Vermont, New York, and Pennsylvania; Thompson et al. 2013). In eastern Canada, balsam fir displayed all possible responses and spruce was stable or declined (Jackson et al. 2000; Leadbitter et al. 2002; Dupuis et al. 2011; Danneyrolles et al. 2016; Terrail et al. 2019). The current disturbance regime of overstory tree removal by logging at <100 years (Pan et al. 2011) is relatively comparable to the historical disturbance regime experienced by northern white-cedar, balsam fir, and spruce of severe overstory disturbance (i.e.,

crown fires, all fires are now suppressed; Cleland et al. 2004) at return intervals less than the lifetime of dominant tree species. Northern white-cedar, balsam fir, and spruce were able to escape or reduce fire exposure in locations near firebreaks caused by water or topography, extending fire rotations, but for example, northern white-cedar may live 400–600 years, allowing exposure to long fire intervals (Heinselman 1973; Cleland et al. 2004). Termination of the overstory trees at regular intervals (i.e., 100 years, but with great variability; Cleland et al. 2004) resulted in origination of similar forests cycling through structural, rather than compositional, succession (Heinselman 1973). Likewise in boreal forests of Alaska, Johnstone and Chapin (2006) and Johnstone et al. (2010) found that if fire intervals were >75 years, stands auto-replaced by seedlings that recruited immediately after fire, with postfire tree seedling composition reflecting the overstory prefire forest stands. If fires burn more severely or frequently, then tree composition after fire may change. The type of tolerance by these shade-tolerant boreal species to overstory disturbance, both stand-replacing historical fire and current land use, suggests a life history strategy and associated traits that combine post-disturbance establishment with competition for growing space and shading.

Current forests have changed from 23% beech-hemlock in the past to about 3% beech-hemlock. Both a shade-tolerant deciduous and coniferous species declined. Likewise, beech decreased by about 20% and hemlock by about 5% to 6% in the northern forests of the Northeast (i.e., the northeastern US states of Maine, New Hampshire, Vermont, New York, and Pennsylvania; Thompson et al. 2013). Hemlock and beech become more competitive as time from stand origination extends to more than a generation of trees, which currently is a rare disturbance regime (Pan et al. 2011). In southern Michigan, open ecosystems of grasslands, oak savannas, and wetlands, now are remnants (Comer et al. 1995; Chapman and Brewer 2008). In conjunction with loss of historical forests, understory plants often decline (Rooney et al. 2004; Wiegmann and Waller 2006; Chapman and Brewer 2008). Declining plants particularly are forbs pollinated by animals, while sedges, grasses, and non-native plants have increased (Wiegmann and Waller 2006).

Most of the Lower Peninsula and some of the Upper Peninsula of Michigan have become a mix of early-mid successional species, particularly red maple, generally expanding from eastern broadleaf forests of the central-eastern US ('other species'; Figure 3). Red maple and quaking aspen have increased to about 20% of all species compared to <2% of each red maple and aspen in the past. Aspen has been a new dominant species in these forests since the turn to the twentieth century, gradually declining over the years (Cleland et al. 2004). Conversely, increased distribution and abundance of red maple appear to be an emerging, consistent development throughout eastern North America (Abrams 1998; Leadbitter et al. 2002; Dupuis et al. 2011; Thompson et al. 2013; Hanberry et al. 2014, 2019; Hanberry 2019). Current overstory removal is frequent enough to prevent progression over time from colonizers to shade-tolerant competitors of beech and hemlock (e.g., Pan et al. 2011). Red maple is extremely successful within current disturbance regimes arising from forestry and land use as opposed to historically when red maple was a rare species (Abrams 1998). Although expansion of southern species northward may appear to be a signal of climate change, a variety of eastern broadleaf forest species are moving south as well while also replacing oaks in the central-eastern US, as happened in the southern Lower Peninsula (e.g., Hanberry et al. 2014; Hanberry and Hansen 2015; Hanberry 2019). Additionally, some boreal species increased in this landscape.

Qualitative assessment of novel ecosystems in Michigan and the eastern US

In addition to exceeding the squared chord metric (0.19, which is > the 0.15 threshold), ecosystems in Michigan meet qualitative measures. Murcia et al. (2014) defined novel ecosystems as 'a new species combination that arises spontaneously and irreversibly in response to anthropogenic land-use changes, species introductions, and climate change, without correspondence to any historic ecosystem'. They also listed characteristics of novel ecosystems, albeit while critiquing the concept because of concern that novel ecosystems provided justification for lack of restoration efforts. Nonetheless, the qualifiers of novel ecosystems apply to both Michigan and the eastern US.

1. Novel ecosystems are ubiquitous and constitute a new normal (Murcia et al. 2014). Eastern broadleaf forests, or comparably the southern and northern mixed forests with conifer constituents, are comprised of diverse species with typically an abundance of red maple and may present a classic example of acceptance of novel ecosystems as baseline shift. Excluding pine plantations, the eastern US and Canada commonly are composed of forests with new species combinations, particularly of red maple and diverse early- and mid-successional tree species (e.g., Leadbitter et al. 2002; Dupuis et al. 2011; Thompson et al. 2013; Hanberry et al. 2014, 2019; Danneyrolles et al. 2019; Hanberry 2019). The invading species are native species that formerly were constricted to firebreaks of wetlands and

rocky outcrops generally in the central-eastern US. In contrast to current diverse forests, historical forests were dominated by pines in the southern US, oaks in the central US, and a mix of either (1) sugar maple, American beech, and eastern hemlock, (2) tamarack, birch, and aspen, or (3) northern white-cedar, spruce, and fir in the northern US and southern Canada (e.g., this study, Hanberry and Nowacki 2016).

2. Novel ecosystems result from predictable and unavoidable responses in species distributions (Murcia et al. 2014) caused by disturbance or land-use change. The overall current disturbance regime is frequent overstory removal at <100 years (e.g., Pan et al. 2011), indicated by the reduced mean diameter of trees (Table 4), which may be within the historical range of severe overstory disturbance in boreal forests (e.g., Heinselman 1973). However, overstory disturbance historically occurred in cycles of hundreds to thousands of years in beech-sugar maple-hemlock forests and open oak forests (e.g., Lorimer and White 2003). Both of these forest types decreased in Michigan and have decreased throughout the eastern United States (e.g., Thompson et al. 2013; Hanberry and Abrams 2018; Hanberry 2019). While frequent overstory removal may be similar to the high severity fire regimes of both cedar-spruce-fir and tamarack-birch-aspen, early- and mid-successional eastern broadleaf species also are extremely competitive under current disturbance. Forests of early- and mid-successional eastern broadleaf species have increased both in Michigan and throughout the eastern United States (see references above).

3. Novel ecosystems tend to self-organize and retain their novelty because they have crossed thresholds (Murcia et al. 2014) that are challenging to correct. Once early- to mid-successional eastern broadleaf species reach a certain threshold of abundance in the overall tree matrix, similar to other invasive species, they become increasingly difficult to remove because there is limited control on tree growth, without the historical disturbances of fire and/or competitive top-down control by continuous overstory tree presence that capture growing space (Nowacki and Abrams 2008; Hanberry et al. 2017). In general, novel forests do not depend on continued human intervention for their maintenance (Hobbs et al. 2006; Nowacki and Abrams 2008). However, if frequent overstory tree removal hypothetically was to stop and beech and hemlock were not facing diseases, progression from current forests to late-successional beech-sugar maple-hemlock forests would be expected to occur without human intervention after centuries, based on slow compositional succession. In addition, given great enough human intervention through restoration, most current ecosystems could be restored.

Murcia et al. (2014) also expressed that 'there is no clear message as to what practitioners should do with a "novel ecosystem"'. Restoring novel ecosystems is not a futile endeavor simply because restoration requires resources (Murcia et al. 2014). Current forests require substantial effort to restore without the controlling effects of fire and overstory trees and some forests are changed enough that they are not cost-effective targets to prioritize for restoration. Restoration and management of historical ecosystems is an adaptive, and not always successful, process that supports declining species and yields a variety of social and economic benefits (Thompson et al. 2018). The greater the financial effort in restoration, the greater the reward in terms of conserving biodiversity. Critically, restoration will help support forbs, insects, and birds associated with historical forest conditions, particularly with additional stressors of warming temperatures and precipitation variability. The implications of climate change make restoration of historical ecosystems more crucial, rather than less so, and strategies exist to support adaptation to climate (e.g., Falk 2017). Restoration and management of historical ecosystems may make ecosystems more resilient to climate change because historical ecosystems withstood the test of climate over a wide range of time, considering that historical forests typically were stable in composition, whereas novel ecosystems are products of the past century. Additionally, historical forest structure may have been more resistant to a variety of disturbances (Mitchell and Duncan 2009). Future climate in Michigan may not support northern species, but American beech (although prone to beech bark disease) extends to Texas, which is within the range of future climate.

Conclusions

Historical baselines allow identification of the nature of change to new baselines. Most of Michigan, corresponding with the eastern US and Canada, has transitioned to diverse early- to mid-successional forests of eastern broadleaf species, with red maple as the most abundant species. This is likely due to a change of disturbance regime, given that frequent overstory tree removal has become widespread for longer than a century. Additionally, historical baselines provide better guidance for at least small-scale restoration and management opportunities; at minimum, red maple need not be planted deliberately for landscaping purposes (Michigan Department of Natural Resources 2020) or protected from deer through the use of metal cages. Some amount of restoration is essential to support declining plants and animals associated with historical ecosystems, particularly under increasing pressures. The task is difficult and

conditions have changed and will continue to change under climate change, but economic and social thresholds and not ecologic thresholds should define the restoration limitations (Murcia et al. 2014).

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ORCID

Brice B. Hanberry http://orcid.org/0000-0001-8657-9540

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