

Forest Disturbance Types and Current Analogs for Historical Disturbance-Independent Forests

Brice B. Hanberry

USDA Forest Service, Rocky Mountain Research Station, Rapid City, SD 57702, USA; brice.hanberry@fs.fed.us

Abstract: Forest classifications by disturbance permit designation of multiple types of both old growth forests and shorter-lived forests, which auto-replace under severe disturbance, and also identification of loss of the disturbance type and associated forest. Historically, fire and flooding disturbance regimes, or conversely, infrequent disturbance, produced unique forests such as disturbance-independent forests of American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), and sugar maple (*Acer saccharum*) in the Eastern United States. However, disturbance has changed to primarily frequent mechanical overstory disturbance, resulting in novel forests. To demonstrate the transition to no-analog forests after disturbance change, I compared historical tree surveys (ca. 1837 to 1857) to current surveys in the Northern Lower Peninsula of Michigan. To establish widespread disturbance change effects, I also located where beech and hemlock are currently most abundant throughout the Eastern US compared to historical distribution of beech–hemlock forests. In the Northern Lower Peninsula of Michigan, beech and hemlock historically were about 30% of all trees, but currently, beech and hemlock are 2% of all trees. Red maple (*Acer rubrum*) increased from 1% to 11% of all trees and aspen (*Populus*) increased from 2% to 13% of all trees. The squared-chord difference between historical and current surveys was 0.40, or dissimilar forests. Areas with $\geq 20\%$ beech and hemlock or $\geq 15\%$ of either species decreased from about 52 million to 6 million hectares, with current distribution restricted to the Northeastern US. Current forests are dissimilar to historical forests, and this transition appears to be driven by disturbance regimes without historical analogs. Disturbance change may provide perspective in forest management for climate change.

Keywords: analogue; climate; climate change; disturbance; maple; no-analog; novel; old growth



Citation: Hanberry, B.B. Forest Disturbance Types and Current Analogs for Historical Disturbance-Independent Forests. *Land* **2021**, *10*, 136. <https://doi.org/10.3390/land10020136>

Academic Editor: Eusebio Cano Carmona

Received: 18 December 2020

Accepted: 24 January 2021

Published: 1 February 2021

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1. Introduction

Disturbance generates a system to differentiate types of old growth forest that persist under minimal or low severity disturbance and shorter-lived forests that auto-replace under severe disturbance (Figure 1). Archetypical closed old growth forests are relatively unaffected both by understory and overstory disturbance and instead, dominant tree species are long-lived and shade-tolerant, while their structure is complex due to the extended time since the last disturbance. Stand-scale replacement occurs after centuries to millennia and is likely to be patchy even then. For example, in the Eastern United States, American beech (*Fagus grandifolia*), eastern hemlock (*Tsuga canadensis*), and sugar maple (*Acer saccharum*) represent disturbance-independent upland and even wetland forests, according to limited disturbance, shade tolerance, longevity, and complex internal structure [1]. Stand-replacing disturbance, primarily by wind, may have returned approximately every 1400 years [2–4]. Surface fires did not occur to remove small diameter trees, but larger diameter trees controlled the growing space for long intervals, which overall caused either mortality or suspension of growth in tree regeneration. Small-scale disturbance of individual larger trees (“gap dynamics”) allowed recruitment of shade-tolerant tree species. Structure consisted of large trees, presence of old trees near maximum longevity, dense multiple canopy layers, canopy gaps and anti-gaps, snags, coarse woody debris with accumulated moisture, mosses, and epiphytes [5,6]. American beech, eastern hemlock,

and sugar maple are long-lived species; in particular, eastern hemlock may live for over 800 years [7]. Each of the three species has a unique distribution, and depending on region, one species may be absent or less dominant relative to the other two. American beech spans the latitudinal gradient of Eastern United States from Eastern Texas to Eastern Wisconsin [8,9]. Eastern hemlock and sugar maple do not extend as far south, but these species currently extend further west than American beech.

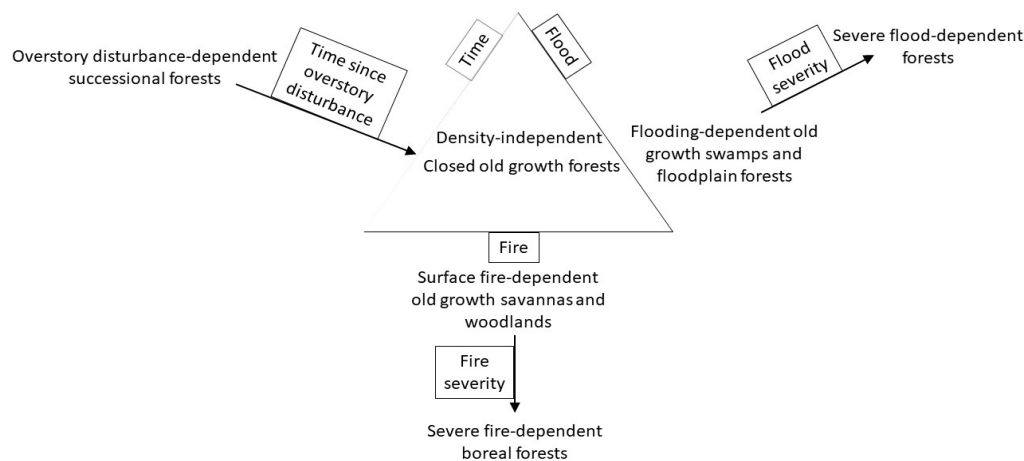


Figure 1. Forest types based on dependence on disturbance type and disturbance severity in the Eastern United States.

Other old growth and naturally less enduring, short-lived forests are filtered by different disturbance types and severity. Frequent surface fire is an understory disturbance that is critical for maintaining a bilayer of fire-tolerant trees and herbaceous vegetation in tropical and temperate savannas and woodlands, but because overstory disturbance is rare, these forests are also old growth with long-lived tree species [10]. In contrast, severe fire removes both understory and overstory trees every 50 to 150 years in boreal forests, favoring auto-replacement by the pre-fire tree species, which have traits for rapid post-fire recovery [11,12]. Disturbance interacts with vegetation dynamics and site conditions to shape the composition and structure of forests. Fire is generally more frequent in conditions that are exposed to wind and sun, with sandy, dry soils, and flat terrain, which contribute to drying vegetation for ignition and spreading fire. For example, in the Eastern United States, grasslands and fire-tolerant pine savannas are typically located where fire is most frequent. Fire becomes less frequent in dry, rocky locations with limited vegetation or as conditions become increasingly protected with soils that have greater water capacity, more rugged terrain, and trees that provide coarse fuel for fire replace abundant herbaceous vegetation that provide fine fuel. As fire-free intervals extend, biomass accumulates and when ignition occurs, fire may be severe enough to spread through tree canopies, killing overstory trees.

Similarly, long-lived trees of swamps and floodplains are flooding-tolerant, but relatively frequent severe flooding favors auto-replacement by short-lived *Salix* and similar species (e.g., *Populus deltoides*; [13]). In the Eastern United States, the lower Mississippi River Alluvial Valley and tributaries such as the Missouri and Wabash Rivers once produced enormous trees, both in height (60 m) and in diameter (4 to 5 m; [14]). However, many of the swamps of the past do not functionally exist anymore, both at small and large scales, such as the Great Black Swamp of Northeast Ohio, due to wetland drainage.

Wind and herbivory are other disturbances that directly contribute to stand-scale replacement or interact with surface and crown fires and flooding to remove trees at different vertical profiles. For example, strong winds spread fires, whereas blown-down trees supply coarse fuels for severe fires. Trees in saturated soils after flooding may be vulnerable to wind. Herbivores that browse and trample small diameter trees maintain open forest densities, similarly to surface fire. Insect herbivores and various pathogens are

well-known for killing large trees. Although wind and herbivory alone do not appear to maintain unique forests at landscape scales in the Eastern United States [15], wind may be the primary disturbance of pine forests of tropical islands [16], and megaherbivores (Elephantidae) may maintain tropical savannas.

The effects of disturbance and disturbance change may receive less consideration than the effects of climate and climate change; nonetheless, disturbance change has already caused widespread declines in historical forests. Currently, widespread overstory disturbance, with minimal understory disturbance, for forest products creates a cycle of short-term closed forests, which tend to be non-analogous in composition and structure compared to historical forests [10]. During Euro-American settlement and particularly between 1850 and 1920, the combination of increased population and improved tools of industrialization led to forest removal for different forest products and land uses, primarily agriculture, throughout the Eastern United States. Other changes include exclusion of surface fire, suppression of flooding processes through river regulation, and wetland drainage for agriculture. Compared to historical disturbances, continued mechanical removal of overstory trees has increased frequency of overstory disturbance, while fire and flooding exclusion have decreased frequency of understory disturbance [17]. Historically, common tree species have been replaced by a variety of early-successional and mid-successional tree species that were formerly rare and, furthermore, changed structure by decreasing tree diameter and increasing tree density [18]. Most notably, red maple (*Acer rubrum*) and eastern redcedar (*Juniperus virginiana*) have increased [18–21].

In disturbance-independent forests, although clearing for agriculture did occur, disturbance change overall occurred by logging. Some disturbance-independent forests were concentrated in rugged or cold locations protected from fire that were less suitable for agriculture. For example, Whitney [22] described that for hemlock forests located in Northern Pennsylvania (Figure 2A; green area in agriculture <15% in Pennsylvania), farming was limited by the short growing season and steep terrain, but lumbering was intensive starting about 1880 due to mechanical innovations of bands saws and railroads. By then, preferred pines had been selectively harvested but hemlock was abundant and bark was valuable for the tanning industry. Between 1880 and 1900, hemlock constituted more than two-thirds of the lumber production in Pennsylvania, whereas Northern Pennsylvania had the greatest tannery concentration in the world. Logging railroads allowed removal of the heavy broadleaf species, and sugar maple and beech specifically were removed for charcoal and organic chemicals. Equally, in the Northern Lower Peninsula of Michigan (Figure 2A), lightweight and valuable pine was selectively harvested, and then during 1890 to 1920, hemlock and the heavier broadleaf species were harvested for a variety of products, including tannins and chemicals, while agricultural cultivation was sparse and unproductive [2]. Extensive cutting allowed fast establishment by light-seeded and sprouting sugar maple and also aspen initially, which started a pulpwood industry. These landscapes have remained forested and relatively unfragmented by other land uses but are perforated by clearings (Figure 2B). Flatter landscapes, such as parts of Indiana, Ohio, Pennsylvania, and New York, have been converted to agriculture (Figure 2).

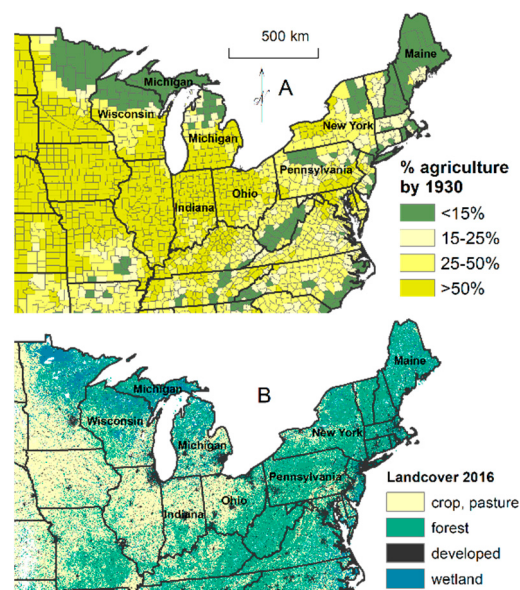


Figure 2. Percentage area in agriculture for 1930 (A; [23]) and 2016 land classes (B; [24]).

To illustrate the effects of disturbance change, I first provided a detailed example of transition after tree harvest from disturbance-independent American beech and eastern hemlock forests to no-analog forests in the Northern Lower Peninsula, a 4.5 million ha ecological section of Michigan (Figure 3; [25]). I evaluated forests surveyed by the General Land Office (GLO; 1837 to 1857) and USDA Forest Service Forest Inventory and Analysis (FIA; 2010 to 2015; [26]). To scale these results of disturbance change to the Eastern United States, I mapped the historical distribution of beech–hemlock forests, as identified by studies to this point, and located where beech–hemlock analogs may exist today at landscape scales, according to all current FIA surveys, by ecological subsections or landscape scales of hundreds of thousands of hectares throughout the Eastern United States (Figure 3). Other spatial maps may be available, and for example, to extend historical coverage, I added sites identified as beech or hemlock from expert-based models (Biophysical Settings, [27,28]), which represent vegetation that may have been dominant historically. Lastly, I addressed how disturbance change from pre-Euro-American settlement forests to current no-analog forests helps to provide a context for climate change.

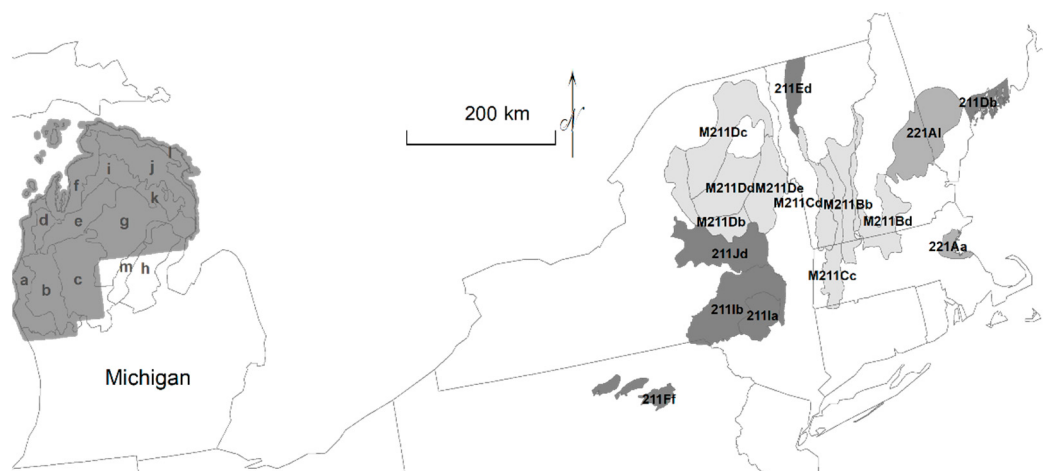


Figure 3. The ecological section (212H) of the Northern Lower Peninsula, Michigan, with ecological subsections (outlined and labeled with subsection suffix letter) and extent with historical tree surveys (shaded). Additionally, subsections (outlined and labeled with complete subsection designation, shaded by ecological provinces of M211, 211, 221) where beech and hemlock are currently $\geq 20\%$ of all trees or either species are $\geq 15\%$ of all trees.

2. Materials and Methods

2.1. Transition to No-Analog Communities in the Northern Lower Peninsula

For historical surveys, the General Land Office was established in 1812 to direct the surveying, platting, and selling of public lands 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, improving on surveys based on the Land Ordinance of 1785 [29]. Surveyors recorded tree species, diameter, distance, and bearing for two to four trees selected at survey points in the corners and middle of each section line (i.e., every 0.8 km) and also recorded the species and diameter of line trees, or trees encountered along section lines. When selecting trees at survey points, surveyors may have had preferences for tree species that were easier to access (i.e., no low branches) and blaze (i.e., smoother bark) and were also following survey instructions, such as to record trees of moderate diameter, whereas trees intercepted along the survey lines were recorded without selection. The difference between these two survey methods can help to detect bias in trees at survey points and provide a general indication of the differences that can occur between two sampling methods. In the Northern Lower Peninsula of Michigan, surveys from 1837 to 1857 contained about 100,000 of both line and survey point trees, after exclusion of trees that were <12.7 cm in diameter because smaller trees were rarely recorded by surveyors in GLO surveys. Not all of the Northern Lower Peninsula was recorded in the dataset, and therefore, the southern four of the thirteen ecological subsections were partially incomplete (Figure 3). I determined tree composition for both survey types in the Northern Lower Peninsula of Michigan and for line trees by ecological subsection. I proportionately distributed the tree number for unidentified species within each genus to compare to current composition.

For current surveys, the USDA Forest Service Forest Inventory and Analysis was established to monitor long-term plots, which occur about every 2500 ha [30]. Personnel visit each plot on a five-year cycle. I used available plots from the complete cycle of 2010 to 2015 (~36,000 trees ≥ 12.7 cm) to determine tree composition in the Northern Lower Peninsula of Michigan and by ecological subsection.

In addition to comparing changes in composition of historical and current surveys, I demonstrated the novel status of current forests using the squared-chord distance metric ([31]; R Core Team package *analog*, [32]) Historical and modern forests that differ in composition tend to have squared-chord distance ≥ 0.15 , and given that thresholds divide continuous data, values between 0.12 and 0.15 indicate divergence ([31]). I also compared the squared-chord distance metric between historical line and survey point tree surveys to display the similarity arising from two different survey methods, one of which may be more biased, of the same forests.

2.2. Current Analogs for Beech–Hemlock Forests in the Eastern United States

I then searched USDA Forest Inventory and Analysis surveys for ecological subsections that currently contain both beech and hemlock as $\geq 20\%$ of all trees or either species as $\geq 15\%$ of all trees. This threshold is a low standard, but necessary to find any current American beech–eastern hemlock forests. I summed the subsection areas to calculate the distribution extent. To map the historical distribution of beech–hemlock, following the rule of at least 20% beech and hemlock or $\geq 15\%$ of each species, I used databases of published historical tree survey research [33–36] and then summed areas to calculate the extent. Although the distribution may increase as more historical tree surveys become available, I also added sites identified as beech or hemlock from expert-based Biophysical Settings [27,28] that extended beyond the survey bounds. Most of the map was based on survey point surveys because line surveys are often not available or limited in sample.

3. Results

3.1. Transition to No-Analog Communities in the Northern Lower Peninsula

Eastern hemlock, sugar maple, and American beech were the three most abundant species historically, comprising about 45% of all trees in the Northern Lower Peninsula

of Michigan (Table 1). Surveyors had a marked bias for marking smooth-barked beech trees, based on the difference between beech composition in the line and survey point surveys, which were encountered or selected by surveyors, respectively. Beech percentage in line surveys was only 60% of beech in survey point surveys. When beech and hemlock are combined, their combined percentage in line surveys was 84% of that found in point surveys. The three pine species and northern white-cedar (*Thuja occidentalis*) comprised another 37% of all trees, such that seven species were 80% of all trees. The squared-chord distance was 0.029 between line and survey point surveys, which indicated that forests were the same, or analogs, despite known biases.

Table 1. Most abundant tree species (≥ 12.7 cm in diameter) of historical trees from 1837 to 1857 encountered by surveyors along survey lines (line), historical trees selected by surveyors (points), and the ratio of line to point trees in the Northern Lower Peninsula of Michigan.

Species	Scientific Name	Historical Line		Historical Point		Ratio
		Count	%	Count	%	
eastern hemlock	<i>Tsuga canadensis</i>	14,481	16.06	12,029	12.35	1.30
sugar maple	<i>Acer saccharum</i>	12,467	13.83	9587	9.84	1.40
American beech	<i>Fagus grandifolia</i>	12,408	13.76	22,698	23.30	0.59
pine		26,950	29.89	24,090	24.73	1.21
pine—unidentified		7741	8.58	4784	4.91	N/A
eastern white pine	<i>Pinus strobus</i>	7105	7.88	5978	6.14	1.28
red pine	<i>Pinus resinosa</i>	6301	6.99	6752	6.93	1.01
jack pine	<i>Pinus banksiana</i>	5803	6.44	6576	6.75	0.95
northern white-cedar	<i>Thuja occidentalis</i>	6349	7.04	7595	7.80	0.90

In contrast, current forests contained about 9% eastern hemlock, sugar maple, and American beech, primarily due to declines in hemlock and beech (Table 2). Only 2% of all trees were eastern hemlock and American beech compared to 30% of historical composition (Figure 4). A major increase occurred in the aspen group of quaking aspen and bigtooth aspen (+11 percentage points from 2% of all trees to 13%), red maple (+10 percentage points), and the red oak group (+4 percentage points). If the unidentified pine species group contains representative proportions of eastern white (*Pinus strobus*), red (*P. resinosa*), and jack pine (*P. banksiana*), then red pine has increased (+7 percentage points), while the other two pine species have declined. The squared-chord distance between historical line tree surveys and current tree surveys was 0.40, which demonstrated different, no-analog forests.

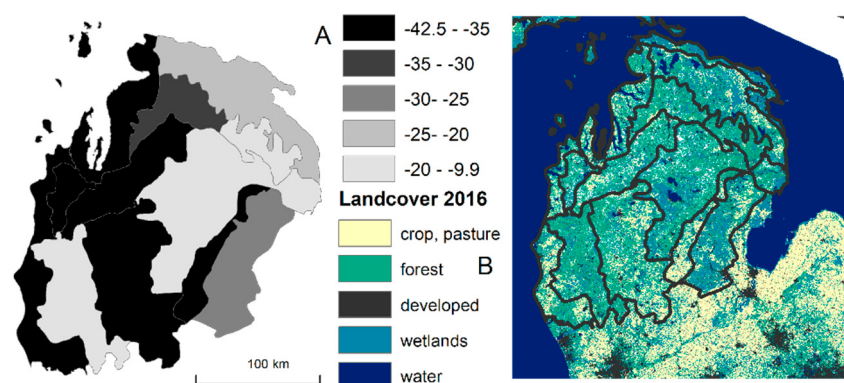


Figure 4. Decrease in percentage points of American beech and eastern hemlock between historical and current surveys (A) and 2016 land classes (B; [24]).

Table 2. Percent composition ($\geq 1\%$ of total stems in one survey; trees ≥ 12.7 cm in diameter) of historical trees encountered by surveyors along survey lines (after allocation to unidentified species) from 1837 to 1857 and current trees from 2010 to 2015, and ratio of current to line trees in the Northern Lower Peninsula of Michigan.

Species	Scientific Name	Historical %	Current %	Ratio
red pine	<i>Pinus resinosa</i>	9.85	16.90	1.72
red maple	<i>Acer rubrum</i>	0.85	11.24	13.22
northern white-cedar	<i>Thuja occidentalis</i>	7.04	9.80	1.39
bigtooth aspen	<i>Populus grandidentata</i>	1.04	7.24	6.96
sugar maple	<i>Acer saccharum</i>	14.66	7.13	0.49
quaking aspen	<i>Populus tremuloides</i>	1.04	6.07	5.83
jack pine	<i>Pinus banksiana</i>	9.30	5.61	0.60
eastern white pine	<i>Pinus strobus</i>	10.74	4.84	0.45
northern red oak	<i>Quercus rubra</i>	0.36	4.22	11.72
white oak	<i>Quercus alba</i>	1.39	3.92	2.82
balsam fir	<i>Abies balsamea</i>	0.93	2.41	2.59
black oak	<i>Quercus velutina</i>	0.36	2.25	6.24
northern pin oak	<i>Quercus ellipsoidalis</i>	0.36	2.15	5.96
black cherry	<i>Prunus serotina</i>	0.09	1.54	17.56
American basswood	<i>Tilia americana</i>	1.21	1.46	1.20
green ash	<i>Fraxinus pennsylvanica</i>	0.12	1.35	10.88
American beech	<i>Fagus grandifolia</i>	13.76	1.20	0.09
paper birch	<i>Betula papyrifera</i>	1.99	1.17	0.59
black ash	<i>Fraxinus nigra</i>	1.44	1.12	0.78
white ash	<i>Fraxinus americana</i>	0.12	0.92	7.42
white spruce	<i>Picea glauca</i>	0.57	0.88	1.55
silver maple	<i>Acer saccharinum</i>	0.85	0.83	0.98
eastern hemlock	<i>Tsuga canadensis</i>	16.06	0.79	0.05
black spruce	<i>Picea mariana</i>	0.57	0.79	1.38
tamarack	<i>Larix laricina</i>	3.36	0.64	0.19
American elm	<i>Ulmus americana</i>	1.88	0.38	0.20

3.2. Current Analogs for Beech–Hemlock Forests in the Eastern United States

Currently, a total of 16 ecological subsections contain $\geq 20\%$ both beech and hemlock or $\geq 15\%$ of either species, which are all located in the Northeastern United States (Table 3, Figure 5). No subsections in the Northern Lower Peninsula contain $>6.5\%$ of both species. Beech and hemlock forests cover an area of 6.1 million hectares.

Table 3. Historical (1837 to 1857) and current percent composition of American beech, eastern hemlock, and sugar maple (trees ≥ 12.7 cm in diameter) by subsection in the Northern Lower Peninsula of Michigan (section 212H) and analogous subsections in the Eastern US that contain $\geq 20\%$ beech and hemlock or $\geq 15\%$ of either species.

Historical Line Surveys				Current FIA Surveys			Current Analogs from FIA Surveys in the Eastern US				
Sub	% Beech	% Hem-lock	% s. Maple	% Beech	% Hem-lock	% s. Maple	Province	Sub	% Beech	% Hem-lock	% s. Maple
a	22.8	20.6	14.5	2.5	2.0	7.5	Northeastern Mixed Forest	211Db	1.5	15.6	0.7
b	7.7	11.7	4.3	0.2	1.0	1.3	Northeastern Mixed Forest	211Ed	1.1	17.4	13.0
c	20.0	22.7	14.4	3.3	1.6	12.8	Northeastern Mixed Forest	211Ff	11.8	8.0	10.1
d	21.8	20.1	30.8	0.5	0.1	18.6	Northeastern Mixed Forest	211Ia	11.6	10.3	16.7
e	19.0	19.6	28.1	1.2	0.9	16.0	Northeastern Mixed Forest	211Ib	10.2	10.3	17.6
f	25.7	19.6	33.3	3.0	1.8	32.6	Northeastern Mixed Forest	211Jd	4.7	14.6	13.1
g	3.1	7.3	1.3	0.4	0.1	0.6	Eastern Broadleaf Forest	221Aa	6.9	17.2	0.0
h	5.5	21.2	2.5	0.0	0.0	0.2	Eastern Broadleaf Forest	221Al	8.8	19.2	3.0
i	18.8	19.5	34.5	2.6	1.2	31.9	Adirondack-New England Mixed Forest	M211Bb	7.7	22.6	10.0
j	10.1	14.9	9.1	1.5	0.7	3.7	Adirondack-New England Mixed Forest	M211Bd	4.7	18.8	2.8
k	8.0	10.6	4.5	0.2	0.0	1.2	Adirondack-New England Mixed Forest	M211Cc	8.7	18.8	15.0
l	6.4	11.3	5.7	0.3	0.7	1.1	Adirondack-New England Mixed Forest	M211Cd	17.8	3.4	21.0
m	13.2	32.0	9.7	2.6	0.2	4.9	Adirondack-New England Mixed Forest	M211Db	19.8	8.0	15.5
mean	14.0	17.8	14.8	1.4	0.8	10.2	Adirondack-New England Mixed Forest	M211Dc	18.9	2.8	11.6
							Adirondack-New England Mixed Forest	M211Dd	26.5	2.8	17.2
							Adirondack-New England Mixed Forest	M211De	9.8	18.0	13.6
							mean		10.7	13.0	11.3

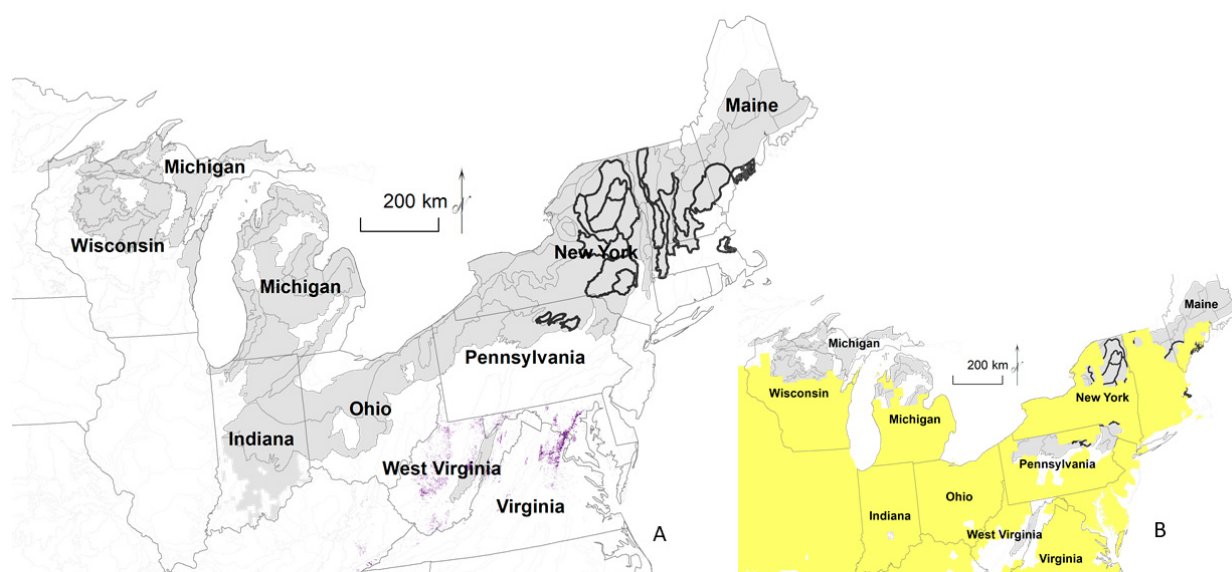


Figure 5. Historical distribution (ca. 1620–1900; light shading) of American beech and eastern hemlock forests, compared to current distribution (dark outline), where beech and hemlock were $\geq 20\%$ of all trees or either species was $\geq 15\%$ of all trees (A). Purple indicates locations of Appalachian Hemlock-Northern Hardwood Forest from Biophysical Settings [28]. Agricultural area did not exceed 25% in some locations before 1940, which was typically followed by agricultural abandonment in the Eastern United States (B, [23]).

A distribution map shows the best available beech and hemlock historical distributions (Figure 5). Historically, 9 of 13 ecological subsections in the Northern Lower Peninsula alone contained $\geq 20\%$ both beech and hemlock or $\geq 15\%$ of either species, based on line trees. This area covered 51.8 million ha. Due to surveyor preference for beech, the map may be too expansive; however, where beech and hemlock intersect, a bias for beech may be counterbalanced by a bias against hemlock. Based on Biophysical Settings [28], the main remaining landscapes that may meet these thresholds are the Appalachian hemlock forests.

4. Discussion

4.1. Key Findings

The three most abundant tree species in the Northern Lower Peninsula of Michigan were American beech, eastern hemlock, and sugar maple, which historically comprised about 45% of all trees. In the absence of overstory disturbance, generations changed at scales of hundreds of years, often to the same species given that overstory trees were positioned to supply seed sources and sprouts to the understory. The species require long disturbance-free intervals to become dominant (Figure 1). Shade-tolerant beech and hemlock decreased in current forests to only 2% of all trees from 30% of historical composition. Most forests in the Eastern US have been disturbed by multiple cycles of harvest since Euro-American settlement. Current forests are typically within a tree generation from origination and will require hundreds of years, or several tree generations without disturbance to restore a historically low disturbance regime and allow compositional and structural succession to old growth forests. Compositional succession occurs slowly, such that successional stages in composition are not particularly applicable, similar to high severity disturbance regimes in short-lived forests that auto-replace with pre-disturbance species (Figure 1; [11,12,17])

Sugar maple declined but remained relatively stable despite disturbance change. Sugar maple grows relatively well in gaps from overstory disturbance and is often the first of the three species to become abundant [2,37]. As time increases since overstory disturbance, sugar maple, then beech, then hemlock may rotate in dominance [38], although American beech may have been the most historically abundant shade-tolerant species in the Eastern United States within an oak and pine open forest matrix [21,33]. Propagule sources may be a problem in some locations. Reports of sugar maple declines and beech increases occur in

other locations, perhaps in some cases due to beech sprouting that suppresses other tree regeneration [37,39–42].

Historically, the Northern Lower Peninsula of Michigan alone contained almost as much area of beech and hemlock forests as the entire US contains currently (Figure 5). The area with minimum thresholds of beech and hemlock decreased from about 52 million to 6 million hectares. Limited current vegetation analogs exist of composition comparable to historical eastern old growth forests of American beech and eastern hemlock. Given land use and rates of tree removal, the archetypal structure of old growth forests is also not likely present throughout most of the ecological subsections that approach historical composition, even in mature forests [43].

Within the historical beech–hemlock distribution developed here, caveats include that the distribution is likely to expand as more historical surveys become available. Nonetheless, the main remaining landscapes may be identified as Appalachian hemlock forests [28]. Additionally, survey point surveys, composed of trees selected by surveyors, contained 1.7 times more beech trees than line tree surveys, which means that historical beech abundance is likely to be inflated because survey point surveys with surveyor bias are typically the only available source of information. The map incorporates hemlock and thus should help offset the bias in favor of beech.

In order to locate current vegetation analogs, I used low thresholds of at least 20% beech and hemlock or $\geq 15\%$ of each species because increasing this threshold to $\geq 30\%$ beech and hemlock produced only one subsection. However, at this minimum threshold, upland oaks were likely to be more abundant than beech where there was historical overlap. Historically, beech was abundant in landscapes with fire-tolerant oak species, perhaps due to fine-scale variation in understory fire disturbance [35,44]. Aside from understory disturbance by fire, open oak forests shared a similar infrequent overstory disturbance regime with closed beech forests (Figure 1).

Biodiversity and ecosystem function are affected by the loss of disturbance-independent beech and hemlock forests because dominant species most influence ecosystem properties and processes [45]. Large trees, the presence of old trees near maximum longevity, and snags are all rare across the Eastern US and elsewhere [46,47]. These structural characteristics are desirable for a wide range of associated taxa, which are declining in the absence of mature forests [10,48]. Beech generates nuts, or hard mast, for wildlife; due to concurrent decreases in oak species, which provide acorns, beech declines prevent substitution of one type of hard mast for another [49]. Functional redundancy cannot be compensated for if the major suppliers of hard mast all are declining. Native understory plants have also decreased in this region [50]. Both beech and hemlock produce leaf litter that decomposes more slowly than most other species of eastern forests and influences soil processes [51]. Older forests provide greater recruitment of large woody debris to streams, forming debris dams and pools [43,52]. Furthermore, hemlock is an evergreen species and may stabilize shading, temperature, and humidity and even available water throughout the year, perhaps allowing streams to have increased water flow [52].

Hemlock and beech additionally face new diseases from the wooly adelgid (*Adelges tsugae*) and beech bark disease (beech scale insect, *Cryptococcus fagisuga*, followed by lethal fungal infections by *Neonectria* spp.; [9]). In Michigan, hemlock wooly adelgid is not a widespread problem and beech bark disease was first detected in 2000, and thus, any losses have been recent [53]. Beech is a sprouting species, and when beech bark disease affects larger diameter trees, beech trees become thickets or in some cases, pole-sized trees, somewhat analogously to American chestnut transformation in life form to a shrub due to disease [52]. Beech is extremely shade-tolerant and can survive as thickets in dense understory conditions. Indeed, tree removal exposes resistant American beech to open conditions that may lead to mortality, although selective removal of infested beech may be beneficial [9,42,54]. Beech thickets appear to be undesirable, recalcitrant vegetation that prevents development of either an herbaceous understory or forest [55]. However, impenetrable thickets, similar to shrub ecosystems, often provide valuable nesting and

protective cover for wildlife. Additionally, in some cases, the loss of beech in the canopy may allow hemlock, which has extreme longevity, to increase with less competition from a long-lived competitor. Hemlock similarly is dealing with the hemlock woolly adelgid, but hemlock has exhibited development of resistance in the past. Rapid hemlock decline, attributed to insects, perhaps Lepidoptera, to about 5400 BP depressed pollen composition for millennia or several tree generations, but hemlock increased again in about 3500 BP [56]. Developing resistance followed by recovery is a long process [9].

4.2. Disturbance Change, Climate Change, and Novel Forests

Identification of compositionally similar analog communities or compositionally dissimilar no-analog communities typically occurs under the context of climate, with links to analog or no-analog climates [57]. Although concerns about climate change effects on forests are justified, historical forests have already been replaced by non-analogous forests in composition and structure throughout the Eastern US during the past century or two, due to changing disturbance. The limited extent of the potential current analogs of beech–hemlock forests demonstrates the loss of disturbance-independent beech–hemlock forests throughout most of the 52 million ha range. The current analogs may not even be very similar to historical beech–hemlock forests, but these may be the most disturbance-free landscapes in the Eastern United States.

Similarly to the loss of disturbance-free forests, surface fire-dependent pine, pine-oak, and oak open forests that historically covered most of the Eastern United States also have decreased to remnants without fire as a frequent disturbance to filter out fire-sensitive species and remove small trees, and with increased overstory disturbance that favors other traits [10,58]. For example, longleaf pine (*Pinus palustris*) woodlands, which dominated (60% to 95% of all trees) about 37.5 million ha of the Coastal Plain in the Southeastern United States, have transitioned to a combination of planted loblolly pine (*Pinus taeda*) forests and eastern broadleaf forests, while longleaf is currently 3% of all trees [59,60]. The Northern Lower Peninsula of Michigan may be one of the few locations in the Eastern US where upland oak species, particularly northern red oak, are increasing. However, historical oak dominance extended only into the Southern Lower Peninsula. Oaks grow well replacing pines in the pine understory, as seemed to be the case here, and northern red oak may share more traits with red maple and other increasing species than other fire-tolerant oak species [61].

The current disturbance regime of forestry favors species that reproduce vegetatively or produce prolific seeds for rapid establishment after overstory disturbance, and grow rapidly, including planted species such as red pine in Michigan and the Northern US and loblolly pine in the Southeastern US. Multiple eastern broadleaf species from the Central–Eastern US have expanded both north and south, not apparently due to climate change [15,62,63]. For example, in the Northern Lower Peninsula Michigan, severe, repetitive fires after logging at the turn to the 20th century that removed organic soil layers and cones first benefitted aspen, an established boreal species, resulting in a pulpwood industry, in which aspen stands are clear-cut on a rotation cycle of 30–60 years [2,4]. More recently, red maple in particular has expanded and increased in this near-boreal landscape and throughout most of the Eastern United States, including the Southeast [18–21,50,58]. Historically, red maple was limited to wetland areas between fire and flooding disturbances but currently succeeds in frequent gaps and clear cuts after overstory disturbance with limited understory disturbance.

Climate change may not be any worse for historical forests than disturbance change has already been and introduction of diseases for beech and hemlock specifically, which are still in progress. Climate change will interact with disturbance change, in unexpected ways, to both amplify and dampen disturbance change [64]. Future rates of change of forests in the Eastern US may not be likely to exceed rates of change that occurred during the exploitation era of Euro-American settlement and subsequent disequilibrium as species have been re-sorted by disturbance change. Moreover, tree dynamics respond slowly to climate change [65,66], which is why climate may not have a very apparent effect on tree

distributions relative to direct disturbance [15,67]. Climate change is expected to shift forests in a poleward direction and expand southern forests, but replacement of established trees by more heat-adapted species will occur slowly due to requirements for propagule dispersal and successful competition for growing space after natural tree mortality or tree removal.

Forests are now novel, which helps to contextualize change and perhaps alters how forests could be managed to reduce the effects of climate change. Biodiversity and ecosystem function have been affected by disturbance change and many species associated with historical forests are not being supported by current forests in the Eastern United States, which include longleaf pine, a biodiversity hotspot [10]. Management and restoration of historical forests and historical disturbance regimes will support declining species and provide ecosystem types that may be more resistant and resilient under the pressure of climate change. Historical forests have persisted throughout millennia of climate change, but current no-analog forests have assembled during the past hundred or so years and have not withstood the climate variation that historical forests have experienced. Additionally, forest management practices, such as protection of overstory trees and species-specific cutting and planting, may slow compositional change. Without acceleration of overstory turnover by tree removal, it may take hundreds of years for climate change effects on competitive dynamics to materialize. Management and restoration of fire-tolerant pine and oak species currently helps to maintain these species against competition from fire-sensitive species now that fire regimes are no longer in place.

5. Conclusions

The effects of Euro-American settlement and altered disturbance change are registered in the environmental records of disturbance-independent forests in Michigan, with similar large-scale effects on disturbance-independent forests in the Eastern United States. Mature forests composed of late-successional beech and hemlock have been removed across the Eastern US, due to mechanical disturbance of overstory trees, which has influenced forests to states that are not representative of historical forests. Forests continue to change in response to land use pressure in a trajectory of increased early to mid-successional species of eastern broadleaf forests. Even where current composition meets minimal thresholds of similarity to historical forests, current forests may not be likely to have the same structural and functional properties that are critical to associated species. Historical ecology and knowledge of the magnitude and trajectory of change from pre-Euro-American settlement forests to current forests help to provide a context for changes due to climate.

Author Contributions: The author performed all authorship tasks. The authors have read and agreed to the published version of the manuscript.

Funding: No funding was provided.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: All data are available.

Acknowledgments: I thank the anonymous reviewers. The findings and conclusions in this publication are those of the author and should not be construed to represent any official USDA or U.S. Government determination or policy.

Conflicts of Interest: The author declares no conflict of interest.

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