Composition, structure, and trajectories of Great Lakes coastal pine forests in relation to historical baselines and disturbance history

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Abstract

Limited information exists on the historical distribution and regeneration dynamics of native pine species in Great Lakes coastal environments. The project detailed here utilized historical surveys and modern stand data to assess the necessity for restoration of native pines to coastal environments in the Great Lakes region by comparing original composition and structure to that of modern stands. Modern stand data were also used to asses likely trajectories of compositional change and to assess the legacy effect of historical logging disturbance on modern stand composition. Composition of modern coastal pine stands was generally similar to that evident in pre-settlement land surveys across the region. There was not a large difference in pine dominance between the two data sets, and the major differences in composition involved species other than pines and were consistent with region-wide patterns. Analysis of modern stand composition and age and size structure indicated that some stands may be currently transitioning away from pine dominance, but this pattern likely represents standard successional processes on more mesic sites. Drier sites also exhibited successional trends, but the transition in these sites was from red pine to white pine dominance. Legacy effects of logging-era disturbance intensity on pine dominance were evident, with stands that underwent moderate levels of disturbance during the pine logging era having lower pine dominance than those that had little disturbance or nearly complete canopy removal. The findings of this research provide a baseline of data that could be very useful in designing and implementing restoration experiments and management treatments in coastal pine forests. As an outcome of this work experiments are being initiated to assess possible restoration treatments and to investigate local adaptation in Great Lakes coastal pine populations.

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Introduction

Historically, native pine species (white pine - *Pinus strobus,* red pine - *P. resinosa,* and jack pine - *P. banksiana*) were an important component of the coastal ecosystem in much of the Great Lakes region, especially in dune and beach ridge environments (Albert 2006). Many of these habitats have been severely altered by human influences, some of which have resulted specifically in removal of pines from these locations (e.g., early logging, especially for white and red pine; Lichter 1998). Even where pines were not removed by logging, *in situ* regeneration is not occurring in some pine stands (Menges and Armentano 1984). Some have attributed this to successional processes, but human alterations of natural processes, such as fire suppression, may also have had an effect. In some locations exotic species such as Austrian pine (*Pinus nigra*) occupy habitats formerly associated with native pine species, and have been shown to negatively impact the coastal ecosystem (Leege and Murphy 2001) and potential for restoration of other native species such as Pitcher's thistle (*Cirsium pitcheri;* Gulezian and Nyberg 2011). Non-native tree species can provide wildlife habitat and their outright removal is therefore often not ideal from a management standpoint. A phased approach, in which native pines are established in areas currently dominated by non-native species and eventually released to form a new canopy, may be most acceptable for both wildlife habitat and ecosystem restoration objectives.

Knowledge of the historical range of native pines in coastal habitats and their composition and structure is needed, both to support the necessity of restoration activities and to guide the development of experimental restoration research. A wealth of historical information on the Great Lakes forests (including those in coastal areas) exists (Albert 2006), but this resource has not been fully utilized to understand the extent and dynamics of the coastal pine forest. Wyse (2004) used pre-settlement and modern vegetation maps prepared by the Michigan Natural Features Inventory (Albert et al. 2008a, Albert et al. 2008b) to compare the area covered by coastal pine forests between the two eras and concluded that area of coastal pine forests had been reduced by more than half (to ~ 43%) both through development and forest conversion. Historical documents such as original land surveys, early writings, and timber company records can also be used to develop historical baselines for restoration of forest ecosystems by assessing structure and composition of the original forest (Schulte and Mladenoff 2001, Bollinger et al. 2004). A more thorough analysis of historical documents is needed to provide the rationale for regional-scale restoration experiments, and to situate these restoration experiments in appropriate environments (Howell 2001).

Historical data can also be useful in describing the magnitude of change in conditions relative to the original landscape (Rhemtulla et al. 2009), but such data is not always of use in assessing the drivers of this change and in forecasting future conditions. The combination of modern stand information and dendrochronological data can be especially useful in assessing such trajectories and their drivers (Frelich 2002). The forests of the Great Lakes region were heavily impacted by harvesting and subsequent slash fires that occurred during the late nineteenth-century (the "logging era"). This massive regional-scale disturbance has had long-lasting effects on the composition and structure of the forests of the Great Lakes region (Whitney 1994, Rhemtulla et al. 2009). The legacies of this disturbance may have an influence on the modern composition and structure of coastal Great Lakes forests, and could strongly influence the necessity of pine restoration in these ecosystems. Locations that underwent intense disturbance during the pine logging era may be likely to have a reduced level of modern pine dominance (Lichter 1998). Sites that have had more canopy established by lower intensity harvesting in the post-logging era would be expected to have increased dominance by shade-tolerant, sprouting competitor species such as red maple (*Acer rubrum*) and red oak (*Quercus rubra*).

The objectives of the work presented in this report were to 1) define historical baselines for restoration of coastal Great Lakes pine forests, 2) evaluate the necessity for restoration of composition and structure in modern coastal forests, and 3) assess the impact of historical legacies on modern composition and structure of coastal pine forests.

Methods

Historical Data

The US General Land Office Public Land Survey (PLS) records were used to evaluate the composition of pre-settlement coastal forests that had a pine component. In the PLS, surveyors recorded bearing trees at intersections of the township/range/section land grid system, and also recorded species and communities along survey lines. Bearing trees were also recorded where survey lines intersected water features, thus coverage of coastal environments is especially good. PLS data were collected for legal and economic rather than ecological purposes, and the data that resulted has some limitations including surveyor biases in tree selection, species misidentification, and data fabrication (Schulte and Mladenoff 2001). However, despite these shortcomings these records have proved to be very useful for reconstructing forest composition, structure, and disturbance regimes prior to significant alteration by Euro-american settlers (Bourdo 1956, Whitney 1986, Schulte and Mladenoff 2005). For this analysis, bearing tree species, diameter, and distance data were collected from maps prepared by the Michigan Natural Features Inventory on which data from the original land survey notes were transcribed onto USGS topo quad maps. These maps formed the basis for a published delineation of pre-settlement plant communities (Albert et al. 2008b). Data for use in the present study were recorded within coastal pine forest areas delineated by Albert et al. (2008b).

Modern Stand Data

Based on pre-settlement and modern vegetation data described above, sampling plots were located in areas currently or previously occupied by native pines in various locations around the Great Lakes region (Fig. 1). Study areas included in this report were located in Pictured Rocks National Lakeshore, Wilderness State Park, Ludington State Park, Big Knob State Forest, The Huron Mountain Club, and Hiawatha National Forest. Additional study areas, for which data collection/analysis is in progress, are located in Indiana Dunes National Lakeshore (IN), Sleeping Bear Dunes National Lakeshore (MI), Warren Dunes State Park (MI), P.J. Hoffmaster State Park (MI), and Saugatuck Dunes State Park (MI). Survey plots (0.1ha - 50 x 20m) were randomly located within coastal pine forest areas that were delineated based on modern vegetation data, aerial photographs, and historical data. Within each plot, all trees (≥10cm dbh) were measured and mapped. Saplings (>1m in height, <10cm dbh) were tallied across the entire plot in two size classes (0-5 and 5-10cm). Snags, stumps (<2m in height, evidence for harvest origin), and downed woody debris were measured and decay classes were recorded. Increment cores were collected from all canopy trees (trees in dominant, co-dominant, or intermediate canopy positions) to evaluate disturbance history and age structure of the canopy. Cores were also collected from a subset of sub-canopy trees and larger saplings to estimate the range of ages present in the understory. Cores were mounted on grooved wood blocks and sanded with progressively finer sand paper to help distinguish rings. Annual growth increments were measured to 0.001mm using a Velmex stage micrometer and Metronics Quick-Check 4100. Growth ring series were visually crossdated against regional master chronologies to identify possible missing or false rings (Yamaguchi 1991).

Data analysis

Relative basal area (dominance) for all species was calculated for both modern stand data and two pre-settlement data sets, one that included all coastal pine forests and another that was limited to those areas sampled in the modern data set. Species dominance data were compared between time periods using 2xC contingency table analyses (Agresti 2007). Relative density in the modern stand data was calculated for all species and by 5cm diameter classes (0-5, 5-10cm, etc.). Relative density was calculated only for the modern data because most of the pre-settlement trees were "line trees" which lack any distance information. Importance value for each species was calculated as the average of the relative basal area and density values (Cottam and Curtis 1956). Downed woody debris volume was determined based on length and large and small end diameters using the equation for volume of the frustrum of a cone.

Figure 1. Map of study locations for analysis of modern coastal pine forest composition, structure, and disturbance history.

Establishment dates for all canopy trees were determined based on increment core data, in cases where the core did not directly intercept the pith, the number of missed rings was estimated based on the growth rate of rings in the innermost 5cm of the core. Using these establishment dates, the proportion of total basal area on each plot that was established in each decade was calculated as a measure of canopy disturbance over time. The proportion of basal area established was then summed for three time-periods: the pre-settlement era (1660-1869), the pine logging era (1870-1919), and the post-logging era (1920-present). Basal area proportion for each period was then regressed against pine dominance to assess the effect of disturbance intensity and timing on modern pine dominance in these forests.

Ordination was conducted on modern stand overstory and understory composition to investigate compositional differences among stands and likely successional trajectories in these forests. A "plots x species" data matrix was constructed in which the overstory (≥10cm dbh) and understory (<10cm dbh) in each plot were included as separate sample units. Non-metric multidimensional scaling ordination was conducted on this matrix with PC-ORD v.5 (McCune and Mefford 2006) using the "Slow and thorough" autopilot setting. To assess the robustness of the ordination solution this setting makes a comparison with 250 iterations of randomized data using Monte Carlo analysis. To assess successional trajectories the overstory and understory samples for each plot were connected with successional vectors in the ordination space (McCune and Grace 2002).

Results and Discussion

Composition and structure of modern stands

There was considerable variation in structure among the modern coastal pine forest stands (Table 1). Overstory (≥10cm dbh) density varied between 440 and 840 stems per hectare, and overstory basal area between 26.3 and 50.7 m^2 per hectare. Levels of coarse woody debris also varied strongly among stands with snag basal areas between 2.8 and 5.7 m^2/ha and down woody debris volumes between 3.2 and 28.8 m^3/ha. Sapling density was also highly variable with density of stems >1m in height and <10cm dbh between 420 and 1740 stems/ha. Stump basal area also differed greatly among stands with levels as low as 3.2 m^2/ha and as high as 25.8m^2/ha.

Table 1. Characteristics of vegetation in modern coastal pine forest study areas.

Study Area	*0-5 Den/ha*	*5-10 Den/ha*	*>10 Den/ha*	*Live BA/ha*	*Canopy BA/ha*	*Understory BA/ha*	*Snag BA/ha*	*Stump BA/ha*	*DWD Vol/ha*
Big Knob	300	120	840	50.7	32.3	18.4	3.5	7.1	6.9
Huron Mtns.	330	90	440	26.3	21.0	5.3	5.7	3.2	25.7
Ludington	307	173	587	34.3	27.8	6.5	5.1	8.4	9.2
Pictured Rocks	1140	220	690	31.6	24.6	7.1	3.2	21.2	3.2
Pointe aux Chenes	1100	260	840	43.6	28.3	15.3	2.8	25.8	28.8
Wilderness	1389	351	566	32.7	23.5	9.2	4.6	10.1	9.8
Total	936	249	604	33.9	24.9	8.9	4.5	11.1	11.9

Overstory density and basal area were strongly and negatively correlated with snag basal area (R^2 = 0.8289 and 0.4291 respectively), but not with stump basal area. This finding suggests that recent natural mortality is more influential on current structure than harvesting-related mortality that occurred in the late nineteenth and early twentieth centuries. However, snag basal area was strongly negatively correlated (R^2 = 0.6817) with stump basal area, suggesting that there was a legacy effect of harvesting on the previous generation that is manifested in the modern forest as lower levels of coarse wood. Sapling density was not strongly correlated with overstory density or basal area, suggesting that the canopy played a relatively minor role in driving understory conditions in these forests.

Pine species were highly important in the modern canopy of the stands (Table 2), with an average relative basal area of 64.2 and relative density of 55.3 for all pine species combined (combined IV = 59.8). There was some variation among sites in the degree of pine dominance, but all except Big Knob and Ludington had pines dominating in both basal area and stem density (Fig. 2). The most important non-pine species were red oak, red maple, and hemlock (*Tsuga canadensis*; Table 2), but there was considerable variation among stands in the importance of these species as well (Fig. 2). Red maple occurred at low levels in all sites except for the Huron Mountains stand. Red oak, on the other hand, only occurred in two of the stands (Ludington and Wilderness), but was highly dominant in those locations. Hemlock occurred in four stands but was only an important component at the Big Knob and Pointe aux Chenes sites. Pines were highly dominant among snags and stump accounting for 86.6% of combined basal area (although identification of species was not always possible; Table 3). This dominance may be somewhat misleading, because pines are much more resistant to decay than the hardwood species that occur in this forest type (although similar to the other conifers, which make up a large portion of the current stand composition).

Table 2. Live tree basal area, density, and importance (Rel. BA + Rel density/2) of tree species overstory (>10cm dbh) in modern coastal pines study areas.

Species	*Acronym*	*Basal area ha^{-1}*	*Relative basal area*	*Density ha^{-1}*	*Relative density*	*Importance value*
White pine	PIST	10.28	30.4	136.25	22.6	26.5
Red pine	PIRE	9.19	27.1	136.25	22.6	24.9
Red oak	QURU	5.76	17.0	87.50	14.5	15.8
Jack pine	PIBA	2.26	6.7	61.25	10.1	8.4
Red maple	ACRU	1.87	5.5	51.25	8.5	7.0
Hemlock	TSCA	1.52	4.5	37.50	6.2	5.3
Cedar	THOC	1.19	3.5	27.50	4.6	4.0
Paper birch	BEPA	0.83	2.4	23.75	3.9	3.2
White spruce	PIGL	0.54	1.6	16.25	2.7	2.1
Balsam fir	ABBA	0.16	0.5	13.75	2.3	1.4
Black spruce	PIMA	0.10	0.3	7.50	1.2	0.8
Yellow birch	BEAL	0.05	0.2	2.50	0.4	0.3
Aspen	POTR	0.08	0.2	1.25	0.2	0.2
Black Cherry	PRSE	0.03	0.1	1.25	0.2	0.1
Total		33.85	100	603.75	100	100

Table 3. Snag and stump basal area, density, and importance (Rel. BA + Rel density/2) in modern coastal pines study areas.

Species	*Acronym*	*Basal area ha^{-1}*	*Relative basal area*	*Density ha^{-1}*	*Relative density*	*Importance value*
Pine		11.04	70.8	71.25	39.9	55.3
Jack pine	PIBA	0.82	5.3	25.00	14.0	9.6
Red pine	PIRE	0.88	5.7	12.50	7.0	6.3
White pine	PIST	0.76	4.8	12.50	7.0	5.9
Paper birch	BEPA	0.42	2.7	16.25	9.1	5.9
Red oak	QURU	0.66	4.2	11.25	6.3	5.3
Balsam fir	ABBA	0.29	1.8	13.75	7.7	4.8
White spruce	PIGL	0.23	1.5	7.50	4.2	2.8
Hemlock	TSCA	0.16	1.0	2.50	1.4	1.2
Cedar	THOC	0.15	1.0	2.50	1.4	1.2
Aspen	POTR	0.15	1.0	2.50	1.4	1.2
Unknown		0.04	0.3	1.25	0.7	0.5
Total		15.58	100	178.75	100	100.0

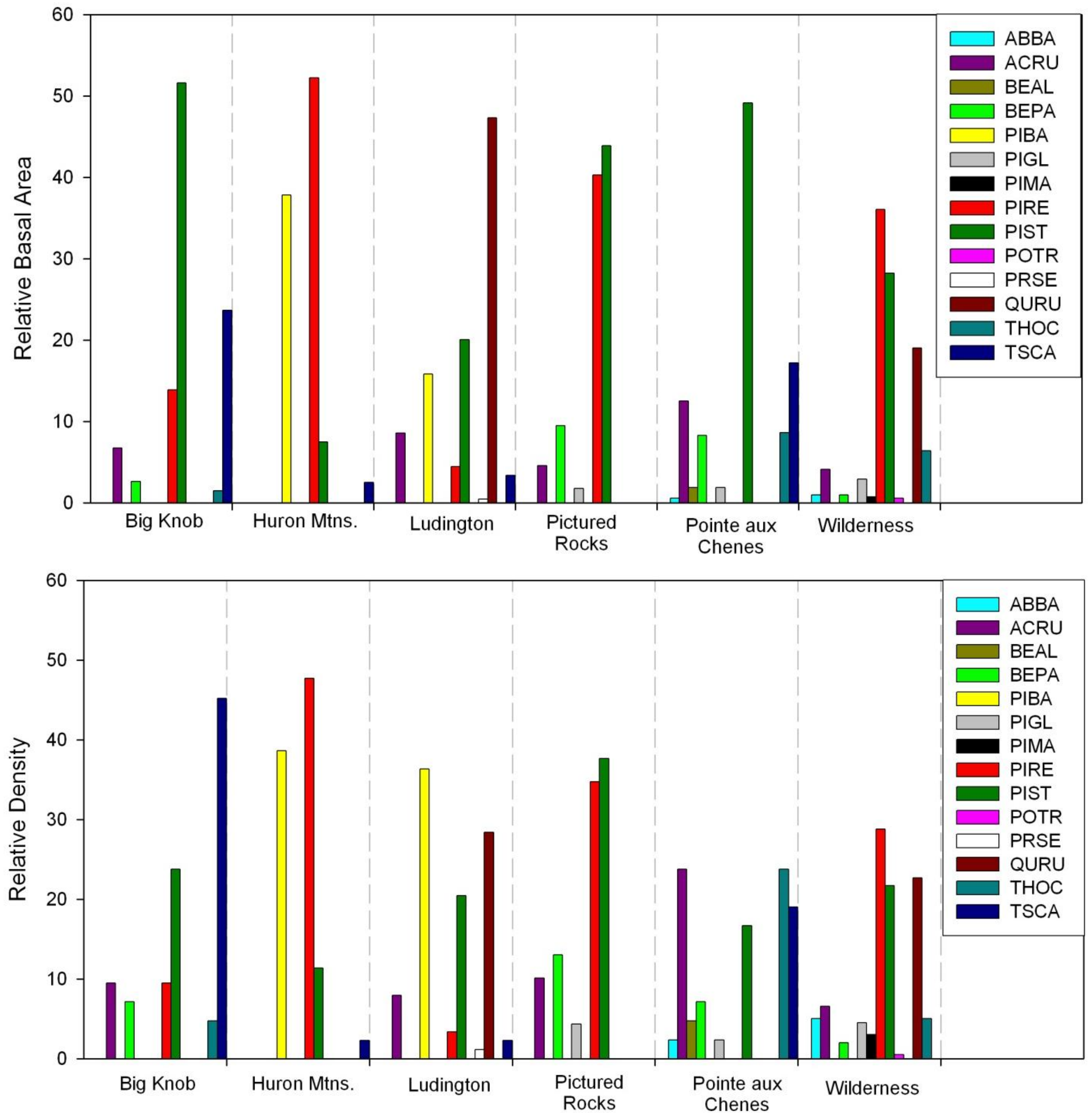

Figure 2. Relative basal area and density of overstory trees (>10cm dbh) in modern coastal pines study areas.

The data set as a whole had a strong negative exponential diameter distribution, with very few stems greater than 50cm in diameter (Fig. 3). To some extent this lack of large trees likely reflects the history of harvesting disturbance in the sites, which would have focused on the larger stems and is evidenced by the frequent occurrence of large stumps in the sites. The lack of large stems is also probably partly associated with the environment, which does not support rapid tree growth. The smallest diameter classes (saplings) were dominated by balsam fir (*Abies balsamea*), white and black spruce (*Picea glauca and P. mariana*), and white pine (Fig. 3). There was little regeneration of red and jack pines, especially as compared to their dominance in the canopy layer. The larger size classes were dominated by red pine, white pine, and red oak, while red maple was largely limited to the mid size classes. These data do not provide strong evidence of transition from pines to red maple and other shade tolerant species, but a general transition may be occurring from red and jack pine dominance to stands dominated by white pine with an understory of spruces and fir.

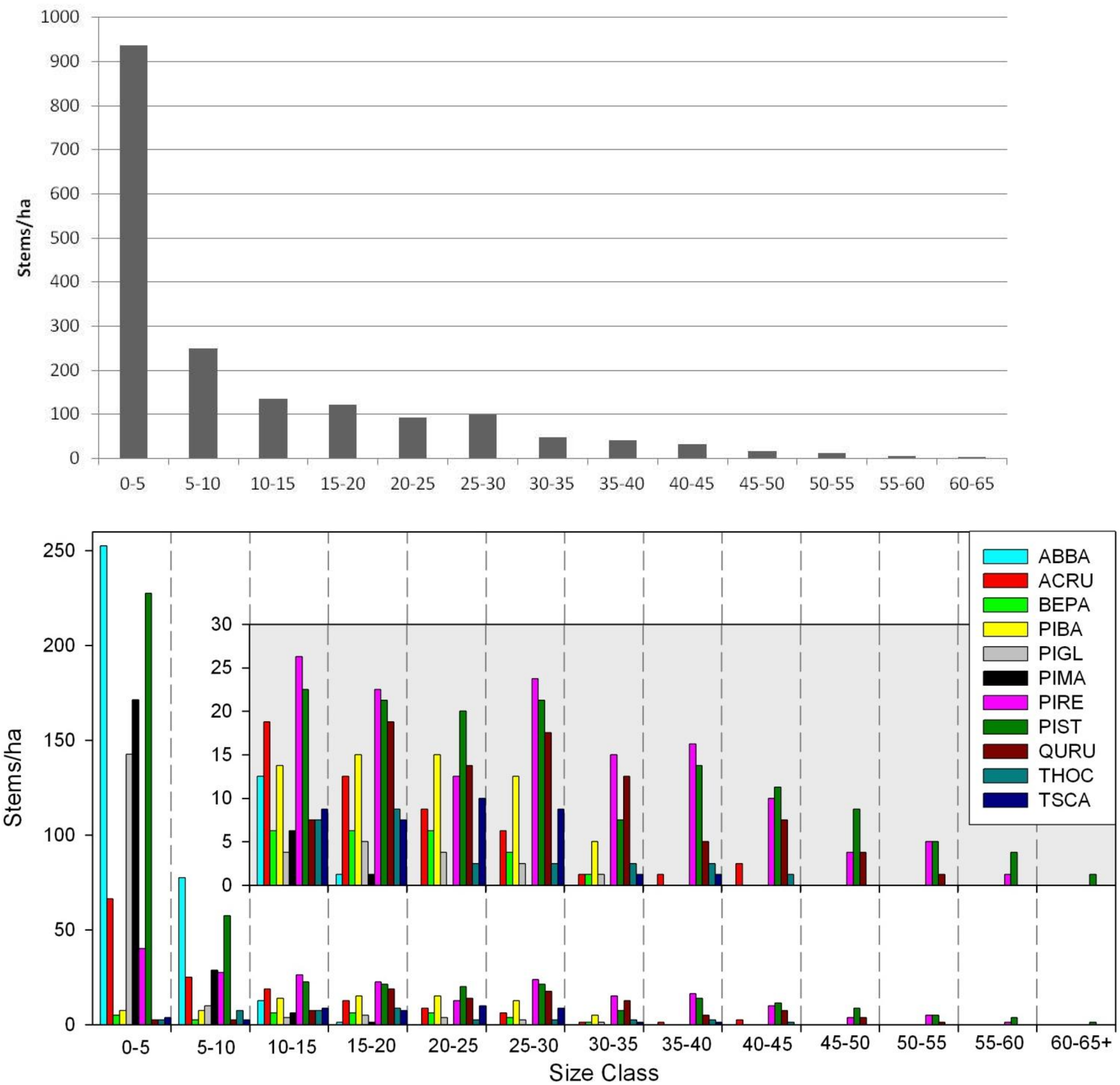

Figure 3. Diameter distributions of stem density for all species combined (top panel) and for individual species (bottom panel)

Ordination of the combined overstory and understory composition matrix resulted in a three-dimensional solution that was significantly more explanatory than randomized data (Stress = 12.05, p = 0.004) and explained 89.1% of the variation in the original data matrix. The strongest axis was Axis 1 (46.4%), which illustrated a strong separation of a number of understory plots and was highly related to a separation between red pine (r = -0.618) and balsam fir (r = 0.788) dominance (Fig. 4). The next strongest axis was Axis 3 (25.9%), which illustrated a gradient within the overstory composition with separation between plots dominated by red pine (r = 0.474) and jack pine (r = 0.393) from those dominated by white pine (r = -0.799).

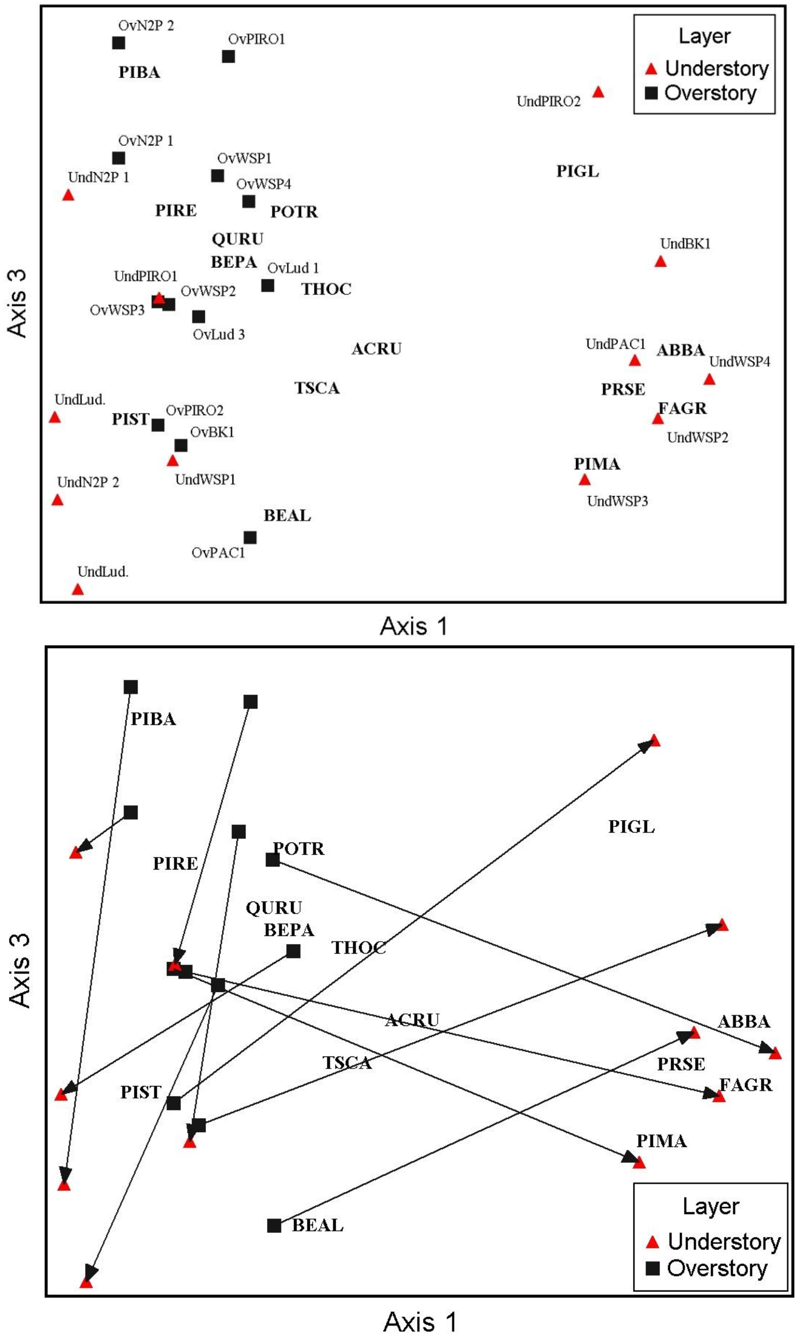

Figure 4. Non-metric multidimensional scaling ordination of overstory and understory composition by plot with species centroids overlayed and plot overstory and understory points connected by successional vectors (bottom).

Vectors connecting overstory and understory plots illustrated two separate successional patterns likely associated with environmental differences between plots (Fig. 4). Sites with strong red pine and jack pine overstory dominance indicated a successional trajectory towards white pine dominance in the understory. However, sites with an overstory of white pine or mixed between white and red pine had an understory dominated by fir and spruce. This dichotomy is likely associated with moisture conditions at the plot level, with the first trajectory (red pine-jack pine to white pine) associated with more xeric microclimates and the latter condition (white pine to spruce-fir) associated with wetter sites.

Pre-settlement composition and comparison with modern stands

Pines were dominant in most of the coastal forest areas in which they were found (91% of areas examined; Table 4). Only two southern locations (Saugatuck and Warren Dunes) had a non-pine species as the most dominant species (American beech, *Fagus grandifolia*, and white oak, *Q. alba*, respectively; Table 5). The other locations had mix of red and white pine dominance, and a variety of secondary species (including hemlock, oaks, swamp conifers, and beech), the abundance of which differed strongly by location.

Table 4. Characteristics of pre-settlement land survey coastal pine forest areas defined according to maps prepared by Albert et al. (2008)

Location	Total Stems	Total Basal Area	Pine Basal Area	Pine Dominance (Rel. BA)
Alpena	124	5.9	2.3	38.5
Au Train Bay	88	7.6	4.4	57.3
Big Bay	69	6.9	3.6	51.6
Big Knob	83	5.4	2.7	49.5
Grand Marais	531	30.9	27.7	89.7
Little Bay de Noc	119	21.3	18.2	85.2
Ludington	337	31.1	15.9	51.2
Manistique	154	7.9	4.8	60.7
Marquette	70	3.2	2.7	84.8
Muskegon	85	7.1	4.9	68.6
Naubinway	156	4.9	1.8	36.5
Pentwater	120	15.0	11.5	76.6
Pictured Rocks	64	5.9	4.2	71.3
Pointe Aux Chenes	177	10.5	3.3	31.4
Presque Isle	453	30.0	16.1	53.7
Saugatuck	38	1.9	0.1	4.9
Silver Lake	35	5.1	3.1	61.9
Sleeping Bear Dunes	272	25.6	14.3	55.7
Traverse City	68	6.9	3.9	57.5
Warren Dunes	129	14.5	3.8	25.9
Whitefish Bay	38	2.7	1.3	48.1
Wilderness	121	7.9	4.2	53.4
Total/Avg	3331	258.4	154.7	59.9

Table 5. Relative basal area in individual pre-settlement coastal pine areas.

Species	*Alpena*	*Au Train Bay*	*Big Bay*	*Big Knob*	*Grand Marais*	*Little Bay de Noc*	*Ludington*	*Manistique*	*Marquette*	*Muskegon*	*Naubinway*
PIST	19.1	20.4	26.6	30.7	22.4	47.5	47.7	37.5	22.5	68.5	23.8
Pine	0.0	3.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
PIRE	17.7	32.2	22.3	18.9	45.9	36.2	3.5	23.0	53.4	0.0	5.8
TSCA	2.3	20.0	13.6	22.2	1.1	6.6	19.8	17.6	0.0	10.7	9.0
QUAL	0.0	0.0	0.0	0.0	0.0	0.0	5.2	0.0	0.0	5.5	0.0
THOC	30.1	6.0	3.5	6.2	0.5	1.0	2.1	5.1	1.0	1.0	17.1
FAGR	0.0	2.8	0.0	0.2	0.0	0.9	6.9	0.0	0.0	4.0	0.4
PIBA	1.6	1.0	2.8	0.0	21.5	1.6	0.0	0.2	8.9	0.0	7.0
LALA	8.7	1.6	4.3	2.1	0.6	0.1	0.2	2.2	2.1	0.0	12.6
QURU	1.2	0.0	0.0	0.0	0.0	0.1	1.5	0.0	0.0	1.7	0.0
BEAL	4.3	4.2	5.6	6.5	1.1	0.0	0.0	1.6	3.1	0.0	3.6
QUVE	0.0	0.7	0.4	0.0	0.7	1.9	0.6	0.0	0.3	4.1	0.0
BEPA	0.4	0.4	6.3	3.6	1.6	0.0	0.2	1.9	0.6	0.0	4.4
Spruce	2.1	3.6	0.3	2.5	2.1	0.0	0.2	4.2	0.0	0.0	7.0
Birch	1.9	0.0	0.0	0.0	0.0	1.3	0.5	1.7	0.0	0.0	0.0
ACRU	0.0	0.0	7.0	1.8	0.2	0.4	2.1	0.0	0.0	2.1	0.0
POTR	5.8	0.4	1.3	3.9	0.6	0.2	3.8	1.6	2.7	2.0	2.3
ACER	1.5	0.0	2.2	0.0	0.3	0.0	3.9	0.5	3.5	0.0	0.4
ABBA	2.4	0.2	3.9	1.3	1.2	0.0	0.0	2.8	0.0	0.0	3.6

Species	*Pentwater*	*Pictured Rocks*	*Pointe Aux Chenes*	*Presque Isle*	*Saugatuck*	*Silver Lake*	*Sleeping Bear Dunes*	*Traverse City*	*Warren Dunes*	*Whitefish Bay*	*Wilderness*
PIST	76.6	48.6	30.0	18.7	4.8	44.2	45.6	33.7	25.9	6.1	1.3
Pine	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	52.1
PIRE	0.0	22.7	1.4	31.5	0.0	17.7	7.9	23.8	0.0	34.3	0.0
TSCA	3.0	15.3	27.5	4.2	20.3	14.1	21.3	22.7	12.3	33.7	7.3
QUAL	6.1	0.0	0.0	0.0	10.2	1.4	1.5	7.2	27.3	0.0	0.0
THOC	4.2	6.7	6.5	17.6	0.0	0.0	5.8	0.0	1.0	0.0	17.4
FAGR	1.6	0.0	2.3	2.3	43.3	1.4	5.7	8.2	8.7	0.7	0.7
PIBA	0.0	0.0	0.0	3.5	0.0	0.0	2.2	0.0	0.0	7.8	0.0
LALA	0.5	0.9	5.7	3.3	0.0	0.0	3.4	0.0	0.0	0.0	13.3
QURU	0.0	0.0	0.0	0.0	3.2	0.0	0.0	1.9	14.9	0.0	0.0
BEAL	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
QUVE	5.6	0.0	5.1	4.1	0.0	12.3	0.8	0.0	1.3	0.0	2.2
BEPA	0.0	0.0	0.8	3.8	0.0	0.4	0.3	0.0	0.0	10.6	0.0
Spruce	0.0	4.8	2.0	1.3	0.0	0.0	0.2	0.0	0.0	2.8	1.4
Birch	0.1	0.0	11.9	0.8	0.0	2.9	0.0	0.0	0.0	0.0	2.6
ACRU	0.0	0.0	1.1	1.1	6.4	0.4	2.6	0.0	1.0	0.0	0.0
POTR	1.2	0.0	1.7	4.5	2.6	2.5	1.2	0.0	0.7	0.5	1.4
ACER	0.9	0.0	0.7	0.4	4.6	1.4	0.7	1.0	0.0	3.6	0.0
ABBA	0.0	1.1	1.3	0.9	0.0	0.0	0.3	0.0	0.0	0.0	0.4

Comparison with modern composition illustrated surprising consistency between the two eras (Fig. 5), as the distribution of relative basal area by species was not significantly different between the two data sets ($X^2 = 15.27$, $p = 0.084$). Especially interesting was the greater dominance of red pine and jack pine in the modern stands relative to the original forest. White pine had slightly lower dominance in the modern forest than in the pre-settlement surveys, but overall pine dominance was equivalent to that evident in the original forest. There were large increases in both red oak and red maple relative to the pre-settlement landscape, but these increases appeared to come mostly at the expense of hemlock, which declined strongly. This pattern matches regional-scale declines in hemlock abundance that have been attributed to the impact of deer browsing and encroachment by hardwood species such as maples (Mladenoff and Stearns 1993). These patterns suggest that current composition is consistent with conditions in the original landscape despite the intense human disturbance and continued alteration of disturbance regimes that has affected the Great Lakes region forest (Schulte et al. 2007).

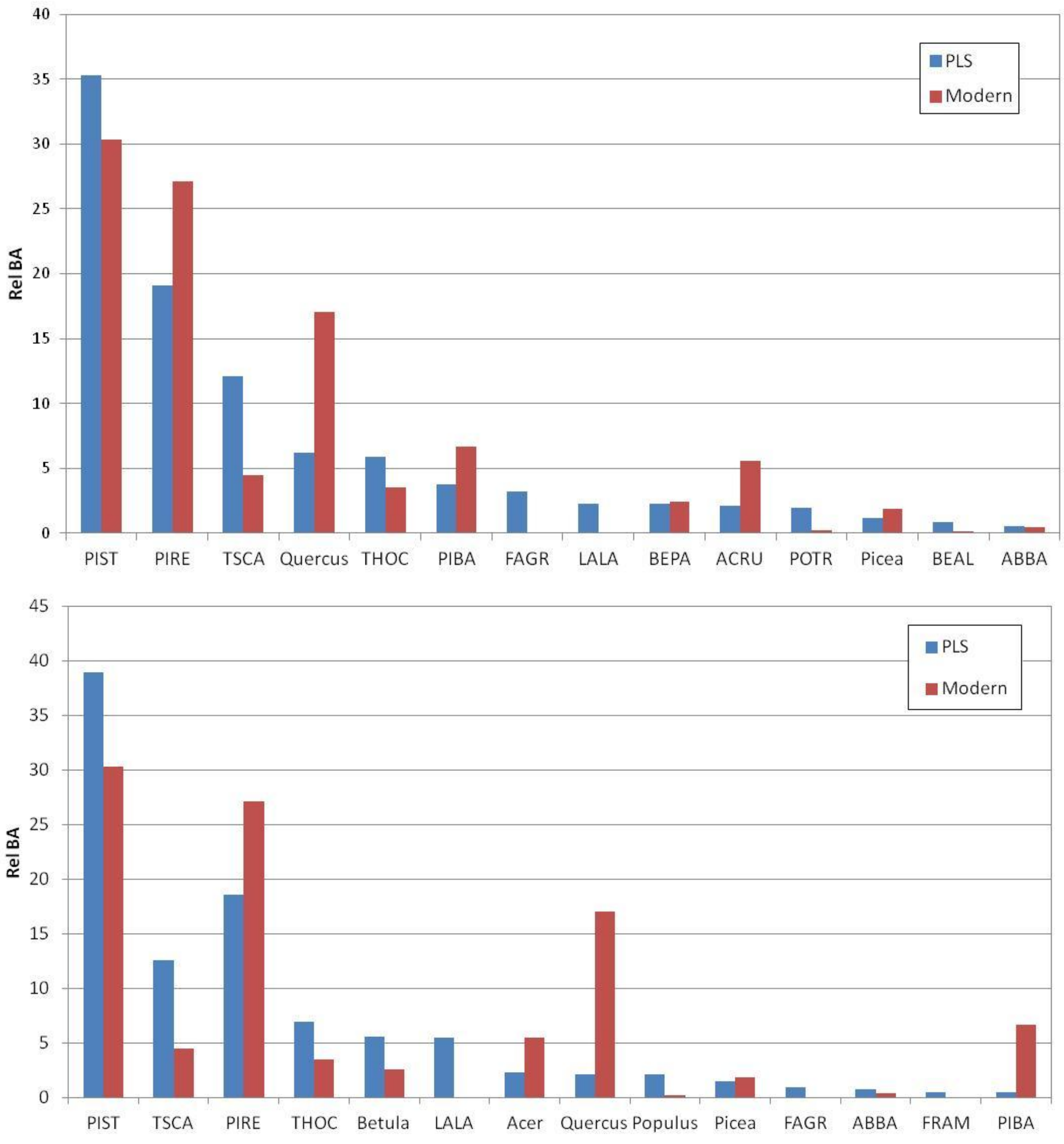

Figure 5. Comparison of basal area in pre-settlement land surveys and modern coastal pines study area, top panel includes all PLS coastal pines areas, bottom panel only those sampled in modern data.

Disturbance histories and legacies

Approximately half of the basal area study-wide was established during the logging era as defined here (1870-1919; Fig. 6). Very few trees established prior to 1850 remained in the forests, and not much basal area was established since the 1930's. This pattern could be somewhat related to the loss of evidence to rot in the center of old trees, which prevents ageing of stems, and the time necessary to establish and access the canopy, which could be quite long on these extreme sites and would preclude the occurrence of young canopy trees. Most stands had very similar timing of establishment (aside from the occasional legacy tree), except for Big Knob, where the majority of canopy basal area was established in the decade prior to the logging-era (Fig. 7). It is possible, but not especially likely, that this study area was logged earlier than most of the surrounding landscape. Instead, a stand replacing disturbance may have affected this site before logging operations could be conducted. The relatively low stump basal area in this site (especially in relation to total stand basal area) could support this interpretation. There were not strong differences among species in timing of establishment (as would be expected with strong successional pressure; Fig. 8). Almost all of the stems established prior to 1870 were pine, which likely reflects the life-span of these species and their fire tolerance. However, pines were established in significant numbers across all decades except for the very recent past (where stems may not have had time to grow to a size where coring was possible, supported by the abundance of pines in the sapling layer) at all but one of the sites (Big Knob; Table 6). This pattern strongly indicates that the canopy of these sites has not been steadily transitioning away from pine dominance.

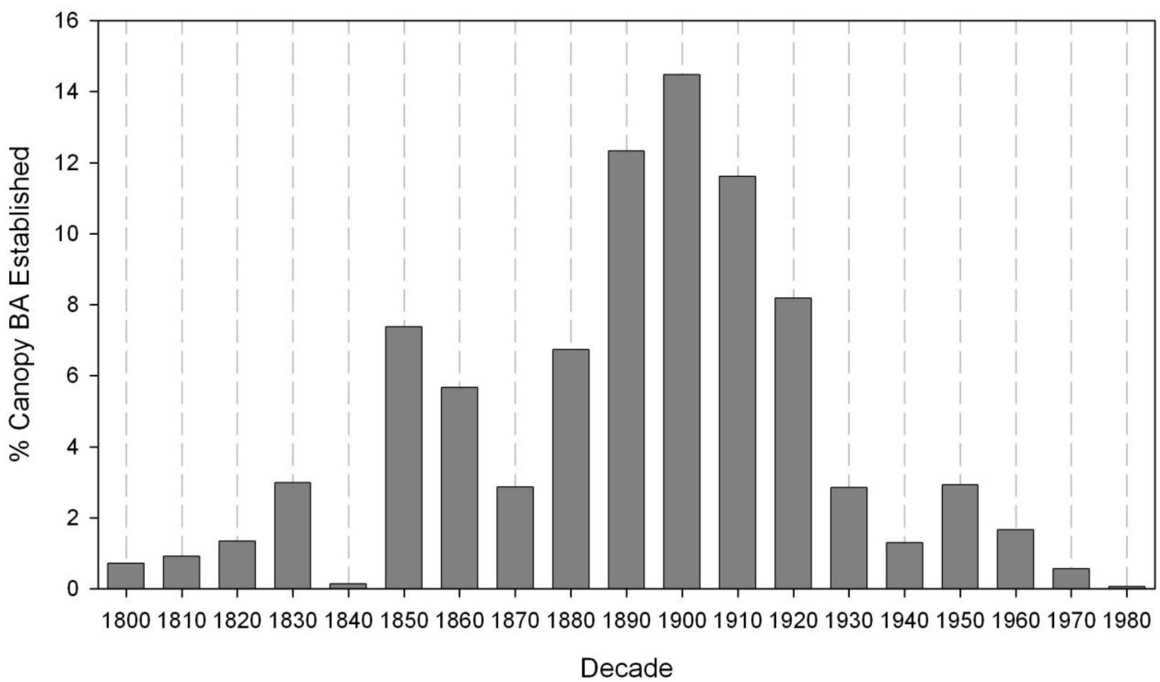

Figure 6. Proportion of study-wide canopy basal area established by decade

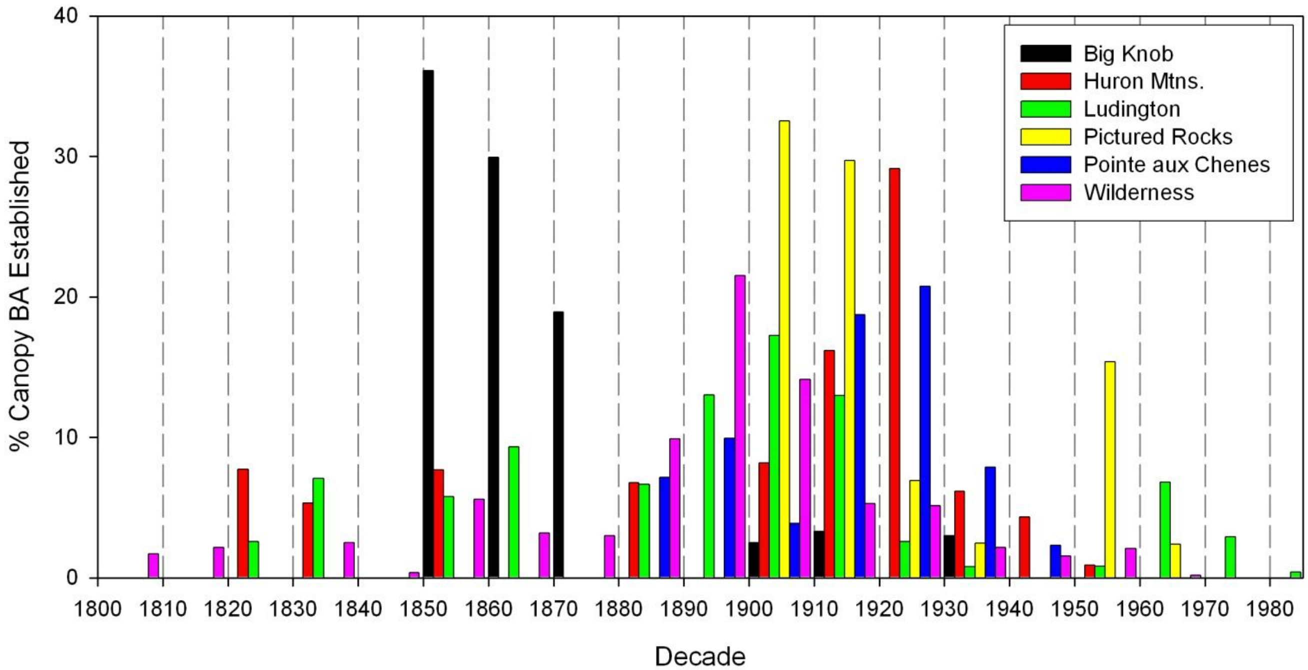

Figure 7. Proportion of stand-level canopy basal area established by decade

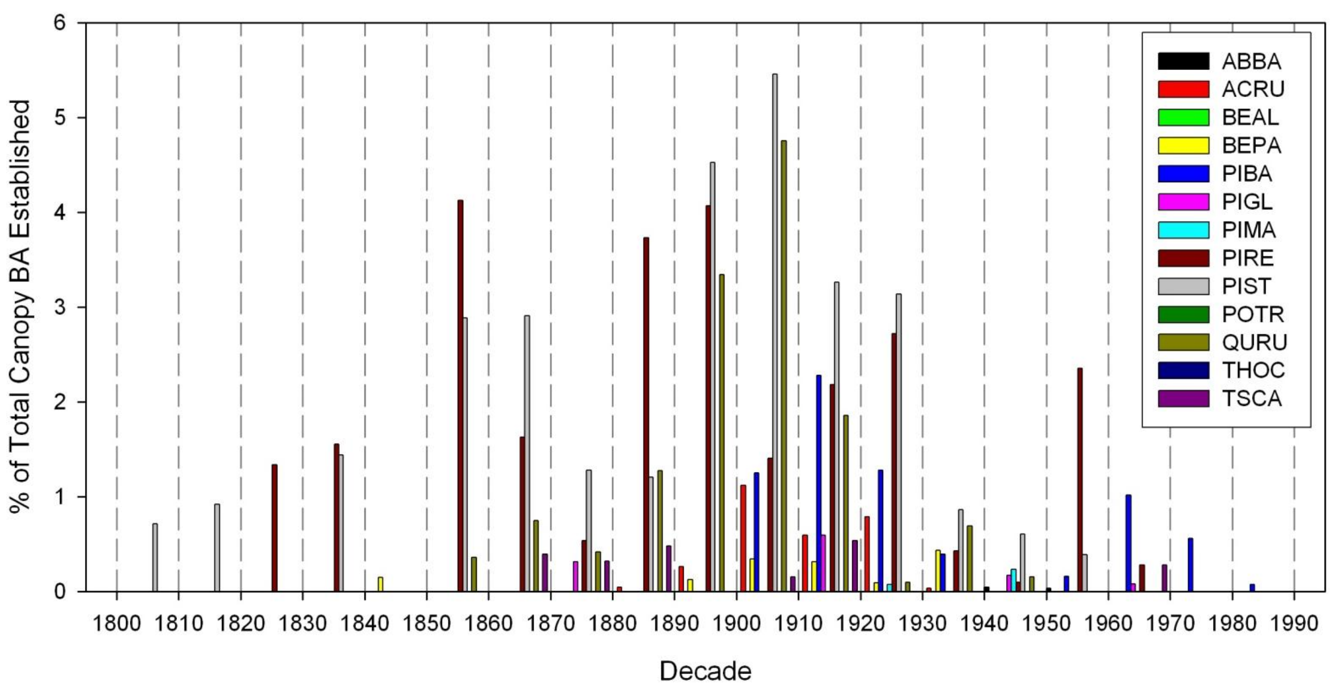

Figure 8. Proportion of study-wide basal area of major canopy species established by decade

Table 6. Relative basal area of pine established by decade and study area.

Decade	Big Knob	Huron Mtns.	Ludington	Pictured Rocks	Pointe aux Chenes	Wilderness	Total
1800	0.0	0.0	0.0	0.0	0.0	1.5	0.6
1810	0.0	0.0	0.0	0.0	0.0	1.9	0.8
1820	0.0	7.2	2.3	0.0	0.0	0.0	1.2
1830	0.0	5.0	6.4	0.0	0.0	2.2	2.7
1850	29.2	7.2	3.5	0.0	0.0	5.0	6.2
1860	20.5	0.0	5.1	0.0	0.0	3.0	4.1
1870	12.3	0.0	0.4	0.0	0.0	1.3	1.8
1880	0.0	6.3	0.0	0.0	0.0	9.6	4.7
1890	0.0	0.0	2.6	0.0	6.7	16.5	7.9
1900	2.6	0.8	0.5	25.8	0.0	7.3	6.5
1910	0.0	0.6	2.0	25.0	11.7	3.1	5.6
1920	0.0	17.4	1.2	5.9	15.0	4.8	5.9
1930	1.0	5.5	0.0	0.0	6.4	0.6	1.4
1940	0.0	4.1	0.0	0.0	0.0	1.0	0.8
1950	0.0	0.8	0.0	15.9	0.0	1.8	2.7
1960	0.0	0.0	0.2	3.1	0.0	0.0	0.4

Disturbance intensity in the different historical eras did not correlate with pine dominance in the expected manner (Fig. 9). Rather than a negative linear relationship between logging era disturbance intensity and modern pine dominance, there was a negative unimodal relationship with high pine dominance where disturbance was low or high and low pine dominance where disturbance was intermediate. This pattern suggests that in situations where canopy removal was nearly complete, pines were able to regenerate in the open conditions, but not in situations with partial canopy disturbance. In locations with little to no canopy removal by logging, pines were able to maintain dominance through the logging period into the modern era. More unexpected was the positive relationship between post-logging era canopy turnover and pine dominance. This pattern suggests that pines have been able to successfully regenerate in these stands in the recent past despite successional pressure and the alteration of landscape disturbance regimes. Some of this effect may be related to post-logging era harvesting, which would have focused on species other than pine, such as hardwoods. Nonetheless, this pattern is not consistent with a system-wide transition away from pine dominance and toward dominance by more shade-tolerant species in the recent past (~1920-present).

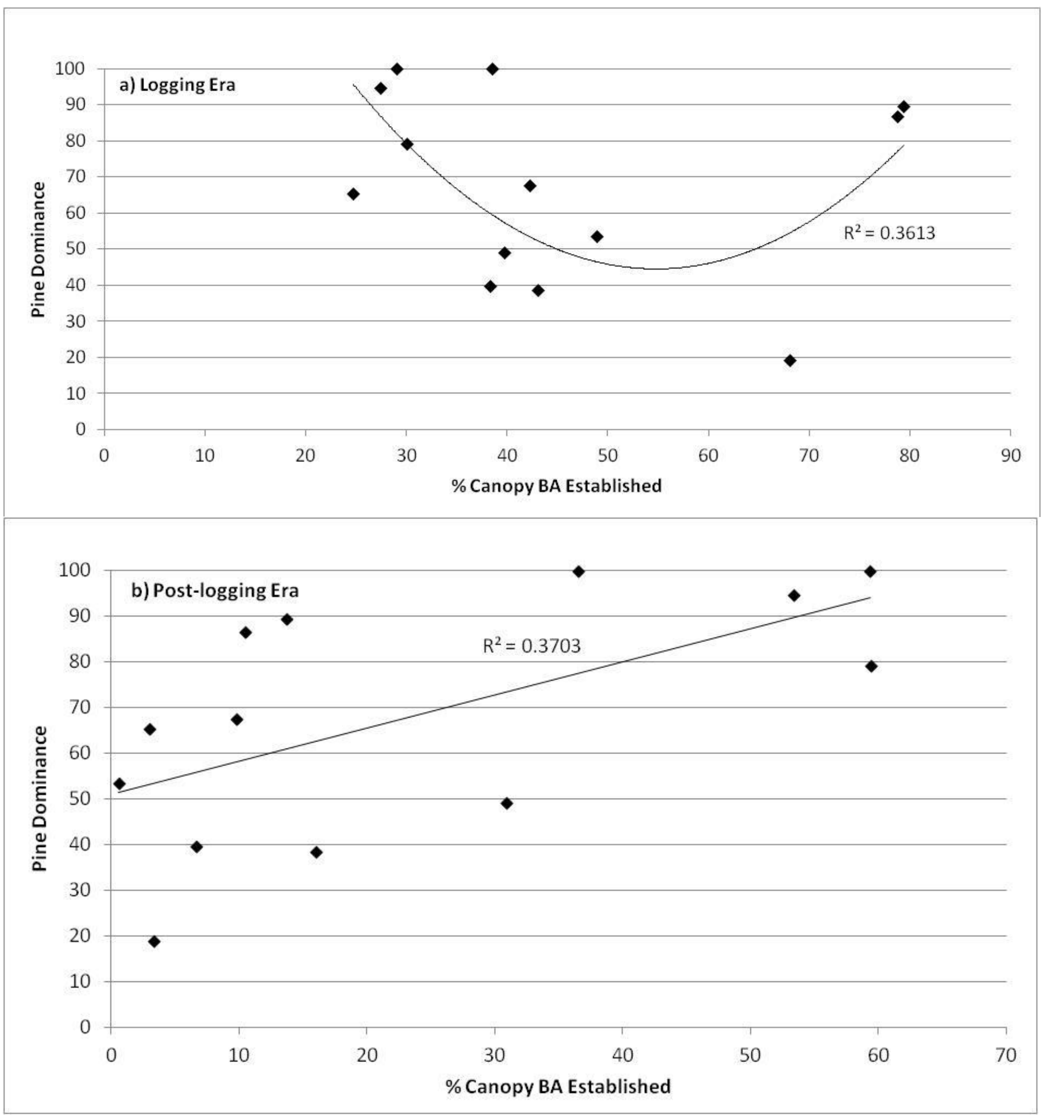

Figure 9. Regression of pine dominance in modern coastal pine forests as a function of canopy turnover during historical eras defined in relation to pine logging activities in the region. Logging era defined as 1870-1919, Post-logging era – 1920 to present.

Conclusions and management recommendations

Composition of modern coastal pine forests was consistent with pre-settlement conditions in this broad sample. An earlier analysis by Wyse (2004) compared maps prepared by the Michigan Natural Features Inventory and estimated that approximately 43% of the area occupied by coastal pine forests in the pre-settlement era also supported pine forests in the modern landscape. Our analysis indicated that, for the most part, the canopy of these stands has not begun transitioning away from pine dominance. However in some of these stands (~50%) the understory is highly dominated by non-pine species, which could indicate an impending transition away from pine dominance. Therefore, in the future landscape less than 25% of the area originally occupied by coastal pine forests may remain dominated by these species. In some of these stands active management (such as prescribed fire, canopy thinning, or seedling planting) would be necessary to maintain pine canopy dominance. However, many of the stands sampled by the PLS were likely in a similar stage of succession toward more shade-tolerant species, and these successional stands are not necessarily outside the historic range of variability. At a landscape-scale, natural disturbance and successional processes could probably maintain coastal pine forests by establishing new early-successional stands in these or similar habitats. Coastal areas may be more fire-prone than the surrounding landscape and without fire-protection are likely to experience somewhat frequent fire (Loope and Anderton 1998). However, in the modern landscape fire-protection is the norm and landscape-scale fire processes have been disrupted, especially in coastal areas where nearby development often limits fire spread. In addition, much of the fire that occurred in pre-settlement coastal areas was likely associated with human influence, and the historic baseline represented by the PLS may be as tied to anthropogenic factors as the modern landscape.

Managers focused on restoration of coastal pine forests need to recognize that the historic baseline is not a “natural” condition any more than the modern landscape, and that the changes occurring at a stand-level are also not necessarily outside the historical range of variability. Despite these caveats, the reduced area encompassed by coastal pine forests at a regional scale suggests that restoration of pines to some forested areas from which they have been lost may be a useful goal. The compositional information from the PLS can provide a useful baseline of information about the makeup of such forests and the variability in composition and structure that occurred there. In addition, reintroduction of fire, both to stands with current pine dominance and those targeted for restoration, would help to maintain some areas in early-successional stages. Such practices are likely to increase landscape-scale diversity and habitat variability that could be important for a number of associated species (Swanson et al. 2010).

Outcomes of seed funding and future directions

In addition to the work presented here, subsequent analysis of the data (including additional data still to be collected/analyzed) will attempt to further solidify our understanding of the history of these forests and its role in driving modern composition, structure, and successional trajectories. The final product of these analyses will be a manuscript prepared for submission to *Forest Ecology and Management.*

In order to effectively implement restoration of pines to coastal environments, tests of regeneration success in different coastal environments and stand conditions need to be conducted. Such analyses could also be useful in evaluating the factors responsible for the lack of pine regeneration in some areas. A project that addresses this need has been initiated and (as a part of this IISG project) seed material necessary for implementation was collected and seedlings are being produced at The Morton Arboretum. The project will be designed to assess possible restoration treatments and also to test local adaptation in coastal pine species using reciprocal transplant experiments (seeds were collected from coastal and non-coastal populations in both northern and southern Great Lakes areas). Treatments will be implemented in 2012-13 and will likely focus on four sites: Illinois Beach State Park (IL), Indiana Dunes State Park (IN), Ludington State Park (MI), and Wilderness State Park (MI). Funding to support this research will be pursued – for example a grant proposal was submitted to the Indiana Lake Michigan Coastal Program in late 2011 to support this work.

References

Agresti, A. 2007. An introduction to categorical data analysis. Wiley, New York.

Albert, D. 2006. Borne of the Wind: Michigan Sand Dunes. University of Michigan Press.

Albert, D., J. Cohen, M. Kost, B. Slaughter, and H. Enander. 2008a. Distribution maps of Michigan's Natural Communities. Michigan Natural Features Inventory. Report.

Albert, D. A., P. J. Comer, and H. Enander. 2008b. Atlas of Early Michigan's Forests, Grasslands, and Wetlands: An Interpretation of the 1816-1856 General Land Office Surveys. Michigan State University Press.

Bollinger, J., L. A. Schulte, S. N. Burrows, T. A. Sickley, and D. J. Mladenoff. 2004. Assessing ecological restoration potentials of Wisconsin (USA) using historical landscape reconstructions. Restoration Ecology **12**:124-142.

Bourdo, E. A. 1956. A review of the General Land Office survey and of its use in quantitative studies of former forests. Ecology **37**:754-768.

Cottam, G. and J. T. Curtis. 1956. The use of distance measures in phytosociological sampling. Ecology **37**:451-460.

Frelich, L. E. 2002. Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge.

Gulezian, P. Z. and D. W. Nyberg. 2011. Naturalized Pine (Pinus nigra) Promotes Growth of Woody Vegetation in Native Sand Prairie: Impacts of Invasion 130 Years After Introduction. Natural Areas Journal **31**:6-13.

Howell, E. A. 2001. The historical ecology handbook: a restorationist's guide to reference ecosystems. Island Pr.

Leege, L. and P. Murphy. 2001. Ecological effects of the non-native Pinus nigra on sand dune communities. Botany **79**:429-437.

Lichter, J. 1998. Primary succession and forest development on coastal Lake Michigan sand dunes. Ecological Monographs **68**:487-510.

Loope, W. L. and J. B. Anderton. 1998. Human vs. lightning ignition of presettlement surface fires in coastal pine forests of the upper Great Lakes. American Midland Naturalist **140**:206-218.

McCune, B. and J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, OR.

McCune, B. and M. J. Mefford. 2006. PC-ORD. Multivariate Analysis of Ecological Data. MjM Software Design. Gleneden Beach, Oregon, USA. Version 5.2.

Menges, E. and T. Armentano. 1984. Successional relationships of pine stands at Indiana Dunes. Proceedings of the Indiana Academy of Science (USA).

Mladenoff, D. J. and F. Stearns. 1993. Eastern Hemlock Regeneration and Deer Browsing in the Northern

Great Lakes Region: A Re-examination and Model Simulation. Conservation Biology **7**:889-900.

Rhemtulla, J. M., D. J. Mladenoff, and M. K. Clayton. 2009. Legacies of historical land use on regional forest composition and structure in Wisconsin, USA (mid-1800s-1930s-2000s). Ecological Applications **19**:1061-1078.

Schulte, L. and D. Mladenoff. 2001. The original US public land survey records: their use and limitations in reconstructing presettlement vegetation. Journal of Forestry **99**:5-10.

Schulte, L. A. and D. J. Mladenoff. 2005. Severe wind and fire regimes in northern forests: historical variablility at the regional scale. Ecology **86**:431-445.

Schulte, L. A., D. J. Mladenoff, T. R. Crow, L. C. Merrick, and D. T. Cleland. 2007. Homogenization of northern US Great Lakes forests due to land use. Landscape Ecology **22**:1089-1103.

Swanson, M. E., J. F. Franklin, R. L. Beschta, C. M. Crisafulli, D. A. DellaSala, R. L. Hutto, D. B. Lindenmayer, and F. J. Swanson. 2010. The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment **9**:117-125.

Whitney, G. G. 1986. Relation of Michigan's presettlement pine forests to substrate and disturbance history. Ecology **67**:1548-1559.

Whitney, G. G. 1994. From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America, 1500 to the Present. Cambridge University Press.

Wyse, T. C. 2004. Vegetation and disturbance history of coastal pine forests in northern lower Michigan, USA. MS Thesis. Ohio State University, Columbus, OH.

Yamaguchi, D. K. 1991. A simple method for cross-dating increment cores from living trees. Canadian Journal of Forest Research/Revue Canadienne de Recherche Forestiere **21**:414-416.