

Forest landscape change in the northwestern Wisconsin Pine Barrens from pre-European settlement to the present¹

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Abstract: Natural disturbance patterns can provide useful information for ecosystem management. Our objective was to provide a detailed spatial picture of the pre-European settlement vegetation cover for the northwestern Wisconsin Pine Barrens and to compare it with the present vegetation cover. We analyzed the presettlement conditions using an extensive data set comprised of U.S. General Land Office surveyor records from the mid-19th century and related it to the vegetation cover in 1987 as depicted in a Landsat satellite forest classification. Changes were quantified by calculating differences in abundance and relative importance of tree species at presettlement time and today. Our results revealed a strong decline of jack, red, and white pine (*Pinus banksiana* Lamb., *Pinus resinosa* Ait., and *Pinus strobus* L., respectively), accompanied by an increase of oak (*Quercus* spp.), trembling aspen (*Populus tremuloides* Michx.), and other hardwood species. Certain vegetation types, e.g., red pine and oak savannas, were removed from the landscape. The forest density gradient of the presettlement landscape with open savannas and woodlands in the South and denser forests in the North disappeared. These changes, especially the increase in forest cover, are ecologically significant because numerous species are adapted to open habitat, which was previously created by fire, and their populations are declining.

Résumé : Le comportement des perturbations naturelles peut fournir des informations utiles pour l'aménagement d'un écosystème. L'objectif de cette étude était de fournir une image spatiale détaillée du couvert végétal précolonial des « Pine Barrens » du nord-ouest du Wisconsin et de la comparer avec le couvert végétal actuel. Les conditions précoloniales ont été analysées en utilisant un lot étendu de données contenues dans les rapports d'inventaire de l'Office général des terres des États-Unis, datant du milieu du 19^e siècle, et qui ont été mises en relation avec le couvert végétal de 1987, tel que représenté par la classification forestière effectuée à l'aide du satellite Landsat. Les changements ont été quantifiés par le calcul des différences de l'abondance et de l'importance relative des espèces arborescentes au temps précolonial et maintenant. Les résultats ont montré une forte diminution des pins gris, rouge et blanc (*Pinus banksiana* Lamb., *Pinus resinosa* Ait. et *Pinus strobus* L., respectivement), accompagnée d'une augmentation des chênes (*Quercus* spp.), du peuplier faux-tremble (*Populus tremuloides* Michx.) et d'autres espèces de feuillus. Certains types de végétation, par exemple des savanes à pin rouge et chênes, sont disparus du paysage. Le gradient de densité des forêts du paysage précolonial, avec les savanes et les forêts claires dans le sud et les forêts plus denses dans le nord, a disparu. Ces changements, surtout l'augmentation du couvert forestier, sont importants du point de vue écologique parce que de nombreuses espèces sont adaptées à un habitat ouvert, créé antérieurement par le feu, et que leurs populations diminuent.

[Traduit par la Rédaction]

Introduction

Recently, natural disturbance pattern and historic vegetation cover have been advocated as an ecological basis for forest management (Hunter 1993; Attiwill 1994; Fulé et al. 1997) and as an attempt to restore former landscape structures (Baker 1994; Fulé and Covington 1998). This requires

determining reference conditions with the greatest detail possible (White and Walker 1997) and identifying how far the current landscape differs from these conditions (Foster 1992; Baker 1992, 1995; Wallin et al. 1996).

Our study objective was to derive a frame of reference for ecosystem management of the northwestern Wisconsin Pine Barrens, to provide a detailed spatial assessment of the vegetation cover before European settlement (beginning around 1860), and to examine the changes that have occurred to the present. Our analysis of the vegetation cover before European settlement (hereafter referred to as presettlement vegetation) was based on the surveyor records of the U.S. General Land Office (GLO; Buordo 1956). The GLO surveys divided unsettled areas into 6 × 6 mile townships (9.66 × 9.66 km), 1 × 1 mile sections (1.6 × 1.6 km), and quarter sections (0.8 × 0.8 km) so that new settlers could be assigned to homesteads, and land could be sold for timber operations, railroads, mining, and other commercial enterprises.

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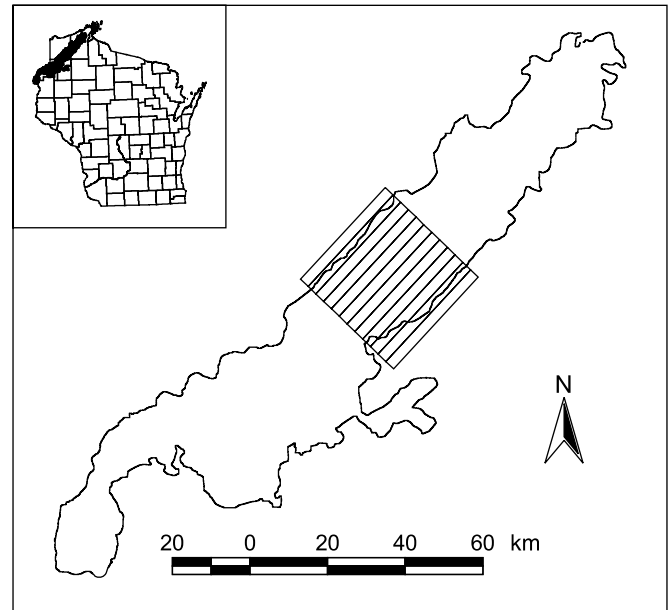
To establish the corners of townships, sections, and quarter sections, survey posts were placed at the exact corner location, and two to four trees ("witness" or "bearing" trees) were marked in the vicinity. The surveyors recorded tree species, diameter (in inches; 1 inch = 2.54 cm; minimum diameter = 10 cm), and distance (in links; 1 link = 22.68 cm) to the survey post (hereafter referred to as "tree distance") in their journals.

The GLO data have been used extensively to study pre-settlement vegetation because they capture a point in time just before drastic changes occurred, and because, in many parts of the United States, they are the only historic vegetation data available (Delcourt and Delcourt 1974; Galatowitsch 1990). Studies based on the GLO data have examined the relationship of soils and vegetation (Whitney 1982, 1986) and disturbance regimes of wind (Lorimer 1977; Canham and Loucks 1984) and fire (Kline and Cottam 1979; Grimm 1984; Radeloff et al. 1998). Comparisons between GLO data and contemporary maps revealed changes in vegetation composition (Iverson 1988; Anderson et al. 1996) and landscape patterns (White and Mladenoff 1994; Nelson 1997). One inherent limitation of the GLO data are that they record only one point in time and not the full range of variability that occurred in dynamic ecosystems. This limitation may be partly overcome by analyzing larger areas, so that all seral stages of a shifting mosaic are incorporated. However, some ecosystems may never experience equilibrium (Sprugel 1991), and one should not assume that the GLO data represent such even of large areas.

The GLO data present unique information about pre-settlement vegetation conditions, but it is important to note that the purpose of the survey was not to sample vegetation. Their main objective was to survey lands of the U.S. public domain so that they could be sold. The GLO data have been criticized for containing possible bias (Buordo 1956), for example, because surveyors may have been inclined to select tree species that were long lived or had bark that was easy to mark. The limited number of trees per surveying point (two to four) mean that the data for a single surveying point represent small samples of species mixtures in forests containing many tree species. However, environmental factors limited the possible choices of tree species and thus the bias introduced by the surveyors (Manies 1997). For example, a surveyor in a jack pine forest on an outwash plain was not likely to make a biased selection favoring mesic hardwoods, because these are very uncommon under such conditions. Furthermore, there is no consistent bias among surveyors (Manies 1997); the bias of a single surveyor influences GLO data analysis less when large areas and thereby the records of many surveyors are investigated.

A trade-off between spatial extent and level of study detail occurs when GLO data are analyzed. This trade-off has forced researchers to either examine relatively small areas in great detail (Delcourt and Delcourt 1996) or to define a few broad vegetation types and map these for a larger region (Finley 1951). This obstacle can be overcome by analyzing GLO data by computer (Grimm 1984). We followed this approach for our study of the Pine Barrens region in northwestern Wisconsin by using a geographical information system (GIS) to store and manipulate an extensive data set while maintaining its full spatial resolution.

Fig. 1. The Pine Barrens region in northwestern Wisconsin and the broad NW–SE transect across the central Pine Barrens used to examine relative importance of pine.



Pine barrens ecosystems, such as the one studied here, occur on poor-quality sandy soils and contain a vegetation cover dominated by grasses, shrubs, and scattered trees (Curtis 1959). Historically, fire was the dominant disturbance determining landscape pattern and vegetation structure typical of pine barrens (Forman and Boerner 1981; Givnish 1981). Pine barrens ecosystems are not unique to Wisconsin (Forman 1979; Abrams et al. 1985) but are generally uncommon and often threatened (Good and Good 1984; WDNR 1995). The Wisconsin Department of Natural Resources (WDNR) has made the Pine Barrens one of its priorities for landscape-scale management (Borgerding et al. 1995) because of the decline of many species that were adapted to the habitat and landscape patterns previously created by fire. One management option that is discussed currently is the aggregation of clearcuts to create larger openings thereby mimicking the habitat patterns of openings previously created by fire. The analysis of pre-settlement conditions and landscape change presented here can be a useful frame of reference for the management and conservation of the northwestern Wisconsin Pine Barrens.

Methods

Study area: the northwestern Wisconsin Pine Barrens

The northwestern Wisconsin Pine Barrens are located on a glacial outwash plain, covering 450 000 ha (Fig. 1). Currently, jack pine (*Pinus banksiana* Lamb.) is the dominant tree species, accompanied by red and white pine (*Pinus resinosa* Ait. and *Pinus strobus* L., respectively); bur, red and pin oak (*Quercus macrocarpa* Michx., *Quercus rubra* L., and *Quercus ellipsoidalis* E.J. Hill, respectively); and trembling aspen (*Populus tremuloides* Michx.). The soils are comprised of coarse sands with low nutrient content. The water-holding capacity of the soils is also low, and they are prone to drought. The topography is flat to gently rolling, surface runoff is uncommon, and streams are rare. The ground

water table is high, and especially the southern part of the Pine Barren contains many lakes. For more detailed descriptions of the Pine Barrens refer to Murphy (1931), Borgerding (1995), and Radeloff et al. (1998).

Historical information on vegetation cover in the region is sparse. The earliest botanical accounts lack spatial detail and were published >15 years after European settlement of the region began (Strong 1877; Sweet 1880; Roth 1898). Later research was based on presettlement data but analyzed only small portions of the Pine Barrens (Fassett 1944; Vogl 1964). No other detailed presettlement vegetation map of the Pine Barrens exists to our knowledge. Little is known about Native American land use of the Pine Barrens (Murphy 1931). However, it is likely that they used fire to increase berry production and facilitate hunting (Lewis and Ferguson 1988; Denevan 1992). Starting around 1860, loggers harvested white and red pine, and farming began shortly thereafter. Slash from the harvesting operations fueled extensive fires. Around 1910, jack pine harvesting for pulpwood production began (Murphy 1931). Up to about 1930, logging, fires, and farm settlement opened the landscape and removed the forest cover almost entirely. This trend reversed after the 1930s because farmers abandoned their nutrient-depleted land. Timber became scarce and reforestation began (Murphy 1931). Fire was seen as a threat to timber resources, and fire suppression also started in the 1930s, despite early research on the importance of fire for the regeneration of pine species (Maissurow 1935, 1941; Vogl 1970). Recent decades have seen an increase in housing density, mainly due to increasing seasonal housing for recreation (Radeloff et al. 1999a). It is important to note that the landscape changes described in this study are the result of all these events.

Land ownership in the Barrens changed also over time. Initially, logging companies owned the rights to harvest timber. Around the turn of the century, farmers and other small private landowners owned the majority of the Pine Barrens (Murphy 1931). This changed during the 1930s, when many farmers could not meet their tax payments, and the land reverted either to the counties and (or) was sold to the U.S. Forest Service or industrial forest corporations. Current landownership patterns vary across the Pine Barrens. The northern portion is part of the Chequamegon National forest, and the central portion contains extensive county forests and private industrial forest holdings. In the southern Pine Barrens, small private holdings are common, as are county forests.

Presettlement vegetation assessment

We entered the GLO point data for 11 153 trees at 5086 corners in our study area into a GIS data base (Manies 1997; Radeloff et al. 1998). This was the database we used to reconstruct the vegetation cover of the Pine Barrens in the 1850s. The small number (two to four) of trees sampled at each corner does not permit analyzing species mixtures at this spatial resolution. We decided to perform two analyses to overcome this limitation. First, we assessed tree species abundance across all surveying corners. We used only the first witness tree for this analysis, because the number of witness trees recorded at a corner varied and was generally too small to allow analyzing species mixtures at this scale. Second, we analyzed species mixtures and relative importance of tree species in larger spatial units to aggregate all witness trees of several corners in the calculations.

Tree species abundance was assessed in 798×798 m grid cells to capture landscape structure in greatest possible detail. The cell size was close to the minimum spatial resolution of the GLO data (0.8 km) and a multiple of the resolution of the satellite classification (see below), thus allowing direct comparison. We first interpo-

lated the GLO point data using the Thiessen polygon interpolation algorithm (Burrough and McDonnell 1998) and assigned the species information of the first witness tree to each Thiessen polygon. The polygon coverage that resulted from the interpolation was converted into a grid with 798×798 m cell size. The location of water bodies cannot be easily obtained from the GLO data, and we superimposed water bodies as classified by the satellite image analysis (see below) on the presettlement vegetation map. The attribute "no forest" was only assigned if the GLO surveyor did not report a witness tree. Our GLO data processing at this scale resulted in the assignment of one tree species for each grid cell, without taking forest density or species mixture into account.

To analyze species mixtures and the relative importance of different tree species, we used a program developed by He et al.³ that summarized the relative importance value (IV; Curtis and MacIntosh 1951) of tree species for predefined spatial units. We chose to calculate IVs for each section (1.6×1.6 km); each section contained six to eight witness trees. The IV is the mean of the relative density (number of trees of a species divided by the number of all trees) and the relative basal area (basal area of a tree species divided by the basal area of all tree species). Conceptually, the IV can be thought of as the relative contribution of a species to the forest canopy (Curtis 1959). Calculating the IV allowed us to compare presettlement forest canopy with current forest cover classified from satellite imagery. A 3-km buffer surrounding our study area was included in this analysis to avoid small spatial units where the Pine Barrens boundary intersects section lines. Furthermore, average IVs for jack, red, and white pine were summarized along a broad northwest-southeast belt transect across the central Pine Barrens (Fig. 1) to examine the occurrence of different pine species in relation to distance from the Pine Barrens edges.

The next task was to combine tree distance and diameter to classify patches of similar vegetation structure in the presettlement vegetation. Tree diameter adds important information for the identification of vegetation structure. For example, oaks can occur in areas of stand-replacing fires, where they resprout, and in savannas of mature bur oak that are large enough to survive ground fires because of their thick bark. Species information alone cannot separate these two vegetation types, but they can be distinguished when diameter information is added. We converted the interpolated GLO point data, similar to the tree species abundance map and also with 798×798 m grid cells but used diameter and tree distance of the first witness tree as attributes for two resulting grids. We then classified tree diameter and tree distance into five classes each and combined the two grids. The final grid was classified into five ecological classes (Table 1).

The last question was the density of the presettlement forests. Tree distance is inversely correlated to forest density. Formulas to derive density from distance measurements have been developed (Cottam and Curtis 1956). We applied these formulas to sections that were dominated by jack pine at presettlement times. We decided to use only jack pine dominated stands for the comparison between presettlement and current forest density, because other mixed stands have no equivalent in the current landscape.

Current vegetation assessment

The assessment of the current vegetation cover was based on a forest tree species classification derived from multitemporal Landsat satellite data by Wolter et al. (1995). This classification (28.5×28.5 m resolution) achieved an overall accuracy of 83% at the tree species level, by identifying phenological changes of different tree species throughout spring and fall in a sequence of satellite images (Wolter et al. 1995). We processed the satellite data so that it could

³He, H.S., Mladenoff, D.J., Wockner, G., Sickley, T., and Guntenspergen, G. Using GIS to analyze pre-European forest from land survey records at varied scales. In preparation.

Table 1. Combination of tree diameter and distance information for the assignment of vegetation types.

Tree distance (m)	Tree diameter (cm)				
	<10	10–18	18–22	22–26	>26
>1000	Prairie	Prairie	Prairie	Prairie	Prairie
100–1000	Prairie	Prairie	Savanna	Savanna	Savanna
10–100	Prairie	Savanna	Savanna	Savanna	Savanna
6.5–10	Fire regeneration	Woodland	Woodland	Woodland	Woodland
<6.5	Fire regeneration	Fire regeneration	Closed forest	Closed forest	Closed forest

Table 2. Transition matrix showing changes in tree species abundance (area in ha) between presettlement times and today.

Current vegetation type	Presettlement vegetation type								
	Jack pine	Red pine	White pine	“Pine” in GLO	Other conifers	Oaks	Aspen	Other hardwoods	No trees
Jack pine	79 091	21 460	3 439	6 177	2 038	2 356	1 083	1 274	2 484
Red pine	10 062	3 439	1 210	64	446	764	446	509	127
Other conifers	7 833	6 241	2 165	0	7 196	700	892	2 101	255
Oak	31 012	22 798	7 833	2 292	4 394	7 896	3 948	6 686	446
Aspen	18 658	20 059	10 826	955	11 080	7 769	5 031	8 979	828
Other hardwoods	11 781	13 946	4 712	1 592	4 330	3 885	3 184	11 717	64
No trees	1 910	892	191	127	127	127	64	255	191

Note: Presettlement vegetation type was based on the interpolation of the first witness tree species; current tree species abundance on the most frequent tree species in the satellite image classification. Both values were assessed using 798×798 m grid cells as smallest spatial units.

be compared with the tree species abundance and the IV estimates that we derived from the GLO data.

Occurrence of the most common tree species in the current landscape was assessed for 798×798 m cells by resampling the satellite classification and assigning the most common tree species to the coarser cells. Each estimate is based on 784 pixels in the satellite classification. The attribute “no forest” was only assigned when no pixel in the satellite classification contained forest.

The relative importance of tree species in the current vegetation was calculated for each section. The polygons of the section boundaries were used to extract the corresponding areas from the satellite classification and to compute the percentage of single tree species relative to all forested pixels in the section.

Change detection

The resampling of the satellite classification was necessary to make it comparable to the coarser GLO data. By adapting the scale of the satellite classification, both could be combined to derive a transition matrix, quantifying the change from presettlement to current tree species abundance.

We also combined the maps of the relative abundance of tree species in GLO and satellite data. The difference between GLO IV and relative importance of a tree species in the satellite data identified spatial patterns of species increase and decrease. In a small portion of the southern Pine Barrens (14 000 ha), where the GLO surveyor (H. Maddin) did not distinguish among pine species, the IV of generic pine was assigned equally to jack pine and red pine.

Current forest density

The forest density estimates for jack pine derived from the GLO data (see above) were compared with current jack pine stand density data derived from the Forest Inventory Analysis database (FIA; Hahn and Hansen 1985) to examine changes in forest density. We limited the estimates of number of trees per hectare to trees larger than 10 cm because the GLO surveyors recorded only

trees above this diameter threshold. Jack pine stand densities were derived from repeated measurements of established plots in both the 1983 and the 1996 inventory, to capture some of the variability over time in the current landscape.

Results

Changes of tree species abundance

The tree species abundance maps in presettlement times and today highlight the changes that have occurred in the Pine Barrens throughout this period (Fig. 2). Whereas jack pine was the most extensive tree species in the Pine Barrens before European settlement, it is now more limited to the central and southwestern portion of the Pine Barrens. Red and white pine are no longer widespread, whereas they represented an important component in the presettlement landscape. Hardwood species, especially oaks and aspen, are now present in large areas that used to be pine ecosystems.

Area statistics of different tree species demonstrate that the three pine species were reduced by 149 000 ha, whereas hardwood species have increased by 152 000 ha (Fig. 3). Jack pine decreased by 30%, red pine by 80%, and white pine could not be detected in the satellite classification. The area of oak increased by a factor of 3.6 and aspen by 5.7. However, even these extensive areas do not represent the full magnitude of changes as revealed in the transition matrix (Table 2). For instance, 10 062 ha of current red pine occur in plantations on sites occupied by jack pine at presettlement times but only 3439 ha on sites that were historically occupied by red pine. Most of the current area of oak occurs on former jack pine sites, whereas aspen is more common on sites formerly occupied by red and white pine.

Fig. 2. Tree species abundance (a) at presettlement times and (b) in the current landscape.

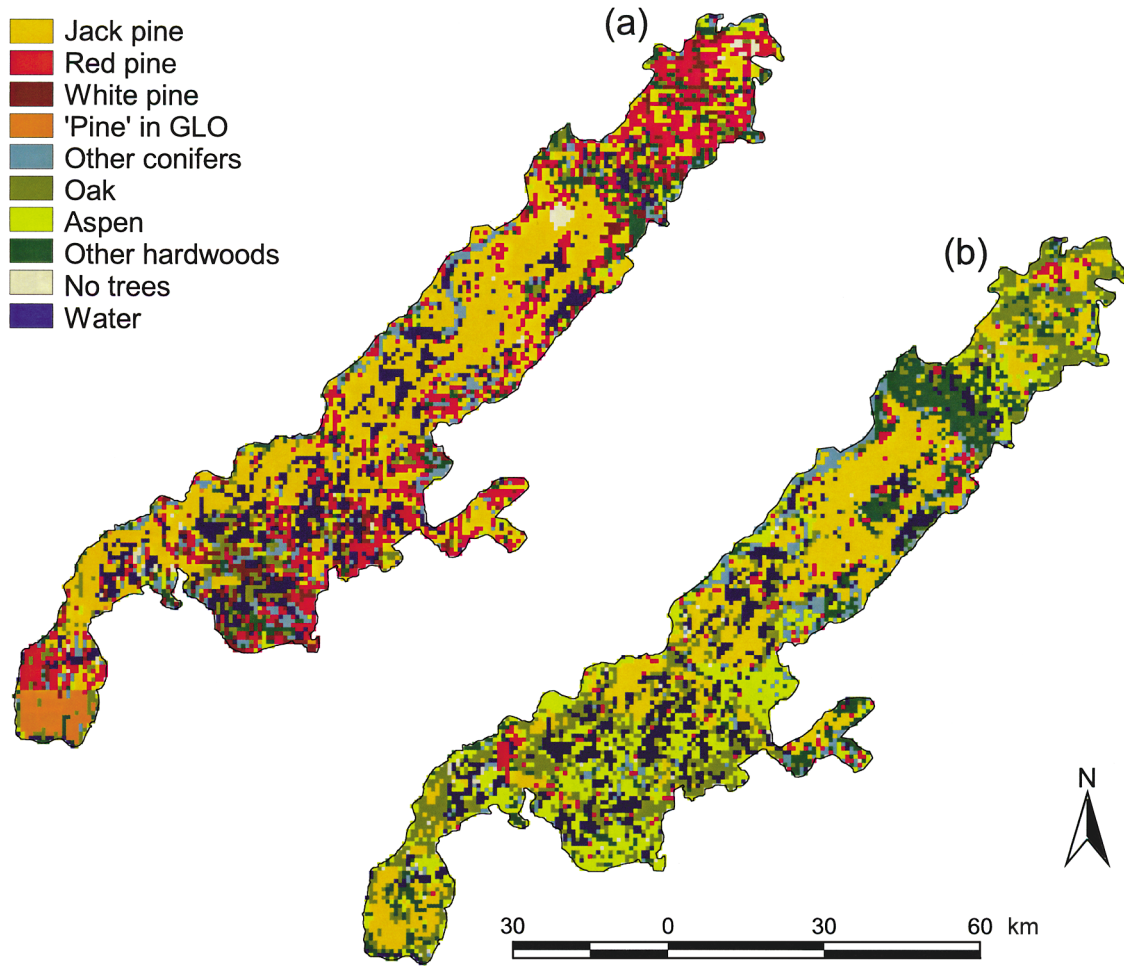
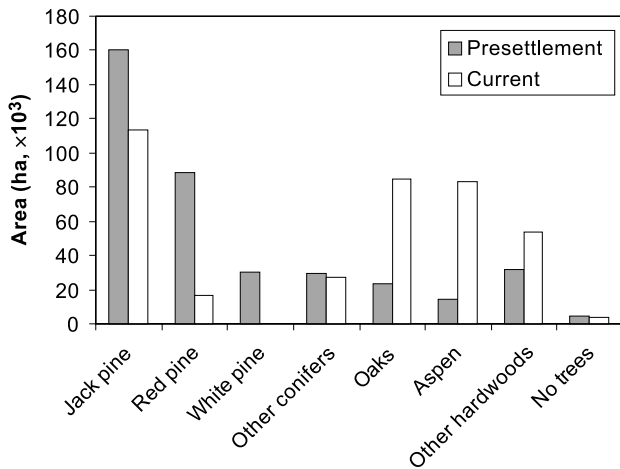


Fig. 3. Changes in area of major tree species and species groups. Other conifers are predominantly white cedar (*Thuja occidentalis* L.), black spruce (*Picea mariana* (Mill.) BSP), tamarack (*Larix laricina* (Du Roi) K. Koch).



Changes of single tree species’ relative importance

The difference between the relative importance values calculated from the GLO data and the percentage of a tree species in the satellite data also reveals strong changes between presettlement times and today (Fig. 4). All pine species decreased, but spatial patterns of their decrease vary. Jack pine decreased mostly in the central Barrens, red pine more in the northeastern and southwestern portions of the study area, and white pine particularly in the south-central portion. Hardwood species generally increased in their abundance within the Pine Barrens, especially oak and aspen species, which exhibited a particular strong increase in the southern and the northern portions of the Pine Barrens. In these areas, oak increased particularly in the core, whereas aspen and the other hardwood species’ increase was strongest along the edges of the study region (Fig. 4).

The spatial distribution of species’ increase and decrease corresponds to spatial pattern present in the GLO data. An example is the distribution of jack, red, and white pine along a broad northwest–southeast belt transect across the central Pine Barrens (Fig. 5). At presettlement times, jack pine was particularly abundant in the center of the transect in the core of the central Pine Barrens. Red pine occurred along the

Fig. 4. Changes in the relative importance of single tree species, using single sections as spatial units for importance value calculations. Positive values indicate an increasing importance value from presettlement to today.

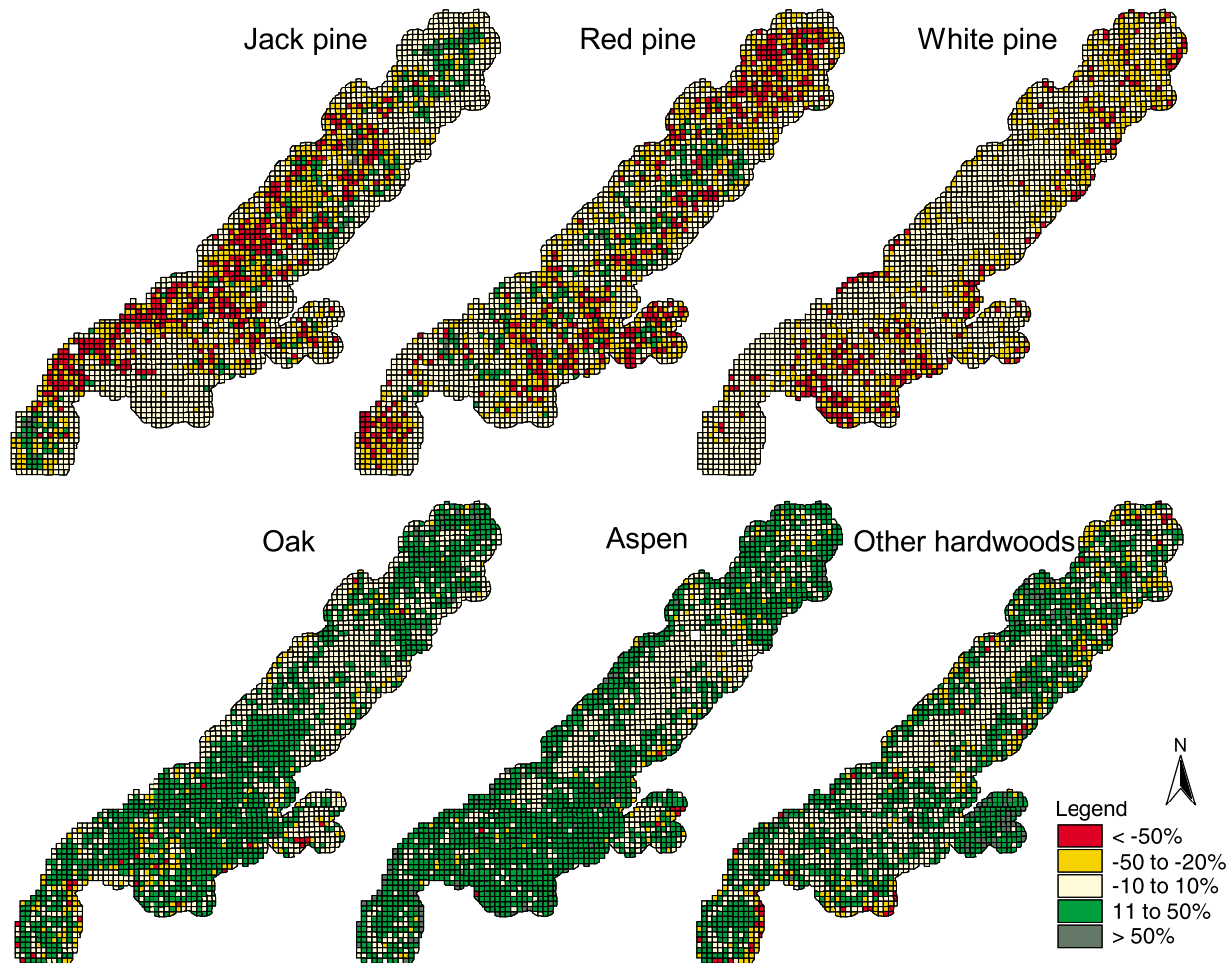
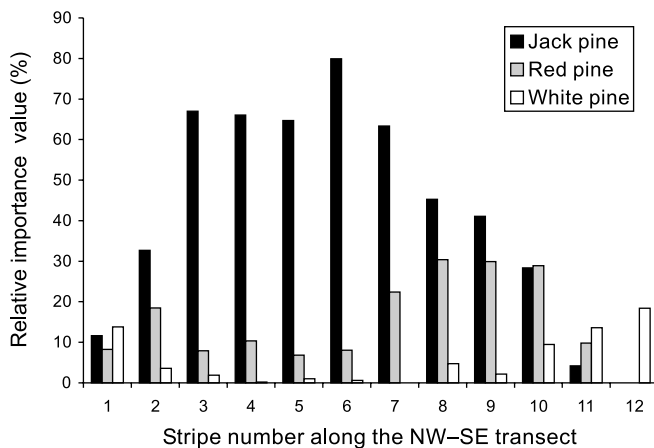


Fig. 5. Relative importance values of jack, red, and white pine in presettlement conditions in a broad NW–SE transect across the central Pine Barrens. Strip 1 is the northwesternmost along the transect, and strip 12 is at the southeastern border of the Pine Barrens (refer to Fig. 1 for location of transect and strips).



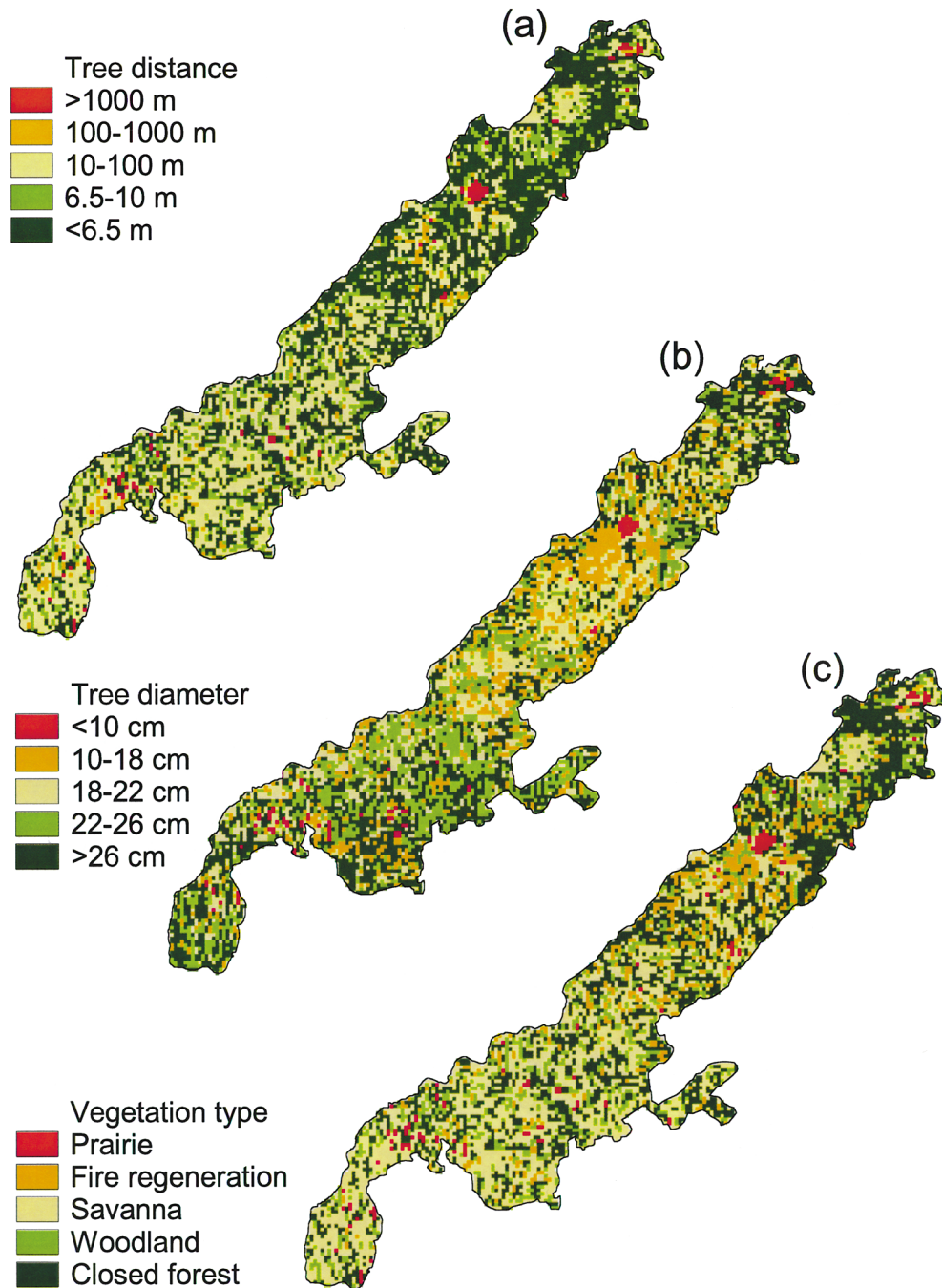
entire transect but was of only negligible importance in the core. However, red pine represented 30–40% of all pines at both transect ends, at the edge of the Pine Barrens, and this was also the area where white pine occurred. This distribution of jack, red, and white pine in the presettlement landscape was reflected in the change maps (Fig. 4). Areas of strong jack pine decrease were in the core of the central Pine Barrens, but red and white pine decrease occurred predominantly along the edges.

Vegetation structure in the presettlement landscape

We reconstructed the vegetation structure at presettlement times from the GLO data on tree diameter and tree distance (Fig. 6). Tree distances exhibited a gradient throughout the Pine Barrens, with distances being smallest in the northeast and largest in the southwest (Fig. 6a). Tree diameters were smallest in the central Pine Barrens but largest both in the southern half and in the northeastern portion of our study area (Fig. 6b).

The map of combined tree diameters and distances highlights patches of similar vegetation structure (Fig. 6c). Combining these two tree attributes allowed separating, for

Fig. 6. Presettlement distribution of (a) tree distances, (b) tree diameters, and (c) vegetation types (for class definitions, see Table 1). The areas mapped as “prairie” also contain few marshes in the southern Pine Barrens, where no trees were recorded.



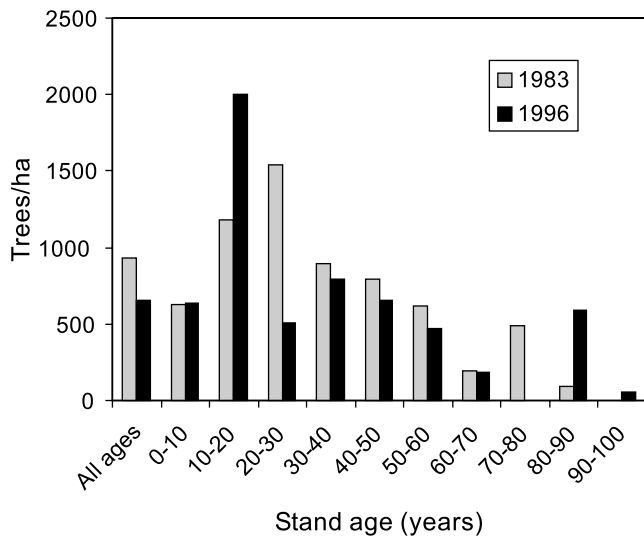
instance, areas of dense regeneration after fire, where tree distances and tree diameters are small, from closed mature forest, where tree distances are small, but tree diameters are larger. The vegetation structure map shows large patches of fire regeneration and of closed forests in the northern half of the Pine Barrens, whereas the southern portion contained more savanna and more localized spatial variation.

Forest density

The mean density of jack pine dominated forests in the Pine Barrens at presettlement times was 937 trees/ha. This value is almost identical to the mean pine stand density in

the FIA data of 1983 (927 trees/ha) but higher than 1996 FIA data (656 trees/ha). Salvage cutting due to a jack pine budworm outbreak from 1991 to 1995 may be mostly responsible for the changing stand density in the FIA data (Radeloff et al. 1999b). The classification of the FIA forest densities by age showed strong differences among age-classes (Fig. 7). Highest jack pine stand density occurred in the 10- to 20-year-old age-class (1999 trees/ha in 1996) and lowest in the 90- to 100-year-old age-class (55 trees/ha in 1996). Variability in jack pine stand density in the GLO data was also high (minimum 1.5 trees/ha, maximum 16 816). Furthermore, the frequency distribution of all jack pine

Fig. 7. Stand density in jack pine dominated stands in the 1983 and 1996 FIA data.



dominated sections was highly skewed; half of all sections exhibited densities of less than 375 trees/ha. Spatial pattern of presettlement density was not random but followed a broad gradient with dense forests in the northeast, and more open forests in the southwest.

Discussion

Ecological significance of the observed changes

Our results revealed major changes in tree species abundance and relative importance from presettlement times to today. The results were consistent for the two types of analysis that we performed, indicating that the changes are not merely a result of the scale and the methods we employed. What is the ecological significance of these changes? We suggest that fire regimes of varying intensity and frequency created a unique ecosystem and areas of open habitat in the presettlement Pine Barrens (Radeloff et al. 1998). The original open pine barrens ecosystem is now limited to a handful of restoration sites, managed by the WDNR (WDNR 1995) and the Chequamegon National Forest (Vora 1993), where prescribed fires prevent forest succession (Radeloff 1999c). These sites are too small to maintain the entire range of successional stages, vegetation structure, and landscape mosaic that existed previously. For example, red pine savannas have almost entirely vanished.

The changes that we detected are the result of many factors, alterations in fire regimes being only one of them. However, fire was likely the single most important factor that shaped the presettlement Pine Barrens. Jack pine regeneration after stand-replacing fires in the central Barrens resulted in very dense, "dog-haired," stands (up to 16 800 trees/ha), much denser than current jack pine plantations. On the other hand, frequent, low-intensity ground fires shaped savanna conditions in the southwest, resulting in vegetation with much lower tree densities than those currently found.

Another probable effect of fire visible in the presettlement Pine Barrens landscape is the distribution of jack, red, and white pine in the central Pine Barrens. The overall domi-

nance of jack pine in the landscape, an early successional and fire-adapted species, suggests that fire disturbance was common. We assume that, because of substrate homogeneity, fire was the dominant factor controlling differences in tree species spatial pattern. Sites in the center of the outwash plain were most likely to have fires spreading into them. The mesic northern hardwood forests neighboring the Pine Barrens were less likely to burn, and therefore, sites at the border of the Pine Barrens had a lower likelihood of fire. This interpretation is supported by the distribution of the three pine species along a transect crossing the central Pine Barrens (Fig. 5). Jack pine is the most fire adapted of the three pine species because of its serotinous cones and the ability to regenerate strongly on burned sites. Accordingly, jack pine is most dominant in the center of the transect, where fires were most likely to occur. Red pine is not adapted to crown fires but can survive ground fires because of its thick bark. It occurs closer to the end of the transect, where fires may have been less frequent because of the neighboring mesic forests. White pine is the least fire adapted pine species in our study area and occurs most where fires were least common, and therefore, the shade-intolerant jack pine was less able to compete.

One point in time versus historic range of variability

When interpreting our results, it must be considered that we were only able to analyze two points in time. Both the current and the presettlement ecosystem were not static but exhibited ranges of variability. The major disturbance during presettlement times was fire, and fire regimes varied through time, following long-term climatic patterns (Clark 1990; Davis 1993). It is unclear to what extent native Americans initiated fires in the Pine Barrens. When different tribes settled in the Pine Barrens, they most likely differed in their use of fire (Clark and Royall 1996). Also, the impact of jack pine budworm (*Choristoneura pinus pinus*) outbreaks on the presettlement landscape is unknown (Volney 1988; Volney and McCullough 1994). However, evidence for spruce budworm (*Choristoneura occidentalis*) in the western United States suggest that budworm defoliation was an important ecological process in conifer ecosystems before European settlement (Swetnam and Lynch 1993). This suggests that jack pine budworm was most likely also part of the presettlement disturbance regime in the Pine Barrens; episodic insect outbreaks may have contributed to higher fuel loads and thus increased fire likelihood and (or) intensity. In the current ecosystem, jack pine budworm outbreaks are a major disturbance force. Salvage cutting of defoliated stands during the most recent outbreak (1990–1995) altered landscape patterns in the central Pine Barrens (Radeloff et al. 1999b).

One question that remains open is whether patch dynamics in the Pine Barrens landscape maintained equilibrium at the landscape scale, or if random catastrophic disturbance events, vast in extent, created nonequilibrium conditions (Sprugel 1991; Turner et al. 1994; Shinneman and Baker 1997). Comparable areas, for instance the 400 000 - ha Boundary Waters Canoe Wilderness Area in northern Minnesota, did not exhibit a steady-state mosaic at presettlement times (Baker 1989). We speculate that the interaction of fire and jack pine budworm defoliation may have resulted in extreme fire conditions and thus episodic catastrophic disturbance

events (McCullough et al. 1998; Radeloff et al. 1999b). The research presented in this manuscript could provide valuable data for modeling disturbance in the Pine Barrens ecosystem in the absence of fire suppression (Potter and Kessell 1980; Baker et al. 1991; He and Mladenoff 1999).

Likely trends

Our analysis did not capture ranges of variability, but the magnitude of change observed over the last 150 years is almost certainly beyond the historic range of variability. Pollen data for the Pine Barrens are scarce but showed strong dominance of jack and (or) red pine and only minor evidence for hardwood species (Wilson 1938).

Furthermore, it is likely that, in the absence of European settlement, the Pine Barrens may have moved towards even stronger abundance of pine species and open habitat across the landscape. Climatic change during this century has exhibited a trend towards warmer and drier conditions and perhaps an increased likelihood of fires (Clark 1990).

Red and white pine were largely removed from the landscape during the early logging phase and the lack of seed sources may be an important factor that limits their natural regeneration today. Fire suppression allowed hardwood species to colonize sites previously covered by pine. Soil quality likely improved because of higher quality leaf litter, providing a positive feedback that may further increase the hardwood component in the landscape. It is unclear which of these factors was most important; however, the combination of these changes has resulted in major landscape changes, and the trend of an increasing hardwood component in the landscape is likely to continue.

Limitations of the data

Careful analysis is crucial when data from different sources are used to detect changes, because differences between data sets are easily confused with landscape changes. The objective of the GLO data was not to survey vegetation but to establish parcel boundaries. Surveyors may have been biased in their selection of witness trees (Manies 1997). Also, the GLO surveyors recorded trees on the ground, whereas the satellite classification is based on canopy reflectance. Species that do not reach the canopy could be part of the GLO surveyor records but will not be detected by a satellite classification. However, forests in the Pine Barrens are relatively simple. The small number of tree species makes surveyor bias less important (Manies 1997) because the number of species they could choose from was limited. Furthermore, the extent of our study area (450 000 ha) surveyed by 17 surveyors makes it less likely that tree species were omitted.

The current forest canopy of the Pine Barrens is mostly single layered. We assume that the jack pine forests that regenerated after stand-replacing fires at presettlement times were also single-layered, which makes the GLO data representative of the forest canopy. The calculation of the relative importance value (IV) from the GLO data was a further step to make GLO data and satellite data more comparable. The IV is based on both relative density and relative basal area. If only relative density was taken into account, species like white pine, which is not very common but large crowned,

would be underrepresented, whereas jack pine and aspen would be overrepresented.

We did not calculate patch statistics using the interpolated GLO data, because we doubt that the GLO data have the necessary spatial resolution to do so in the Pine Barrens. This landscape was dominated by gradients among prairie, savanna, woodland, and closed forest. Defining patches along these gradients would be difficult enough using a vegetation survey designed for such a task; it is probably not feasible using automated methods and the GLO surveyor records.

Jack pine stand density appeared to be almost equal in the presettlement data and current stand inventories when averaged across the Pine Barrens. However, the variability within the presettlement data was high, and density decreases with age. The lack of age information in the GLO data makes comparisons difficult and may have concealed differences between the two periods. Mature jack pine stands in the presettlement landscape might have been less dense, but on average younger, than in the current forests. The presettlement jack pine stand density showed high variability, and few, very dense stands may have caused misleading high mean values. The difference between mean and median presettlement density (937 vs. 375 trees/ha) illustrates this problem.

However, our comparison between GLO data and current satellite classification provides valuable information despite data limitations. The surveyor records allow assessment of large areas with high spatial detail; no other data source can provide such a wealth of information. Furthermore, the magnitude of the changes that occurred since European settlement of the Pine Barrens makes it feasible to compare the presettlement and current landscape using GLO data and a satellite image classification.

Conclusions and management implications

The Pine Barrens have changed dramatically since the beginning of European settlement in the 1850s. The majority of the presettlement landscape was dominated by jack pine and also contained large areas of red pine and oak savannas. Logging removed red and white pine, and fire suppression gave oak, aspen, and other hardwood species a competitive advantage in the previously jack pine dominated landscape. We speculate that the trend of an increasing hardwood component will continue because of fire suppression, current forest management objectives, and soil-quality improvement due to hardwood leaf litter.

The changes in vegetation structure and the general loss of open habitat are detrimental to species adapted to fire-created openings typical of the presettlement landscape. Of special management concern are the endangered Karner blue butterfly (*Lucaedis melissa samuelis*) (WDNR 1995), sharp-tailed grouse (*Pedioecetes phasianellus*) (Hamerstrom 1963), and grassland birds in general, which are not typically found in this forested region and which are currently declining (Mossman et al. 1991; Niemuth 1995). Allocation of future forest harvests to create large openings has been suggested (Borgerding et al. 1995), but it is unclear to what degree forest management actions, such as clearcuts, can fulfill the

ecological role of fire in the presettlement Pine Barrens (Niemuth 1995; Schulte and Niemi 1998). However, such management changes are currently being discussed, and the analysis of the presettlement vegetation and of the changes that have occurred provides an important frame of reference for ecosystem management. This information is one source to consider in the discussion among the public, landowners, and resource managers about the future of this ecosystem (Borgerding et al. 1995).

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