Vegetation development in a southern Maine pitch pine-scrub oak barren[1]

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COPENHEAVER, C. A. (University of Maine, Department of Forest Ecosystem Science, 5755 Nutting Hall, Orono, ME 04469-5755), A. S. WHITE (University of Maine, Department of Forest Ecosystem Science, 5755 Nutting Hall, Orono, ME 04469-5755), AND W. A. PATTERSON III (University of Massachusetts, Department of Forestry and Wildlife Management, Holdsworth Natural Resources Center, Box 34210, Amherst, MA 01003-4210). Vegetation development in a southern Maine pitch pine-scrub oak barren. J. Torrey Bot. Soc. 127:18–32. 2000. We identified factors important to vegetation community distribution within the Waterboro Barrens, an outstanding example of the northern variant of the pitch pine-scrub oak (*Pinus rigida—Quercus ilicifolia*) barrens ecosystem in southern Maine. Plant communities examined included pitch pine-heath, pitch pine-scrub oak, mixed deciduous woodland, scrub oak, and open-canopy pitch pine. We investigated five factors that potentially influence vegetation distribution in the 856-ha preserve: soil texture, moisture, and fertility; topography; and disturbance history. Although analysis of variance revealed significant differences in soils and topography among plots in the five communities studied, multivariate analyses indicated a weak relationship between these environmental variables and species composition and structure. In contrast, disturbance history clearly influenced community and species distribution within the preserve. Effects of historic logging, charcoaling, and cultivation for blueberries persist despite a stand-replacing wildfire that swept through most of barrens in October, 1947. Pollen and charcoal analysis of sediments from a pond near the preserve suggests fire has influenced the barrens for at least the last several centuries, but that prior to European settlement of the area in the 18th century the character of the vegetation differed somewhat from that of today. Our results demonstrate that both fire and edaphic factors have influenced the vegetation of the area, but that historic land use has also played a strong role in determining the present character of the plant communities studied.

Key words: *Pinus rigida*, pine barrens, *Quercus ilicifolia*, Maine, disturbance ecology, land-use history, vegetation distribution.

Pitch pine-scrub oak vegetation is a unique natural ecosystem valued for the rare species of invertebrates that it supports (Widoff 1987). Wildfires historically influenced species composition in barrens of the northeastern United States (Forman 1979). Recurring fires allow fire-adapted, early-successional species such as *Pinus rigida, Quercus ilicifolia,* and *Vaccinium angustifolia* to dominate. Since the mid-1900's, fire regimes throughout the United States have

been altered by fire suppression (Pyne 1982), and although most barrens in the Northeast continue to experience some level of fire most are thought to be in decline due to a lack of burning at historic levels (Widoff 1987).

The Waterboro Barrens (Fig. 1) is part of a larger area in southern Maine that burned during a series of wildfires in 1947. The 1947 fires helped to maintain the area in pitch pine-scrub oak, whereas other barrens areas are being replaced by later successional species (Finton 1998). Fire is not the only factor that influences development of barrens vegetation, however (Motzkin et al. 1996), and management activities that focus solely on the effects of fire suppression may fail to perpetuate current plant communities and the flora and fauna they support (Motzkin et al., unpbl. data).

In 1992–1993, the Maine Chapter of The Nature Conservancy purchased an 856-ha portion of the Waterboro Barrens with the objective of
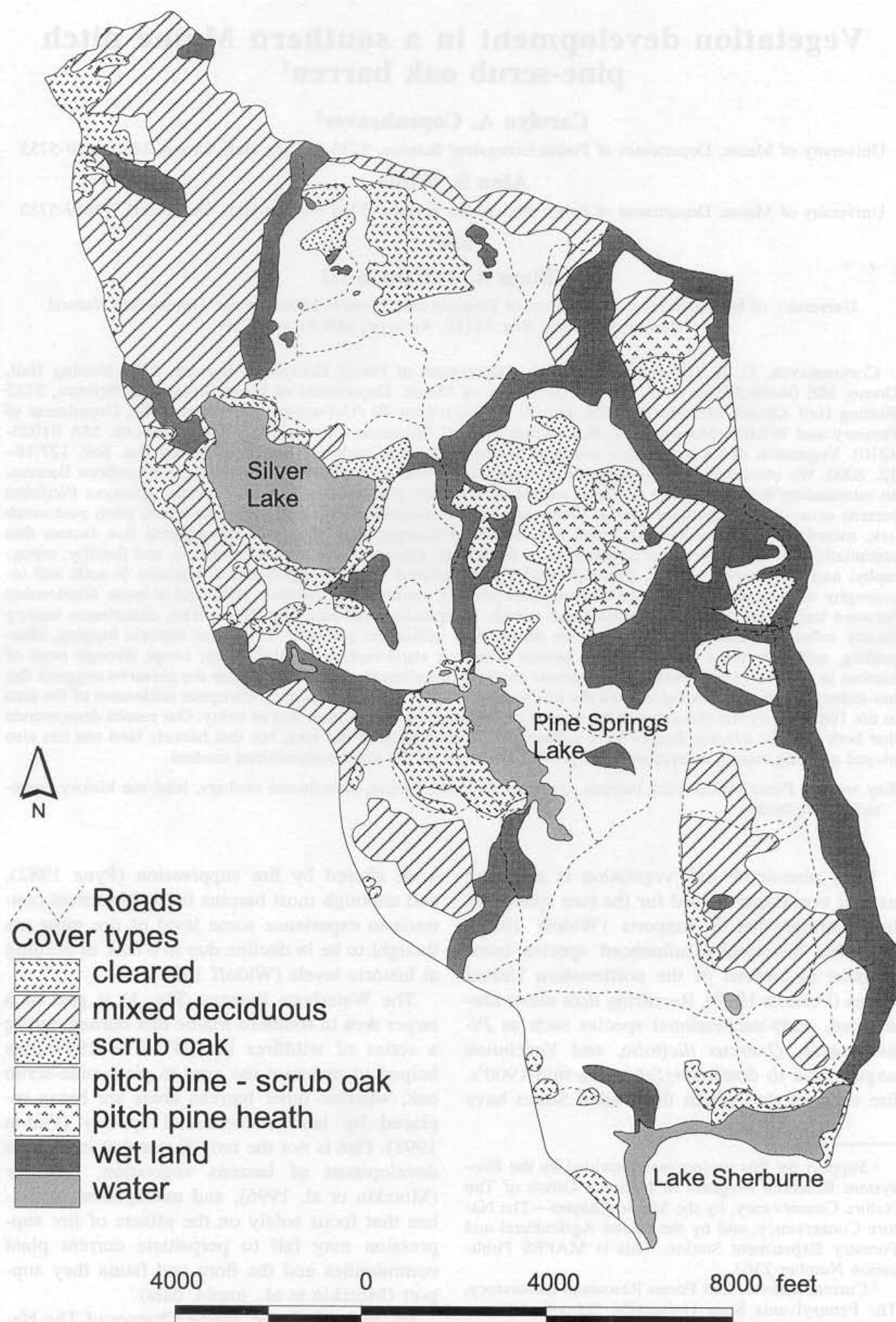
Fig. 1. Vegetation cover type map for the Waterboro Barrens in southern Maine based on 1991 aerial photographs.

maintaining the pitch pine-scrub oak ecosystem. Such an undertaking requires a thorough understanding of the factors responsible for the distribution and development of modern plant communities. Our objective was to examine factors, including soils, topography, and disturbance history, that are widely thought to influence vegetation distribution and development, and to determine how these factors might account for the present character of the vegetation at the Waterboro Barrens. Because the area burned in wildfires fifty years ago and fire suppression has effectively excluded fire since that time, the Waterboro Barrens provides an outstanding opportunity to hold wildfire occurrence and suppression constant for an area as a whole, while studying the effects of soils, topography, and historic land use activities on vegetation development in a large, intact, pine barrens ecosystem.

The distribution of vegetation types across a landscape depends on the factors responsible for the development of individual stands or plant communities. Determinants of vegetation distribution (and by implication, vegetation development) have been assessed for many different ecosystems. Vegetation distribution of pine communities depends on many factors (Richardson and Bond 1991; Barton 1993) including edaphic (Roman et al. 1985; Whitney 1991; Zampella et al. 1992) and climatic factors (Denton and Barnes 1987), and disturbance (Abrams and Nowacki 1992; Bratton and Miller 1994, Latham et al. 1996). For this study, we evaluate the importance of soil (type, moisture, and fertility), local topography (slope, aspect, and elevation), and disturbance (land-use history) as factors influencing the development and current vegetation distribution within the Waterboro Barrens pitch pine-scrub oak ecosystem. We examine long-term patterns of vegetation change by analyzing vegetation cover type maps from 1940 to 1991 using a Geographic Information System (GIS). Fossil pollen and charcoal analysis of sediments from a small pond within the Barrens provide a historic context within which recent vegetation change can be evaluated (Patterson 1993).

Methods. STUDY AREA. The Waterboro Barrens is 45 km west of Portland, in the towns of Waterboro and Shapleigh, York County, Maine. Coarse, infertile, glacially-deposited sand underlies a majority of the preserve. Seventy-five percent of the site is classified as Adams loamy sand with minor coverage by other soil types on the higher elevations and in swampy areas (Flewelling and Lisante 1982). Annual precipitation is approximately 108 cm (NOAA 1993a); mean summer temperature is 18.8°C; and mean winter temperature is −3.3°C (NOAA 1993b).

The Nature Conservancy conducted a preliminary vegetation survey of the Waterboro Barrens and identified nine communities, based on species composition and structure, including three wetland types (Harris 1991). We limited our sampling to Harris' five successionally-related, upland, communities (as determined by Windisch 1992): pitch pine-heath, pitch pine-scrub oak, mixed deciduous, scrub oak, and open-canopy pitch pine. We did not evaluate Harris' sixth upland community—grassy openings—because, although they have been important historically at Waterboro, few good examples remain in the Barrens.

FIELD PLOTS. Within the five communities, we established a total of 60 permanently marked, 10 × 10 m vegetation plots. All were located on soils categorized as Adams loamy sand. Each community was sampled proportional to the area of that community within the whole preserve because of the likelihood that variability was larger in covertypes that spanned larger geographic areas. We included a minimum of five plots within each community. Randomly generated plot locations were rejected if they occurred within 35 m of roads, trails, or previously selected plot locations. Plots were allocated to communities as follows: pitch pine-scrub oak (30), mixed deciduous (15), open-canopy pitch pine (5), pitch pine-heath (5), and scrub oak (5).

Species composition and vegetation structure were characterized for each plot from late-May to mid-July in 1994. We recorded diameter at breast height (dbh = 1.37 m) and species for all living trees >3 cm dbh. Tree heights of three co-dominant canopy trees (as defined by Smith 1986) and canopy closure (using a spherical densiometer) were measured. Increment cores taken at breast height from the three largest (dbh) trees were sanded, and annual rings counted to determine approximate stand ages. Litter depth was measured at each site by inserting a probe into the litter layer until the resistance of the partially decayed duff layer was felt. A variation of the point-intercept method was used to determine species cover. At each plot we established a 1 m × 1 m grid over the entire plot and recorded all woody and herbaceous species that were intercepted by an imaginary vertical line

projected from each of the 121 grid intersections. Data were recorded for three height classes (0 to 0.5 m, 0.5 to 3 m, and >3 m). Nomenclature follows Gleason and Cronquist (1991).

Samples for soil texture analysis and fertility determination were collected. We used a screw auger to a depth of 60 cm at five locations on all plots to test for textural discontinuity or evidence of a plow layer. The University of Maine Plant, Soils, and Environmental Sciences Analytical Laboratory analyzed soil fertility from the organic horizon and the top 15 cm of the mineral soil on a subset of 38 plots. At each of the 38 plots, we collected soil from 5 locations within the plot and combined these into one sample for analysis. The soil pH was measured in distilled water. Available P was extracted using the Modified Morgan Procedure (Westerman 1990) and measured by plasma emission. Ca, K, Mg, and Na were extracted in 1 N ammonium chloride. K and Na were measured by flame emission, while Ca and Mg were measured by plasma emission. Total N was measured by the macro-Kjeldahl method (Westerman 1990). Exchangeable acidity was extracted in 1 N KCl and measured by titration. Percent organic matter was measured by loss on ignition (550°C). Cation exchange capacity was estimated by summing milliequivalent levels of the cations and acidity. We measured soil texture on samples from the top 15 cm of soil and the mineral soil below 30 cm on the same 38 plots using a series of different diameter sieves. The sieves separated coarse sand (>500 mm), medium sand (>250 mm), fine sand (>106 mm), and very fine sand (>75 mm). Clay and silt were not separated, because their combined weight was a minor component (<10%).

Five times throughout the 1995 growing season, we measured relative moisture on 38 plots (the same used for fertility and moisture measurements) using a TRASE Model 6050X1 Moisture Measuring System. Comparisons were made on the rank order of the readings.

Soil fertility, soil texture, and plot structure data were compared across communities by an analysis of variance (ANOVA) on the ranked data using SAS (SAS Institute Inc., Cary, NC). We used the ranked data in the ANOVA because the raw data did not meet the assumption of normality. If the ANOVA revealed significant among-cover-type differences, we performed a protected least significant differences (LSD) means separation. We conducted principle com-

ponents analysis (PCA), canonical correspondence analysis (CCA), and redundancy analysis (RA) using CANOCO (Microcomputer Power, Ithaca, NY) on the vegetation and environmental variables from the 60 plots, as well as the subset of 38 plots for which soil texture, fertility, and moisture data were available. We opted for these analyses of the vegetation data because they use a linear model; the environmental gradient within the Waterboro Barrens is very short and thus the vegetation should take on a linear distribution rather than the normal distribution seen on longer environmental gradients.

LAND-USE HISTORY. We used town histories, maps, and deed research to establish historical land ownership on the preserve. Historical land use was researched through the agricultural census data collected by the State of Maine Department of Agriculture, available in the Maine State Archives for the years 1850, 1860, 1870, and 1880.

GIS DATABASE SAMPLING. Roads, hydrology, and vegetation cover types (based on interpretation of aerial photographs from 1940, 1950, 1960, 1970, 1975, and 1991) were recorded in a geographic information system (GIS) data base (ARC-Info format) by Sewall Company of Old Town, Maine. The Maine Chapter of The Nature Conservancy provided these data. To this database we added the GPS locations of our 60 field plots as well as topography and soil type (Flewelling and Lisante 1982) information for the study area. These coverages were overlaid for analysis of the relationship between vegetation, topography, and soils over time.

POLLEN ANALYSIS. Pine barrens are inherently dry, and thus good sites for fossil preservation (i.e. ponds and bogs are rare). We investigated a small pond in the southern portion of the barrens, but found that it had little sediment. A shallow, seasonally dry wetland to the northwest (referred to here as Newfield Marsh—see Fig. 1) did contain sediments, which we cored with a piston-equipped plastic tube. The 35-cm long core was sampled in 1-cm intervals, with samples processed for pollen and charcoal analysis using standard acetolysis procedures (Faegri and Iversen 1975). Three-hundred-grain counts of fossil pollen, and grid counts for charcoal (Patterson et al. 1987), for adjacent samples through the upper 20 cm of the core provided a record of fire occurrence and vegetation change over the past several centuries for the area surround-

Table 1. Species at the Waterboro Barrens with mean cover greater than 10% or mean frequency greater than 40%. The cover and frequency values are from the dominant height class for each species (either 0 to 0.5 m, 0.5 to 3 m, or greater than 3 m) and are mean values for each of the five communities.

Species	Mixed deciduous		Open-canopy pitch pine		Pitch pine heath		Pitch pine-scrub oak		Scrub oak	
	Cover (%)	Freq. (%)	Cover (%)	Freq. (%)	Cover (%)	Freq. (%)	Cover (%)	Freq. (%)	Cover (%)	Freq. (%)
Species over 3 m tall										
Acer rubrum	12.3	47	0	0	0	0	0.8	17	0	0
Pinus rigida	18.0	73	37.7	20	97.3	100	63.0	100	16.1	100
Populus tremuloides	13.6	40	0	0	0	0	0.1	7	0	0
Prunus pensylvanica	5.0	40	0	0	0	0	0.1	3	0	0
Species 0.5 to 3 m tall										
Amelanchier spp.	2.4	20	23.2	60	5.6	20	0.4	7	0.5	40
Betula populifolia	21.4	80	4.4	20	0	0	10.8	67	1.3	20
Pteridium aquilinum	16.8	73	1.3	60	0	0	20.9	80	12.0	40
Quercus ilicifolia	40.2	100	4.3	100	1.2	40	52.2	100	77.7	100
Species under 0.5 m tall										
Carex spp.	10.5	93	6.9	60	2.6	80	6.0	83	18.5	80
Comptonia peregrina	2.2	40	3.6	100	0	0	1.5	50	1.5	80
Gaultheria procumbens	14.0	60	0.7	20	0.2	20	5.3	43	0	0
Kalmia angustifolia	3.9	40	2.9	60	7.5	40	2.5	13	0.3	40
Lysimachia quadrifolia	1.4	47	0	0	0	0	0.1	7	1.0	40
Trientalis borealis	4.4	60	0	0	0.7	40	0.0	3	0	0
Vaccinium angustifolia	43.6	100	85.6	100	75.3	100	67.3	97	56.2	80

ing the site. Although imprecise with respect to site-specific vegetation development and fire history, fossil data helped to extend our understanding of the history of vegetation of the Waterboro Barrens to the period prior to the arrival of Europeans (before ca. 1750 AD).

Results. SPECIES COMPOSITION OF COMMUNITIES. An upper canopy of hardwood species with a minor *Pinus rigida* component characterized the mixed deciduous community. The most common overstory hardwoods were *Acer rubrum, Betula populifolia,* and *Populus tremuloides* with the subcanopy dominated by *Quercus ilicifolia.* The understory contained *Comptonia peregrina, Gaultheria procumbens, Kalmia angustifolia, Lysimachia quadrifolia, Pteridium aquilinum, Trientalis borealis,* and *Vaccinium angustifolium* (Table 1).

Open-canopy pitch pine stands were dominated by widely-spaced, open-grown *Pinus rigida.* The branches typically grew from the crown to the base with the bottom branches often lying on the ground. The shrub layer beneath canopy trees was unusual compared to the other communities, because *Quercus ilicifolia* was largely absent. Species present included *Amelanchier* spp., *Comptonia peregrina, Kalmia angustifolia,* and *Vaccinium angustifolium* (Table 1).

The canopy of the pitch pine-heath community was almost exclusively dense *Pinus rigida.*

Most trees originated after the 1947 fire, but there were scattered older individuals that probably acted as a seed source for the existing stand. Little subcanopy existed, but there was a thick heath-like ground cover of *Amelanchier* spp., *Kalmia angustifolia,* and *Vaccinium angustifolium* (Table 1).

The pitch pine-scrub oak community had an upper canopy of *Pinus rigida* and a subcanopy of *Quercus ilicifolia.* The understory vegetation was characterized by *Comptonia peregrina, Gaultheria procumbens, Pteridium aquilinum,* and *Vaccinium angustifolium* (Table 1).

The scrub oak community had scattered *Pinus rigida* in a dense thicket of *Quercus ilicifolia.* The ground cover was sparse compared to the other communities and had frequent patches of litter. Major understory species included *Amelanchier* spp., *Comptonia peregrina, Kalmia angustifolia, Pteridium aquilinum,* and *Vaccinium angustifolium* (Table 1).

STRUCTURE. The distribution of diameter classes for living trees >3 cm dbh varied significantly among the communities ($\chi^2 = 9.488$, d.f. $= 5$, $P < 0.05$). The pitch pine-heath, mixed deciduous, scrub oak, and pitch pine-scrub oak types all exhibited reverse J-shaped diameter distributions. In contrast, the open-canopy pitch pine had increasing numbers of stems in the larger diameter classes.

Table 2. Mean canopy height, canopy closure, and litter depth by community for 60 plots sampled at the Waterboro Barrens, Maine. All three measurements showed significant differences between communities. The protected LSD mean separation classes are in parentheses after the values. Values in a column followed by the same letter are not statistically different.

Community	Canopy height (m)	Canopy closure (%)	Litter depth (cm)
mixed deciduous	12.3 (a)	88 (ab)	3.2 (b)
open-canopy pitch pine	10.8 (ba)	44 (c)	3.3 (b)
pitch pine heath	10.5 (ba)	95 (a)	4.3 (a)
pitch pine-scrub oak	9.8 (b)	85 (b)	3.9 (a)
scrub oak	5.0 (c)	62 (c)	3.5 (ab)

The communities differed significantly in canopy height ($P = 0.002$), canopy closure ($P = 0.000$), and litter depth ($P = 0.014$) (Table 2). The mixed deciduous type had the tallest mean canopy height, but this was not significantly taller than the pitch pine-heath or the open-canopy pitch pine. Scrub oak was the shortest. Pitch pine-heath had the highest mean canopy closure, but this was not significantly different from the mixed deciduous community. Open-canopy pitch pine had the lowest canopy closure, which was not significantly different from the scrub oak.

The pitch pine heath community had the greatest mean litter depth, which was not significantly different from that of pitch pine-scrub oak and scrub oak. The mixed deciduous type had the shallowest litter layer, which was not significantly different from the open-canopy pitch pine or the scrub oak.

Soil Characteristics. The organic horizon always had a higher fertility and lower pH than the mineral soil. The mixed deciduous community generally had higher soil nutrient levels than the other four communities and the scrub oak community usually had the lowest soil fertility. Analyses showed significant differences among communities for 13 variables, seven in the mineral soil [pH ($P = 0.000$), Ca ($P = 0.001$), Mg ($P = 0.001$), P ($P = 0.010$), CEC ($P = 0.044$), percent organic matter ($P = 0.012$), total N ($P = 0.010$)] and six in the organic horizon (Ca, Mg, P, CEC, total N, and K) (Fig. 2).

The soil depth to textural discontinuity test revealed that only one plot (in the mixed deciduous community) out of 60 had a plow layer. Seven plots (two in the mixed deciduous and five in the pitch pine-scrub oak) had layers of gravel starting at 15 to 60 cm depth. Soil texture analysis showed an increase in coarseness with an increase in sample depth in all communities (Table 3). Samples from mixed deciduous and pitch pine-scrub oak types had higher percentages of coarse sand than did the other three communities. This appeared to be due to a lower percentage of fine and very fine sand. Six significant differences in soil texture among communities occurred for coarse sand at >30 cm, fine sand at >30 cm, very fine sand at >30 cm, coarse sand at <15 cm, fine sand at <15 cm, and very fine sand at <15 cm.

Soil moisture was consistently higher at shallow depths. The mixed deciduous plots generally had statistically the highest moisture content and pitch pine-scrub oak the lowest (data not shown).

Multivariate Analyses. Principle components analysis (PCA) of the 60 plots revealed some separation of communities (Fig. 3). The mixed deciduous plots are in the upper half of the figure along with deciduous species such as *Acer rubrum* (Acru) and *Prunus pensylvanica* (Prpe). The pitch pine-heath plots are on the left of the figure near the location of *Vaccinium angustifolium* (Vaan) and *Pinus rigida* (Piri). Pitch pine-scrub oak plots are located in the lower half of the figure between *Pinus rigida*, on the left, and *Quercus ilicifolium* (Quil), on the right. The scrub oak plots are on the right side of the diagram as a result of the abundance of *Quercus ilicifolia*.

CCA and RA, which included environmental (soil texture, soil fertility, soil moisture, slope and aspect) and species data, showed no clustering by community (data not shown). A majority of the plots were densely located in one quadrant near two of the dominant species, *Pinus rigida* and *Vaccinium angustifolium*.

Land-use History. Prior to European settlement, the Saco-based Sokokis tribe hunted and

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Fig. 2 Mean soil fertility of organic layer samples collected from 38 plots at the Waterboro Barrens, Maine in August 1994. Each of the six factors differed significantly across cover types ($P < 0.05$). Eight mixed deciduous, 5 open-canopy pitch pine, 5 pitch pine heath, 15 pitch pine-scrub oak, and 5 scrub oak plots were sampled.
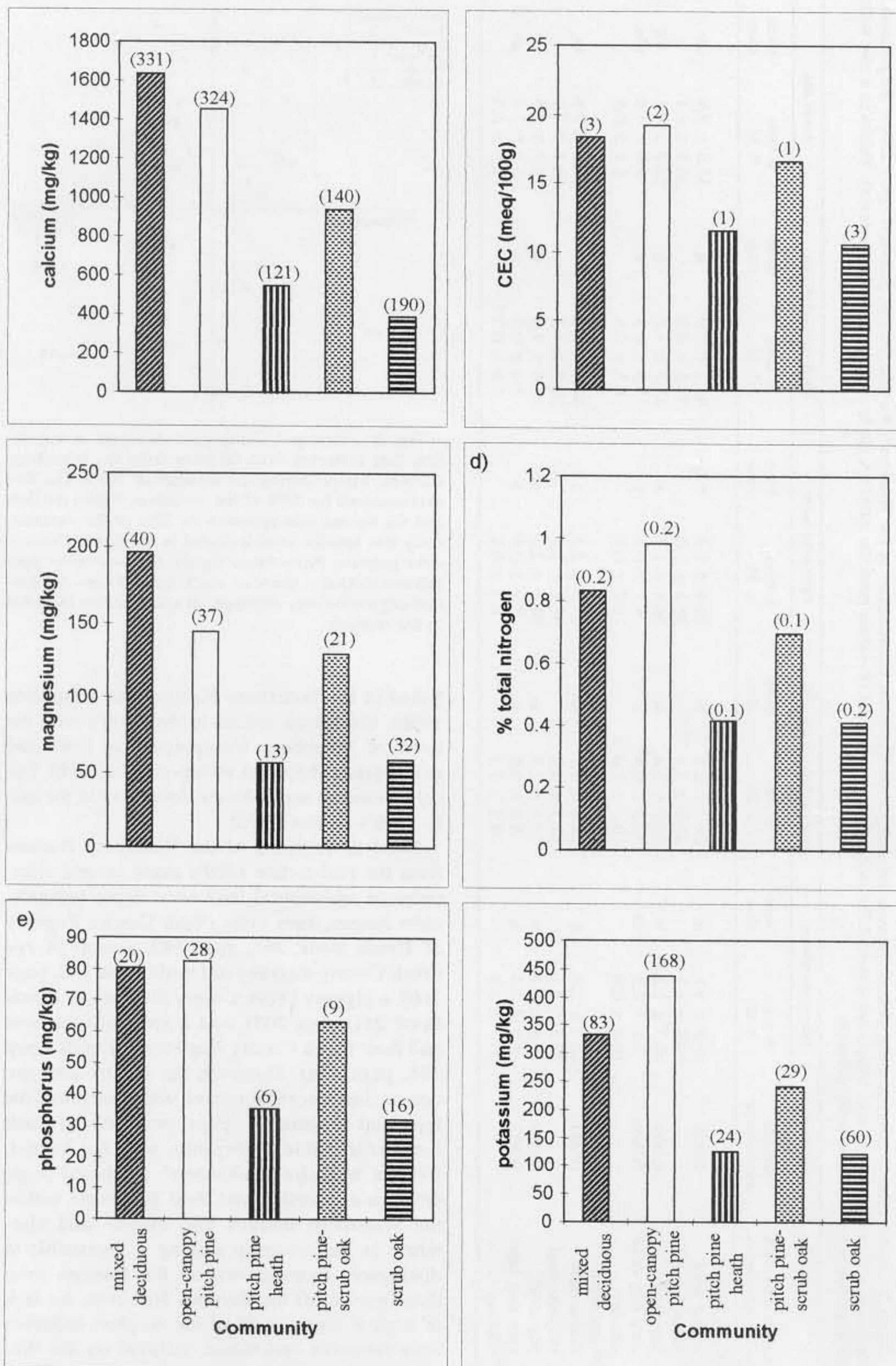
Table 3. Soil texture is given as mean percent by mass for each of the five cover communities at the Waterboro Barrens, Maine. Standard errors follow the percents. The mean separation classes show significant texture differences across cover types (P-values from the ANOVA are located in the second column). Values in a row with the same letter are not statistically different.

| Texture class from two sample depths	Significant P-values between communities	Mixed deciduous % mass ± SE	Mean class	Open-canopy pitch pine % mass ± SE	Mean class	Pitch pine heath % mass ± SE	Mean class	Pitch pine-scrub oak % mass ± SE	Mean class	Scrub oak % mass ± SE	Mean class
15 cm depth											
coarse sand	0.001	39.9 ± 3.1	a	28.7 ± 2.7	b	26.4 ± 1.7	b	41.3 ± 2.0	a	33.8 ± 8.9	ab
medium sand		29.8 ± 1.7		32.0 ± 3.3		34.4 ± 1.0		31.8 ± 0.9		30.8 ± 4.1	
fine sand	0.000	16.3 ± 1.2	b	23.7 ± 1.4	a	26.4 ± 1.7	a	15.7 ± 1.1	b	23.3 ± 8.1	abc
very fine sand	0.006	3.6 ± 0.3	ab	5.3 ± 0.7	c	4.1 ± 0.3	c	3.0 ± 0.3	a	4.0 ± 1.0	abc
silt/clay		10.4 ± 0.9		10.2 ± 1.0		8.7 ± 0.9		8.4 ± 0.6		8.1 ± 0.6	
30 cm depth											
coarse sand	0.000	42.7 ± 2.9	b	29.8 ± 3.7	ac	27.9 ± 2.3	a	46.6 ± 2.8	b	36.1 ± 9.6	bc
medium sand		27.5 ± 2.1		31.7 ± 3.2		33.7 ± 1.3		30.0 ± 1.3		36.1 ± 7.7	
fine sand	0.000	15.4 ± 1.1	b	24.1 ± 2.4	ac	26.2 ± 2.3	ac	13.6 ± 1.2	b	22.7 ± 8.5	bc
very fine sand	0.007	3.6 ± 0.4	b	4.9 ± 0.8	b	3.9 ± 0.4	b	3.0 ± 0.3	a	3.7 ± 1.1	ab
silt/clay		10.7 ± 1.1		9.5 ± 1.3		8.3 ± 0.8		7.5 ± 0.7		7.5 ± 0.4	
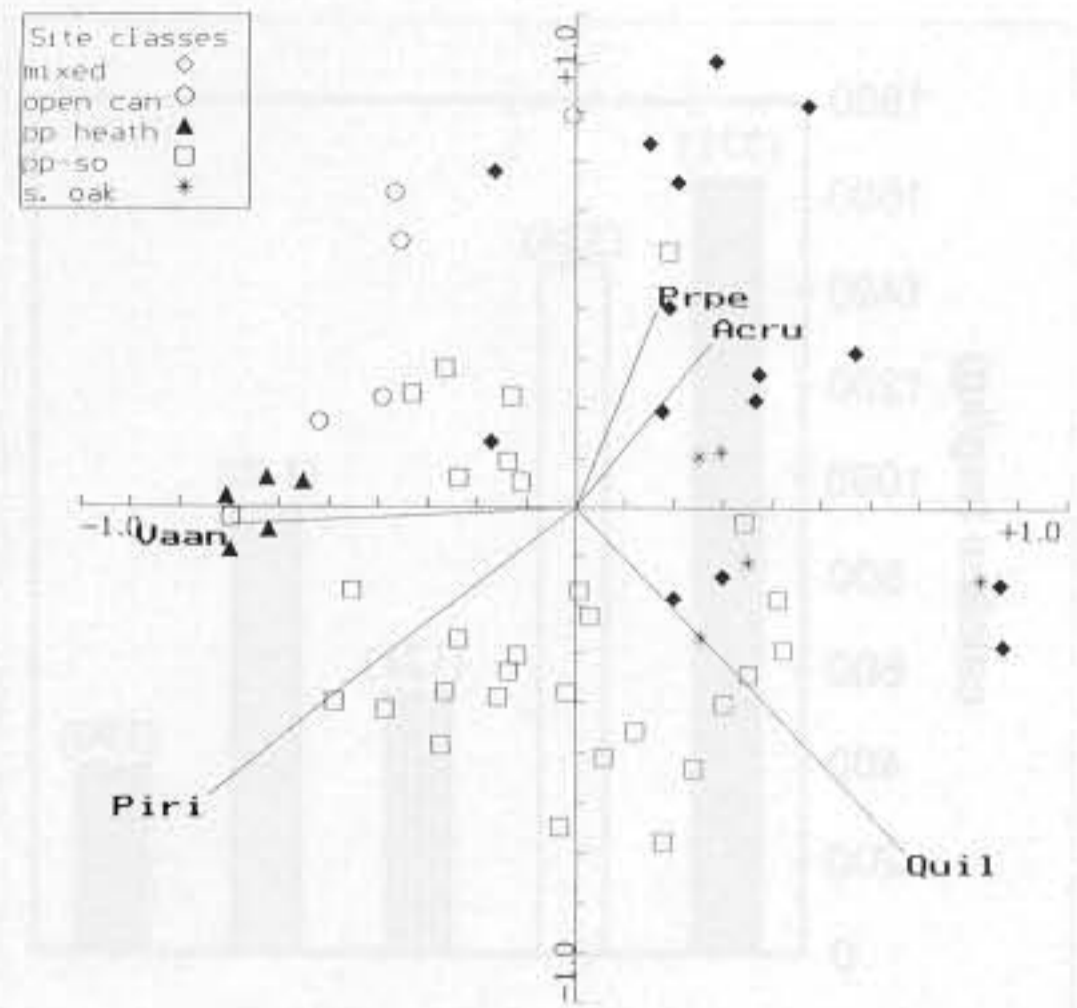
Fig. 3. Principal Component Analysis of vegetation data collected from 60 plots from the Waterboro Barrens, Maine during the summer of 1994. The first axis accounts for 33% of the variations within the data and the second axis accounts for 22% of the variance. Only five species were included in the figure (Acru—*Acer rubrum*, Piri—*Pinus rigida*, Prpe—*Prunus pensylvanica*, Quil—*Quercus ilicifolium*, Vaan—*Vaccinium angustifolium*), although all species were included in the analysis.

fished in the Waterboro Barrens area (Hamilton 1986). Europeans settled in the 1700's with the town of Waterboro incorporated in 1787 and neighboring Shapleigh incorporated in 1785. Local commerce and industry developed in the early 1800's (Libby 1976).

Deed descriptions of the Waterboro Barrens from the mid-to-late 1800's made several references to agricultural land uses: apple orchards, cider houses, corn cribs (York County Registry of Deeds Book 261, page 58), a crop of rye (York County Registry of Deeds Book 312, page 260), a piggery (York County Registry of Deeds Book 241, page 205), and a grist mill for corn and flour (York County Registry of Deeds Book 268, page 414). However, the USDA land-use census data from that period, which recorded the type and amount of crops produced by each landowner within a township, were not helpful. Reports were for landowners' combined properties in a township and most landowers within the Waterboro Barrens also owned land elsewhere in the township making it impossible to distinguish crops grown on the Barrens from those grown off the Barrens. However, the lack of a plow layer on 59 of the 60 plots indicates little intensive agriculture occurred on the Waterboro Barrens.
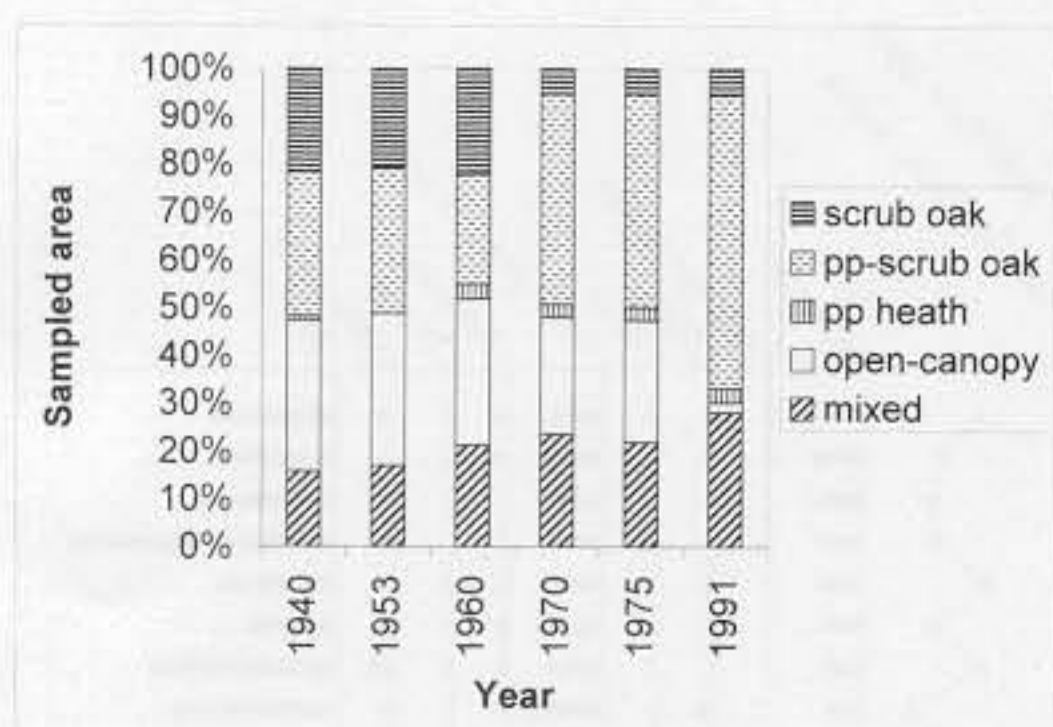
Fig. 4   The present area of the five cover types (mixed deciduous, open-canopy pitch pine, pine health, pitch pine-scrub oak, and scrub oak) at the Waterboro Barrens, Maine, based on GIS coverages created by interpretation of aerial photographs from 1940, 1953, 1970, 1975, and 1991.

Logging however was common. We found several stands with cut stumps in the preserve indicating 20th century logging. Some cutting was for firewood, but the north central section of the preserve contained frequent remnants of charcoal manufacturing pits. Charcoal pits typically consisted of a circular trench about 1 m deep and 8 m in diameter. The trench itself was about 0.5 m wide and encircled a convex, charcoal-rich center.

In the early 1900's, two corporate landowners, Capital Canning Company (123 ha) and Forest Products Company (65 ha), lost their land in the Waterboro Barrens due to non-payment of taxes. During this period, individual landowners likely followed the township-wide trend of decreasing agricultural land-uses. From 1925 to 1940, the farmed area in Waterboro and Shapleigh decreased from 9373 ha to 4208 ha (Washburn 1925; Smith 1940).

In the fall of 1947, a series of fires burned approximately 89,000 ha of forests, fields, and pastures in southwestern and coastal Maine, including much of the Waterboro Barrens (Wilkins 1948). Immediately after the fire, loggers salvaged a portion of the fire-killed logs (Nutting et al. 1949), which may account for some of the stumps that we found, although others clearly represent more recent timber harvesting. Post-fire land use switched from timber harvesting and blueberry cultivation in the early 1900's to recreation and summer homes, which have dominated since 1960.

GIS DATABASE ANALYSIS. GIS analysis revealed four main changes in cover type (Fig. 4).

First, the mixed deciduous cover type almost doubled in area from 1940 to 1991. Second, the pitch pine-scrub oak cover type increased from 30% of the area in 1940 and 1953 to >60% in 1991. The open-canopy pitch pine type decreased by 93% primarily between 1975 and 1991. Open-canopy pitch pine made up a fairly constant proportion (20 to 22%) of the ecosystem from 1940 to 1960, decreased slightly in the 1970's and by 1991 comprised only 1.3%. Finally, the scrub oak cover type declined from >20% during 1940 to 1960, to <7% by 1970 to 1991.

POLLEN ANALYSIS. Pollen and charcoal profiles for the upper 22 cm of Newfield Marsh sediments document changes in fire occurrence and vegetation composition over approximately the past 500 years (Fig. 5). Increases in the abundance of indicators of agricultural activity (chiefly *Ambrosia* and *Rumex*) at a depth of 10 cm in the sediments date the time that settlers moved into the area during the late 18th century (Loring 1983).

The local clearing of pine forests is reflected in the decline, beginning at 10 cm, of total *Pinus* pollen. Charcoal values nearly double (rising from 165 μm to 314 μm) between 11 and 12 cm—just before the rise in agricultural indicators and decline in pine pollen. This suggests that a fire burned the Barrens area just before or in conjunction with the initiation of local logging. Haploxylon *Pinus* pollen (indicating *Pinus strobus*) comprises between one-half and two-thirds of the total *Pinus* pollen before initial logging, but increases to two-thirds to nearly nine-tenths of the total *Pinus* pollen for most post-settlement samples. At the same time, total *Pinus* declines suggesting that locally diploxylon *Pinus* (*Pinus resinosa/Pinus rigida*) were harvested giving way to the regionally more important *Pinus strobus*.

Tsuga canadensis pollen comprises 10–20% of the presettlement pollen with values for *Fagus grandifolia* averaging nearly 5%. Pollen percentages for both species drop by 50% or more with settlement. Both are more typical of mesic than xeric sites; neither tolerates frequent fires well; and both are relatively poor pollen producers. Combined pollen percentages of 15–25% in presettlement sediments suggest more mesic conditions and/or less frequent fires than are known for the area in post-settlement times.

The results of the pollen and charcoal analyses suggest a shift in the vegetation and fire re-
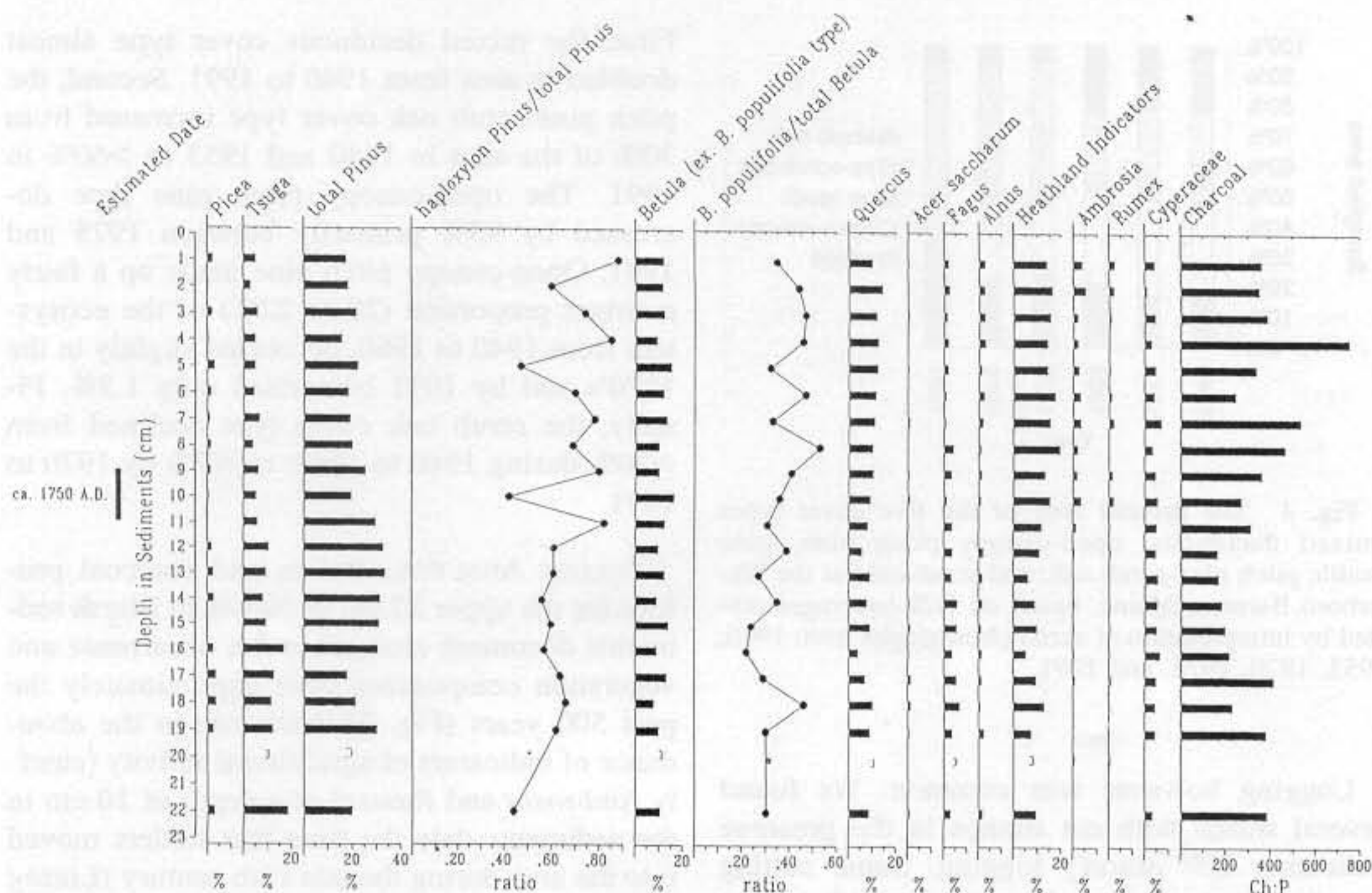
Fig. 5. Charcoal and selected pollen profiles for Newfield Marsh sediments. Pollen data are calculated as a percent of all fossil pollen identified in samples taken at 1-cm intervals from a core obtained in August, 1992.

gimes of the area with settlement. This is supported by detrended correspondence analysis of the pollen data (Fig. 6). DCA locates samples (in this case representing a period of historical time as a function of depth in the sediment core) in the ecological space defined by the abundance of attributes (here, the percentages of different pollen types). For this analysis, we used pollen percentages calculated from a sum that excluded indicators of agricultural activity (i.e. not including *Ambrosia, Rumex, Plantago, Chenopodiaceae,* etc.) The analysis separates presettlement samples from those of younger age. Samples shift from the dominance of *Tsuga, Fagus* and, to a lesser extent, *Pinus,* toward *Betula, Quercus,* and indicators of heathlands. Only sample 11, which represents the pre-/postsettlement transition, is intermediate between these two groups. Prior to European settlement, the analysis documents the shift toward a greater abundance of pine following the fire at 17 cm. The decline in hemlock and increase in pine following this fire are the primary factors responsible for the movement of samples in PCA space (rather than an increase in heath-land indicators, which does not occur until about the time of settlement). Charcoal abundances generally increase with settlement, but fire was also present

before the arrival of Europeans. These presettlement fires may have burned less frequently allowing *Pinus rigida* to exist in a forest rather than a barrens form of vegetation on most sites, with *Tsuga* and *Fagus* important on more mesic or protected sites, and barrens restricted to the most xeric or exposed sites.

There is other evidence for changes in the local vegetation following settlement. Heathland indicators [*Gramineae, Myrica/Comptonia, Pteridium,* and *Ericaceae* pollen] and the proportion of small *Betula* grains (*Betula populifolia* type) increase from 20–30% (of total *Betula* pollen) before settlement to 30–45% after settlement, suggesting more open, early successional vegetation on the landscape.

Although charcoal values fluctuate throughout the core, they are consistently higher above 10 cm than in the several centimeters just before settlement, where they are at their lowest levels in the core. The highest values (at 4 cm) are probably associated with the 1947 fire, although other fires burning in the early 20th century may have contributed charcoal at this level as well. The increased charcoal values at 11 cm and again at 7 and 8 cm could represent the large fires in 1762 and 1854 cited by Harris (1991). Proposed dates for these changes in charcoal

AXIS II

Fagus

Tsuga

Quercus

Betula (populifolia type)

Pre
Settlement

Post
Settlement

Pinus

AXIS I

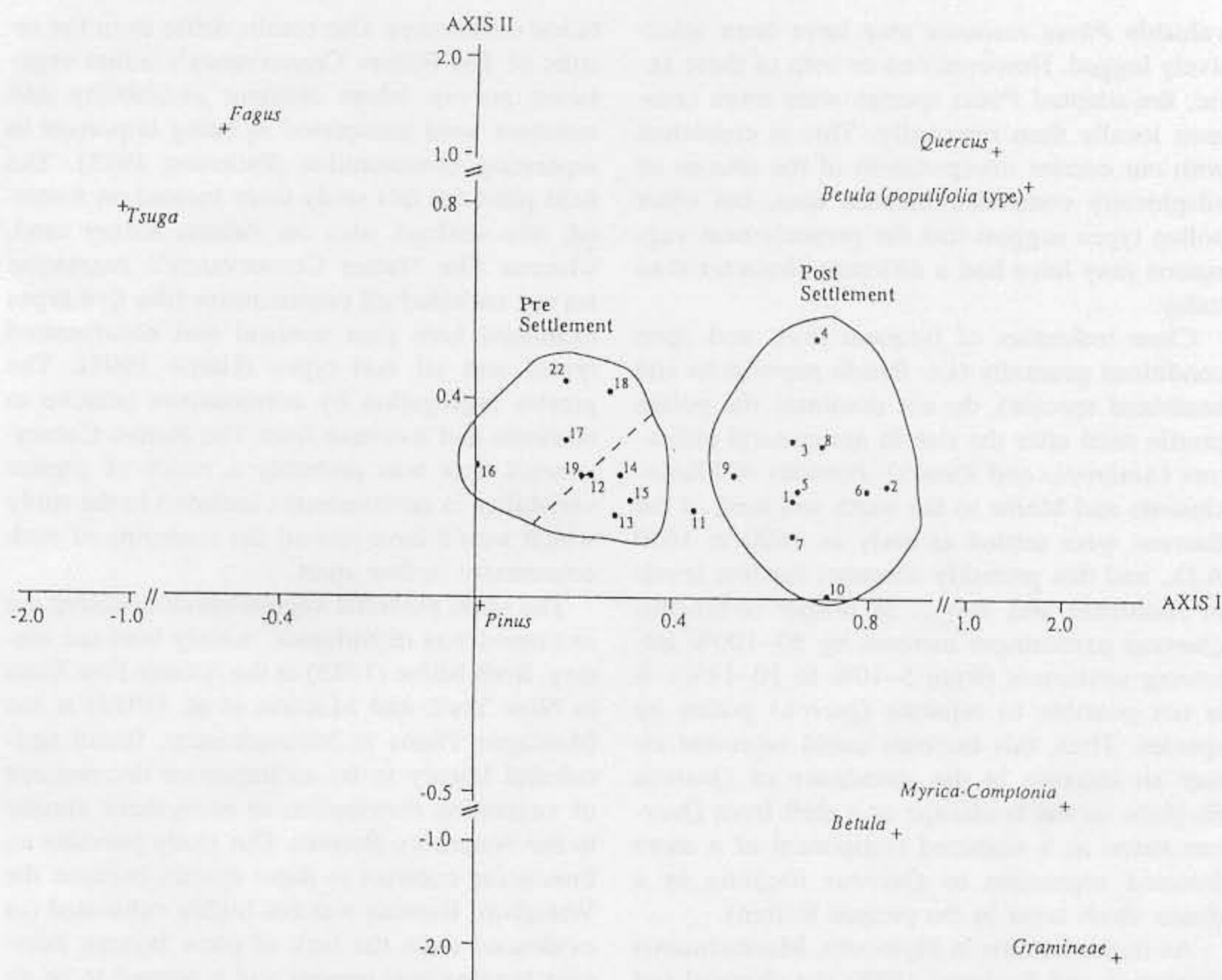Myrica-Comptonia

Betula

Gramineae

Fig. 6. Detrended correspondence analysis of pollen data. Numbers represent sample depths in the sediment core. Values used in the calculations are the percent of selected pollen types expressed as a percent of all pollen minus those types that are indicators of agricultural activity (i.e., *Ambrosia, Rumex, Plantago, Chenopodiaceae, Artemisia, Iva*). The dashed line separates before and after an apparent fire at 17 cm in presettlement time.

abundance are consistent with the chronology for the core based on pollen evidence. The higher charcoal values at the base of the core suggest presettlement fires, with one at 17 cm responsible for regenerating pine forests, to some extent at the expense of hemlock. *Pinus* pollen percentages rise to values consistently above 30% through the 16–11 cm interval, and hemlock percentages fall to less than 10% at 13–15 cm. The charcoal peak at 17 cm probably represents a fire burning in the 14th or 15th century A.D., well before the settlement of New England by Europeans (in the early 17th century).

Discussion. The picture that emerges of the presettlement vegetation of the Waterboro Barrens is a plant community dominated by pines, with diploxylon *Pinus* (*Pinus banksiana, Pinus resinosa,* and *Pinus rigida*) perhaps more important than elsewhere in the region. Mesic forest indicators (*Tsuga* and *Fagus*) were more im-

portant before than following settlement, but their importance in the community had already begun to decline by the time the first loggers and settlers arrived, perhaps reflecting changes in climate (Russell et al. 1993). The apparent increase in importance of *Pinus strobus,* a haploxylon *Pinus,* following settlement may simply reflect the local clearing of diploxylon *Pinus,* given that *Pinus strobus* is the dominant species regionally. Haploxylon *Pinus* pollen (rather than pollen of diploxylon *Pinus*) tends to dominate presettlement samples throughout much of New England, with the only exceptions being areas like Cape Cod where *Pinus rigida* dominates (Russell et al. 1993). The record from Newfield suggests that diploxylon *Pinus* were more important locally than regionally. Currently, *Pinus banksiana* is rare in the Waterboro Barrens area and *Pinus rigida* is more common than *Pinus resinosa*; however, this may not have been true prior to settlement. The more commercially

valuable *Pinus resinosa* may have been selectively logged. However, one or both of these xeric, fire-adapted *Pinus* species were more common locally than regionally. This is consistent with our current interpretation of the area as an edaphically controlled barrens area, but other pollen types suggest that the presettlement vegetation may have had a different character than today.

Clear indicators of frequent fires, and open conditions generally (i.e. *Betula populifolia* and heathland species), do not dominate the pollen profile until after the rise in agricultural indicators (*Ambrosia* and *Rumex*). Portions of Massachusetts and Maine to the south and west of the Barrens were settled as early as 1620 to 1650 A.D., and this probably accounts for low levels of *Ambrosia* and *Rumex* in deeper sediments. *Quercus* percentages increase by 50–100% following settlement (from 5–10% to 10–14%). It is not possible to separate *Quercus* pollen by species. Thus, this increase could represent either an increase in the abundance of *Quercus ilicifolia* on the landscape or a shift from *Quercus rubra* as a scattered component of a more forested vegetation to *Quercus ilicifolia* as a dense shrub layer in the present Barrens.

As in the barrens at Plymouth, Massachusetts (Patterson and Backman 1988), the charcoal and pollen evidence for the Waterboro Barrens suggests a shift toward a more fire-prone, xeric-species-dominated landscape during the past two centuries. The early successional communities occupying the area today may have been present before settlement, but they would have been smaller in area and restricted to the most frequently or severely burned sites, to xeric south- and west-facing slopes, or to areas with exposed bed rock.

The evidence suggests that soils and fire history determined the presettlement existence of the Waterboro Barrens in southern Maine. However, the distribution of species and communities within the current ecosystem may depend on different factors. The five communities somewhat separated into groups when analyzed with PCA (Fig. 3). This indicates differences between communities based on species data. However, when the environmental variables (soil fertility, soil moisture, soil texture, slope and aspect) were included in the analysis (CCA and RA) the community clusters disappeared. Although soil moisture, fertility, and texture all showed significant differences among communities, these variables were not related to the community vegetation differences. Our results differ from the results of The Nature Conservancy's initial vegetation survey where nutrient availability and moisture were interpreted as being important in separating communities (Patterson 1993). The field plots for this study were located on forested, non-wetland sites on Adams loamy sand, whereas The Nature Conservancy's vegetation survey included all communities (the five types examined here plus wetland and non-forested types) and all soil types (Harris 1991). The greater segregation by communities relative to nutrients and moisture from The Nature Conservancy's data was probably a result of greater variability in environments included in the study which would have moved the centroids of each community further apart.

The other potential vegetation determinant we examined was disturbance, mainly land-use history. Both Milne (1985) at the Albany Pine Bush in New York, and Motzkin et al. (1996) at the Montague Plains in Massachusetts, found agricultural history to be an important determinant of vegetation distribution in ecosystems similar to the Waterboro Barrens. Our study provides an interesting contrast to these studies because the Waterboro Barrens was not highly cultivated (as evidenced from the lack of plow layers), however logging was present and it proved to be an important factor.

The Waterboro Barrens experienced two forms of logging: intensive clear cuts for charcoal manufacture and less intensive partial cuts. A north central portion of the preserve appears to have been clear-cut for charcoal manufacture in the 1800's. The nearby Newfield Iron Works opened in 1837 (Libby 1976), and *Pinus rigida* charcoal may have fueled this operation. Numerous remains of charcoal manufacturing pits exist within the pitch pine-heath community but we located only one outside that community. Studies in southeastern Pennsylvania illustrate the long-term effects of charcoal manufacture on forest composition (Mikan and Abrams 1995, 1996). In these studies, charcoal production inhibited forest development for over 100 years by altering soil nutrient availability. Although Mikan and Abrams (1995, 1996) focused on the vegetation within the actual hearth circle, other work in eastern Pennsylvania found evidence for the long-term influence of charcoal production on areas clearcut for charcoal production (Russell and Schuyler 1988) as seems to be the case in the Waterboro Barrens. We hypothesize the charcoal manufacture was the indirect determi-

nant of the pitch pine heath community. The GIS vegetation cover type show the area currently occupied by pitch pine-heath was classified as herbaceous vegetation in 1940. Normally, areas clear cut for charcoal manufacture would have returned to *Pinus rigida,* however because the heath areas did not, we assume there must have been some sort of cultivation, probably related to blueberry production. The Capital Canning Co. owned land in this vicinity in the early 1900's; unfortunately, we were unable to find further information about this company's activities. After the 1947 fires, the areas cut during charcoal manufacture were later presumably cultivated for blueberries. Blueberry cultivation would have involved frequent, low-intensity fires. Following abandonment of these areas, an even-aged pitch pine stand could have seeded in from surrounding stands and developed into the pitch pine heath community.

Less-intensive logging occurred within the pitch pine-scrub oak community and involved the removal of mature *Pinus rigida,* probably in the early to mid-1900's judging from the stumps charred in the 1947 fires. This logging activity appears to have increased the amount of *Quercus ilicifolia* in the pitch pine-scrub oak community. Where logging occurred (in the northern portion of the preserve), the average *Quercus ilicifolia* cover within the 0.5 to 3 m height class was 75%. Where no evidence of logging existed in this type (in the southern portion of the preserve), the *Quercus ilicifolia* cover was significantly lower (23%; T = 4.283, d.f. = 8, P = 0.003). A partial cut would have opened the canopy sufficiently to allow more *Quercus ilicifolia* development than occurred in the unharvested southern portion. A similar pattern of increased *Quercus ilicifolia* cover in partially harvested areas was found at the Montague Plains (Motzkin et al. 1996).

In some barrens, such as the *Pinus rigida* community in the Shawangunk Mountains of New York State, early successional species continue to dominate for hundreds of years due to the edaphic severity of the site (Abrams and Orwig 1995). However, evidence from our study indicates that early successional species continue to dominate the Waterboro Barrens for different reasons. Although we examined a number of environmental factors, the only one that appears to have strongly influence the current community distribution within the Waterboro Barrens was disturbance. The 1947 fires protected the Waterboro Barrens from invasion by fire in-

tolerant species, which occurred in many other fire-dependent ecosystems. The subsequent disturbance history (logging, charcoal manufacture, and blueberry cultivation) allowed those early successional species to continue dominating the site. The importance of disturbance frequency found at the Waterboro Barrens matches work in Pennsylvania (Latham et al. 1996) where the persistence of a *Pinus rigida* and *Quercus ilicifolia* were attributed to frequent disturbance.

Following European settlement, there was an increase in many of the fire-dependent ecosystems such as pitch pine-scrub oak (Thoreau 1993). With the increase of fire suppression however, these ecosystems exist only in the few areas that have experienced wildfire or those currently managed by controlled burning (Latham et al. 1996). The regional pattern of reduction in fire dependent ecosystems is mirrored within the Waterboro Barrens ecosystem where fire dependent communities are being reduced in area and replaced by mixed deciduous forests. Our results show that the environmental conditions of soils and topography may not be sufficient to preserve this ecosystem. The disturbance regime must be preserved as well.

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