**Implications of Land-Use Legacies in the Sand Plain Vegetation
of Cape Cod National Seashore**

A thesis presented

by

Robert William Eberhardt III

to

The Graduate School of Arts and Sciences
of Harvard University

in partial fulfillment of the requirements
for the degree of

Master in Forest Science

February 2001

Harvard University
Cambridge, Massachusetts

ABSTRACT

There is increased recognition that ecological systems are highly dynamic in response to climatic change, disturbance processes, and human activity. Despite the geographical pervasiveness of past land-use, however, an understanding of its long-term ecological impacts often is not considered in the management of landscapes to protect and maintain biological diversity. The study described here used an integrated historical approach to determine the relative impacts of past land-use, fire, and site conditions on woodland vegetation patterns within Cape Cod National Seashore in southeastern Massachusetts. The study area (1) includes expansive coastal sand plains, which are a focus of intense conservation interest since they support a number of uncommon upland habitats including treeless heathlands and grasslands; and (2) has a long history of agricultural activity following European settlement. A comprehensive interpretation of modern vegetation patterns provides a test of theories that emphasize the importance of fire underlying current management of sand plain habitats.

Despite being largely wooded at European settlement, maps from 1846-56 depict the towns of Eastham, Wellfleet, and Truro as extensively settled and 80% open. Historical maps and modern soil profiles indicate that the 5000 ha of woodlands on sand plains in Cape Cod National Seashore were subjected to varied land-uses before agricultural abandonment and subsequent reforestation. Approximately 44% was plowed for crop cultivation or pasture improvement, 42% was cut repeatedly but never cleared, and 14% was subjected to other uses. Previously plowed sites are relatively flat with fine-textured fertile soils, but vegetation/land-use relationships are striking and largely independent of site conditions. Former woodlots support pine-oak woodlands with

abundant low shrubs, whereas previously plowed sites have less canopy oak and a distinct understory that includes the grass *Deschampsia flexuosa* and the shade-intolerant shrub *Arctostaphylos uva-ursi*. Modern compositional patterns and historical sources also suggest that past agricultural activity generated past occurrences of heathland and grassland habitats. In contrast to theories that emphasize the predominance of fire in determining vegetation patterns, the persistent influences of fire are apparent principally in the overstory composition and structure of former woodlots. Overall the results highlight the need (1) to integrate an understanding of past land-use into ecological models underlying the management the biological reserves; and (2) to consider the use of management approaches to perpetuate heathland and grassland habitats that mimic past agricultural practices.

ACKNOWLEDGEMENTS

Jeannette Bowlen, Jack Edwards, Edythe Ellin, Barbara Flye, Linda Hampson, Chris Kruegler, Oscar Lacwasan, Dottie Recos-Smith, and the Wood's Crew.

INTRODUCTION

It is increasingly recognized that ecological systems are highly dynamic in response to climatic change, disturbance processes, and human activity (Picket and White 1985; Clark 1986; Clark 1990; McDonnell and Pickett 1993). One result has been increased consideration of the historical variability of climate and natural disturbances in the interpretation and management of landscapes to protect and maintain biological diversity (Romme 1982; Heinselman 1996; Pickett 1997; Parsons et al. 1999). In contrast ecologists and natural resource managers have not fully embraced the notion that past human activities such as cultivation, grazing, and forest cutting have had long-term impacts on biotic assemblages worldwide (Peterken and Game 1984; Blackmore et al. 1990; Meier et al. 1995; Coffin et al. 1996; Kirby and Watkins 1998; Foster et al. 1999). This omission is particularly striking for those who study and manage the landscapes of northeastern North America, which have been shaped by almost 400 years of intensive, widespread land-use by European colonists (Russell et al. 1993; Whitney 1994; Foster et al. 1998; Foster 1999; McLachlan et al. 2000). There is a clear need to integrate an understanding of past land-use into management policies for biological reserves that have long histories of human activity (e.g. Motzkin et al. 1993; Bratton and Miller 1994).

On the Atlantic coast of southeastern Massachusetts and New York, much private, state, and federal conservation attention has been focused on protecting and managing the distinctive upland habitats that occur on deposits of glacial outwash or "sand plains." In addition to woodlands and shrublands dominated by pitch pine (*Pinus rigida*) and oaks (*Quercus* spp.), these drought-prone sites can support globally-uncommon treeless habitat types referred to as coastal heathlands or sand plain grasslands (Appendix 2 in

Christenson et al. 1996; Dunwiddie et al. 1996). Past research on sand plain and related

ecosystems has focused on the effects of fire on vegetation dynamics and the impact of

fire suppression on landscape structure (Little and Moore 1949; Forman and Boerner

1981; Patterson et al. 1984; Vickory and Dunwiddie 1997). Furthermore it has been

hypothesized that fire was responsible for maintaining extensive heathlands and

grasslands on at least some coastal sand plains before European settlement (Vickory and

Dunwiddie 1997). The research focus on fire has led conservation groups and

government agencies to adopt management policies centered around the use of prescribed

fire to perpetuate uncommon habitat types. However many sand plains have a long

history of agricultural land-use, and no systematic attempt has been made to evaluate the

relative impacts of past land-use, fire, and site conditions on the composition and

structure of modern vegetation.

Identifying the long-term impacts of past human activity often is difficult because

past land-use is poorly documented and strongly influenced by the physical environment

(Glitzenstein et al. 1990; Motzkin et al. 1999b). Using an integrated historical approach,

however, Motzkin et al. (1996, 1999a) identified past land-use as the primary determinant

of modern vegetation patterns across edaphically homogeneous sand plains in central

Massachusetts. The current study uses comparable methods to interpret patterns of

species composition and abundance across a larger, more heterogeneous coastal sand

plain landscape. The study presents the opportunity to evaluate the relative importance of

edaphic factors, land-use history, and fire in controlling modern vegetation patterns to

test theories underlying current management strategies for coastal sand plain habitats.

The following questions were addressed: (1) What were the spatial and temporal patterns

of land-cover, land-use, and fire on eastern Cape Cod since European settlement? (2) How were different land-uses distributed across the study area in relation to initial site conditions? (3) How important is past land-use in explaining modern vegetation patterns relative to edaphic conditions and fire? (4) What are the implications of an interpretation of current conditions for the conservation and management of sand plain habitats?

STUDY AREA

Cape Cod National Seashore (CACO; 42° 30' N, 70° 00' W) is an 10,900 ha area managed by the National Park Service that spans the eastern end of Cape Cod, Massachusetts in the Atlantic Coastal Plain physiographic province (Figure 1a). CACO includes large sections of the towns of Provincetown, Truro, Wellfleet, and Eastham, as well as beaches, wetlands, and several small islands in Orleans and Chatham. Surficial deposits are largely Wisconsinan sand plains and Quaternary dunes but also include areas of ice-contact, marsh, swamp, and beach deposits (Oldale and Barlow 1986). Mean January and July temperatures (1900-1980 from Provincetown) are 0.4° C and 20.3° C, respectively, and precipitation is evenly distributed throughout the year and averages 102 cm (Patterson et al. 1984).

The present study focuses on the sand plains of CACO in Truro, Wellfleet, and Eastham (Figure 1a), which currently support approximately 5000 ha of upland woodlands of the pitch pine-oak zone (Westveld 1956). Pitch pine (*Pinus rigida*; nomenclature follows Gleason and Cronquist 1991) and oaks (*Quercus* spp.) have been important tree taxa in the study area since 9000 B.P. (Winkler 1985). Although elevation only reaches 54 m a.s.l. on the westerly sloping plains, kame and kettle formations and
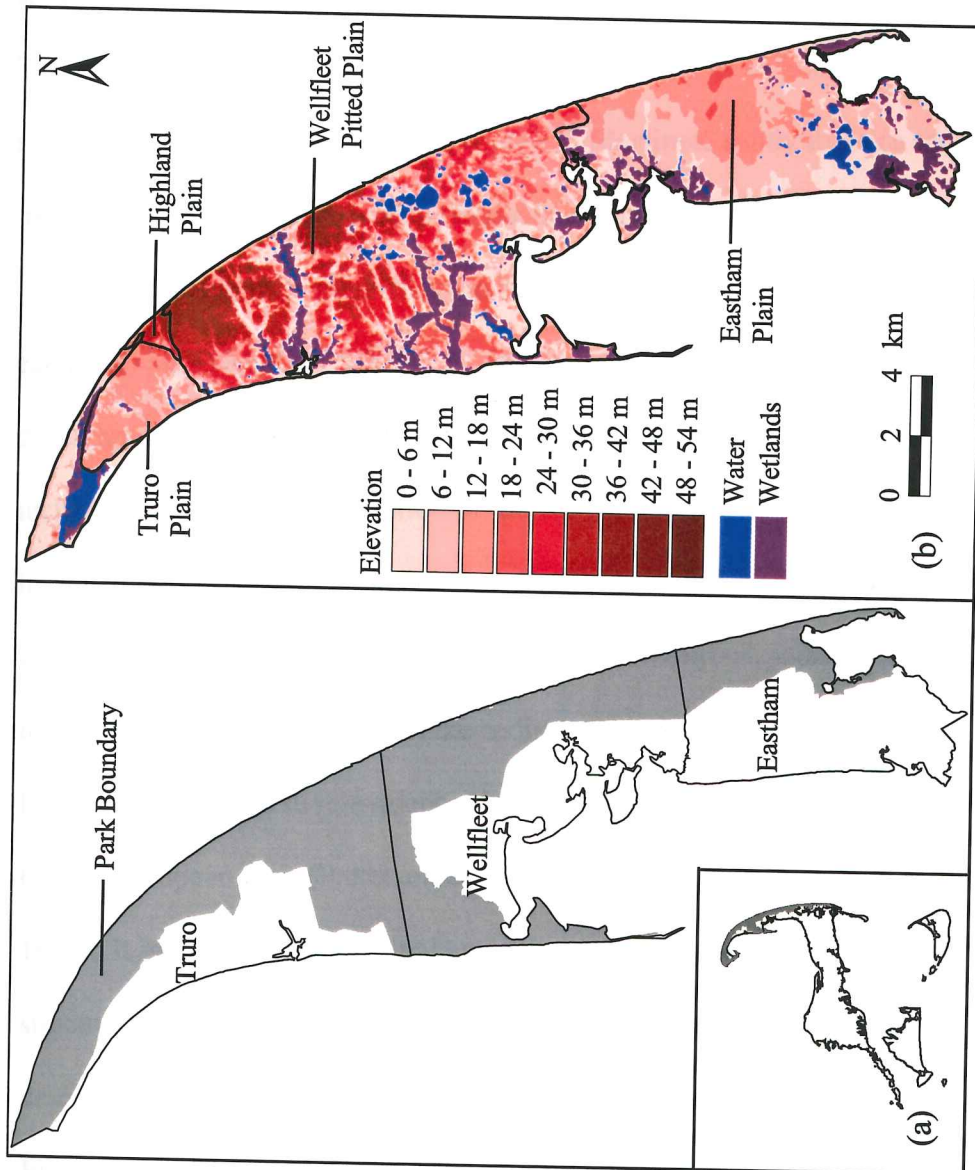
Figure 1. (a) Study area, showing town and park boundaries, and (b) topography of major outwash plains, adapted from Oldale and Barlow (1986). Water and wetlands are from MassGIS (1991).

east-west-trending valleys provide topographic variation, particularly on the Wellfleet Pitted Plain in Wellfleet and southern Truro (Figure 1b; Oldale and Barlow 1986). Ponds and streams occur where depressions intersect the water table at 2-3 m a.s.l.. Upland soils are almost exclusively Carver coarse sands or Hooksan sands, both mesic, uncoated Typic Quartzipsamments, although approximately 80 ha of Eastchop loamy fine sand (a silicaceous, mesic Typic Udipsamment) and Merrimac sandy loam (a sandy, mixed, mesic, Typic Dystrochrept) occur in Eastham and Truro (Fletcher 1993).

The occurrence of prehistoric archaeological sites from every period after the early Archaic (10,000 to 8,000 B.P.) indicates that humans have occupied the study area throughout the Holocene (McManamon 1984). Local aboriginal subsistence economies included hunting, the exploitation of marine resources, and limited horticulture after the introduction of maize to southern New England around 1000 B.P. (Bragdon 1996). Across New England, the relationship between aboriginal population centers and relatively abundant charcoal in lake sediments, along with the present rarity of lightning fires, provides suggestive evidence that Native Americans were major ignition sources for pre-European fires (Patterson et al. 1984; Patterson and Sassman 1988; Motzkin et al. 1996). It is likely that aboriginal agriculture and fire affected the past composition and structure of eastern Cape Cod's vegetation. Palynological evidence and written descriptions indicate, however, that eastern Cape Cod was largely wooded at the time of European settlement (Altpeter 1937; Ruberstone 1985; Winkler 1985; Dunwiddie and Adams 1995; T. Parshall and D.R. Foster, *unpublished data*).

English residents of the Plymouth and Massachusetts Bay Colonies settled Nauset (present-day Wellfleet, Eastham, and Orleans) in 1644 and Pamet (present-day Truro) by

1700. Local geography influenced the relative contribution of agriculture and maritime activities to each town's early economy: favorable soils in Eastham encouraged crop production and animal husbandry, a navigable harbor in Wellfleet supported maritime pursuits, and Truro developed a more mixed economy (Rockmore 1979; Ruberstone 1985). Land-use dramatically impacted upland vegetation in the seventeenth and eighteenth centuries. Forests were cut for forest products and fuel; animals were grazed woodlands and cleared areas; and large areas were cleared and plowed for crop production (Altpeter 1937; Ruberstone 1985; Friedman 1993; Dunwiddie and Adams 1995).

Fishing, shipping, and salt production became increasingly important in the early nineteenth century as international trade increased and regional industrialization began (Ruberstone 1985). Agriculture shifted to dairy and poultry production and more intensive cultivation of fruits and vegetables (Altpeter 1937; Ruberstone 1985; Dunwiddie and Adams 1995; Holmes et al. 1998). Regional economic decline, widespread emigration (Figure 2), and farm abandonment characterized the mid- to late-nineteenth century. Agriculture and maritime activities persisted on eastern Cape Cod until railroad construction in 1872 initiated the development of a summer tourism industry (Holmes et al. 1998). Cape Cod National Seashore was established in 1961 with the objective of protecting natural and cultural resources from development and providing access and resource interpretation for the public.
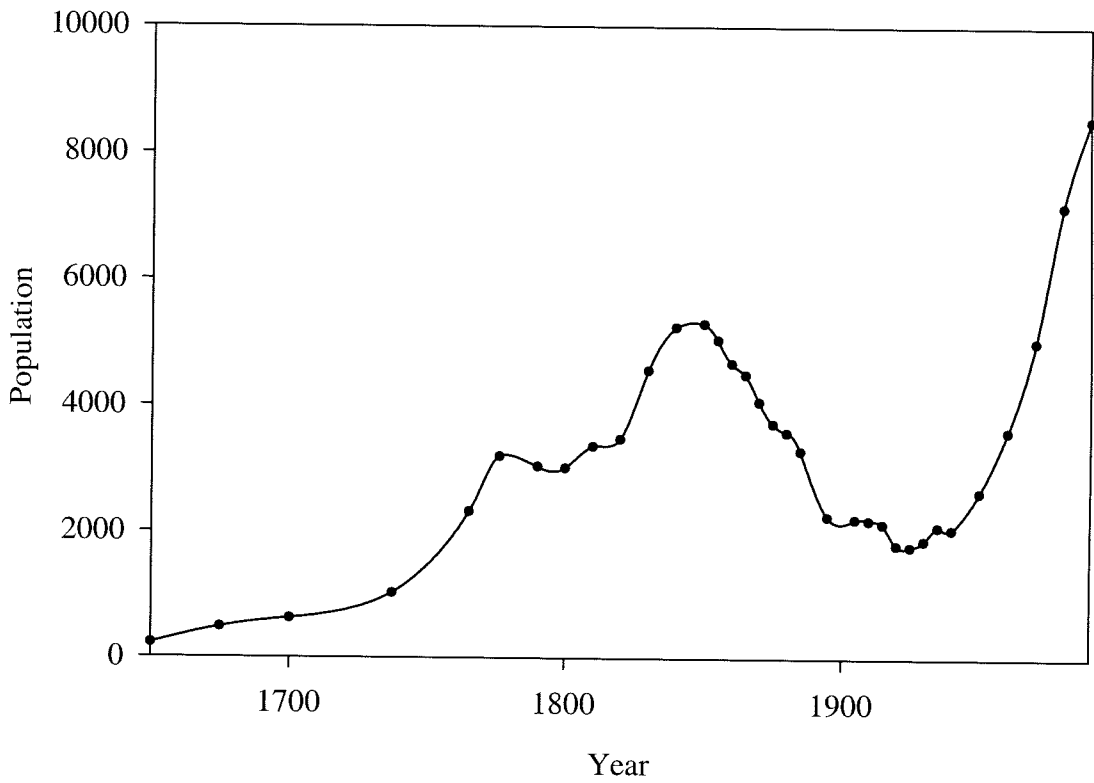
Figure 2. European population trends in Eastham, Wellfleet, and Truro (1650-1990). Data for 1650-1765 are from Altpeter (1937), and state and federal census data are used for later time periods. Aboriginal populations are estimated to have been 450-500 as late as 1698 (Ruberstone 1985).

METHODS

I used a combination of historical maps, aerial photographs, written accounts, and field sampling of vegetation and soils to determine geographic patterns of land-cover and land-use change, species composition and abundance, site conditions, and the past occurrence of fire. Statistical analysis focused on identifying relationships between past land-use and site conditions and the factors that influence modern vegetation patterns.

Land-cover / land-use change and fire history

Maps developed between 1848-1856 by the US Coast and Geodetic Survey were used to identify the extent and location of woodlands and cultural features near the historic peak of forest clearance and land-use intensity (Shalowitz 1964). These detailed maps (1:10,000), which depict woodlands, wetlands, topography, buildings, roads, and fences, were digitized into a geographic information system using ArcView (version 3.1a) and the Data Automation Kit (Environmental Systems Research Institute, Inc., Redlands, CA). Although the 1848-56 maps note some compositional and structural differences among areas covered by woody vegetation, distinctions are inconsistent between maps and surveyors (Allen 1997). For this study, all such cover types were combined into a single "wooded" category; other upland areas were classified as "open."

In grid format in ArcView (pixel resolution of 40 x 40 m), woodland area from the 1848-56 coverage was calculated for Eastham, Wellfleet, and Truro and, separately, for the portion of each town currently wooded and within CACO boundaries (MassGIS 1991). Woodland distribution on the 1848-56 maps was compared with independent maps of each town from 1830 (Massachusetts Archives 1830). Woodlands on the 1830

8

maps were digitized after being transferred onto modern USGS topographic maps (1:25,000) using a zoom transfer scope.

Land cover at each study plot (see below) in the late 1930s was determined from three sources: black and white aerial photos (1:24,000; November 1938) examined under a mirror stereoscope, town maps developed by the Works Progress Administration (WPA 1937), and canopy age estimates (see below).

Information on the occurrence of individual upland fires on eastern Cape Cod between 1897-1961 were compiled from a historical study based on town reports, newspaper articles, and personal interviews (Dunwiddie and Adams 1995), unpublished notes by R.C. Hall, U.S. Forest Service (Harvard Forest Archives, Petersham, MA), 1938 aerial photos, and written historical sources. Whenever possible the location and total area burned were estimated for each fire. Documentary sources were used to infer the extent of fires before the twentieth century.

Modern vegetation, disturbance history, and site conditions

Modern woodland vegetation and site conditions were sampled during summer 1999 at 89 20 x 20 m plots stratified by town and 1848-56 land cover (open or wooded). With the exception of formerly wooded areas in Eastham, which are relatively uncommon, at least 10 plots were sampled in formerly open and wooded areas in each town (Table 1). This design was used to sample vegetation throughout the study area across a range of past land-uses and is compatible with associated vegetation studies of the larger region of Cape Cod, the Islands, and Long Island (D.R. Foster et al. *unpublished data*). All plots were established in areas that had >25% tree cover, showed

Table 1. (a) Number of study plots in woodlands within Cape Cod National Seashore (CACO) sampled in each combination of town and historical land-cover taken from 1848-56 maps. (b,c) Area of woodland shown on 1848-56 maps for the entire towns of Eastham, Wellfleet, Truro (b) and for the portion of those towns currently wooded and within CACO (c). Percentages are relative to total town area (b, MacConnell et al. 1974) and modern woodland area within CACO (c, MassGIS 1991).

	(a) STUDY PLOTS		(b) WOODLANDS IN ENTIRE TOWN		(c) WOODLANDS IN CCNS	
TOWN	WOODED n	OPEN n	Area (ha)	%	Area (ha)	%
Eastham	3	13	540	13	250	40
Wellfleet	18	18	1230	22	800	41
Truro	15	22	1300	23	1100	46
Total	36	53	3070	20	2150	44

no evidence of a seasonally high water table, and were not visibly influenced by significant mid-twentieth century activity including golf course maintenance or military training. Plot locations were chosen using a random point generator in ArcView and found in the field by orienteering from known points.

Vegetation was sampled using methodology comparable to that recommended by The National Vegetation Classification System (Grossman et al. 1998). In each plot, percent cover of each vascular plant species and total lichen and bryophyte cover was estimated using eight cover-abundance classes (1 = <1%, 2 = 1-3%, 3 = 3-5%, 4 = 5-15%, 5 = 15-25%, 6 = 25-50%, 7 = 50-75%, 8 = >75%). Diameter at breast height was recorded for all living (> 2.5 cm dbh) and dead (>10 cm dbh) tree stems, and obvious sprouting patterns (i.e., stems with shared rootstocks) were noted.

Shallow soil pits were dug into the B horizon (mean pit depth = 38 cm) at 1-2 randomly chosen locations in each plot. The depth and boundary characteristics of each horizon were described using standard methods (U.S. Department of Agriculture 1993). Duplicate samples of mineral soil from 0-15 and 15-30 cm were taken with a 5 cm x 15 cm cylindrical steel corer. Samples from each plot were air-dried and combined, and carbon and nitrogen contents were determined using a Fisons CN analyzer (Fisons Instruments, Beverly, MA). Aggregated 0-30 cm samples were analyzed by Brookside Labs, Inc. (New Knoxville, OH) for texture, pH (1:1 in water), extractable nutrients (Mehlich 1984), and percent organic matter (Storer 1984). The following soil parameters were analyzed: pH, % silt + clay, % organic matter, % total nitrogen, % total carbon, C:N, total exchange capacity (TEC; m.e./100 g soil), and extractable concentrations (mg/kg) of phosphorus (as P_2O_5), calcium, magnesium, and potassium.

To categorize physiography, each plot was assigned to one of three dominant outwash plains (the Eastham Plain, Wellfleet Pitted Plain, or Truro Plain; Oldale and Barlow 1986), with the single plot sampled on the Highland Plain grouped with those from the adjacent, edaphically-similar Truro Plain. Mean slope and terrain slope index (TSI; McNab 1989) were used to quantify local topography. Slopes along the ground were measured from each plot center at 45 degree increments starting in the aspect direction. TSI was calculated as the arithmetic mean of slope measurements and describes land surface shape, with negative values indicating convex surfaces that become increasingly concave as values increase.

Field evidence assisted in reconstructing the disturbance history of each plot. The presence / absence of a plow (Ap) horizon, identified as a relatively deep (> 10 cm; mean depth: 17 cm), brown A horizon with an abrupt, smooth to wavy lower boundary, was noted (Motzkin et al. 1996). In contrast, unplowed soils typically had well-developed E horizons (mean depth: 17 cm) immediately below shallow A horizons (mean depth: 2 cm). To provide an estimate of stand age, 1-3 of the largest tree stems per plot were cored as close to their bases as possible. Cores were mounted and sanded in the laboratory, and annual growth rings were counted under 10-30X magnification. Soil profiles and wood were examined for evidence of past fire including presence of macroscopic charcoal or fire scars.

Field evidence was combined with information from the 1848-56 maps to assign plots to broad categories of past land-use. Plots with Ap horizons were considered formerly "plowed," which indicated that the soils were extensively mixed and the original vegetation was eradicated for crop production or pasture improvement. Plots

12

lacking Ap horizons and mapped as wooded on the 1848-56 maps were considered "woodlots," where trees were cut during the historical period but vegetation was never completely eliminated. Plots lacking Ap horizons but shown as open on the 1848-56 maps have varied histories and were designated "open." Some open plots occur in coastal settings or topographic depressions and have disturbed soil horizons resulting from erosion or overwash. Other open plots have no visible soil disturbance yet may have been used as unplowed pastures during the historical period. Three plots are considered woodlots despite being mapped as open on 1848-56 maps, since each occurs within 100 m of a historical woodland border and contains many large oak coppices that apparently develop following centuries of repeated cutting and/or burning (Foster and Motzkin 1999).

Data Analysis

A G-test of independence was used to test whether the three categories of past land-use occurred disproportionately on the Eastham, Truro, or Wellfleet Pitted Plains (Sokal and Rohlf 1995). Kruskal-Wallis tests (with post-hoc comparisons following Conover [1980]) were used to determine whether soil texture, topography, and other soil properties differed among past land-use types. The sequential Bonferroni method was used to adjust the experimentwise error rate for these tests to $\alpha = 0.05$ (Rice 1989).

Classification and ordination of species abundance data were used to characterize variation in vegetation composition. Both analyses were implemented in PC-ORD (versions 2 and 4, MjM Software Design, Gleneden Beach, Oregon) and used the Sørenson (Bray-Curtis) metric to quantify vegetation dissimilarity among plots (McCune and Mefford 1999). For classification, an agglomerative clustering algorithm was used to

group plots into major vegetation assemblages (flexible $\beta = -0.25$; Greig-Smith 1983).

For ordination, plots were arranged in a two-dimensional space using nonmetric

multidimensional scaling (NMDS), where 100 iterations of the NMDS algorithm were

run starting from the output from detrended correspondence analysis (DCA). The

solution was rotated using the varimax procedure to maximize loading on ordination axes

(McCune and Medford 1999). Random starting configurations gave similar ordination

results; the NMDS solution based on DCA is shown here since it has a lower final stress

value than most solutions derived from random starting coordinates. Higher dimensional

NMDS solutions showed little reduction in final stress values.

 G-tests of independence were used to determine whether the vegetation types

identified by classification occurred disproportionately at sites of specific categories of

past land-use or where evidence of past fire was found in the field. Kruskal-Wallis tests

were used to determine whether the vegetation types had different canopy stem ages or

occurred on sites with different topographic or edaphic characteristics. The

experimentwise error rate for this group of tests is $\alpha = 0.05$.

 Analyses of overall vegetation variation showed strong relationships between

species composition and abundance and past land-use (see below). To further explore the

influences of past land-use on species distributions, presence/absence data for species

occurring in 13-87% of plowed and woodlot plots were analyzed using G-tests to identify

the land-uses affinities of individual species. Open plots were not considered in these

analyses. The experimentwise error rate for these tests was adjusted to $\alpha = 0.05$.

RESULTS

Land-cover and land-use change

Between 1848 and 1856 eastern Cape Cod was extensively settled and largely deforested, with only 20% of Eastham, Wellfleet, and Truro wooded at this time (Table 1b; Figure 3b). Buildings and fences were concentrated in the western portion of the towns, although settlements also were present throughout the study area in east-west trending valleys (Figure 4). An extensive road network ran across the landscape through both open areas and woodlands (Figure 4). Only 44% of the present-day woodlands in CACO were wooded in 1848-56 (Table 1c).

Field evidence, independent historical sources, and contemporary maps suggest that the 1848-56 maps provide an accurate description of land-cover during the mid-nineteenth century. All but one of the 38 study plots with a Ap horizon are mapped as open on the 1848-56 maps, which indicates that direct evidence of agricultural activity is highly concentrated in areas depicted as having been cleared. The distribution of woodland on the 1848-56 maps also coincides with contemporary written descriptions that describe a woodland dominated by pine and oak in northern Eastham on the border of Wellfleet (Figure 3b; MA Historical Society 1802; Dwight 1969; Thoreau 1987). The general agreement with the 1830 map series provides further independent evidence that the 1848-56 maps accurately depict land-cover (Figure 3a,b). I suggest, however, that the 1848-56 maps provide a more accurate depiction of land-cover of the two map series, since they are more detailed and conform better to historical references to the large woodland in northern Eastham, which is not depicted on the 1830 maps (Figure 3a).
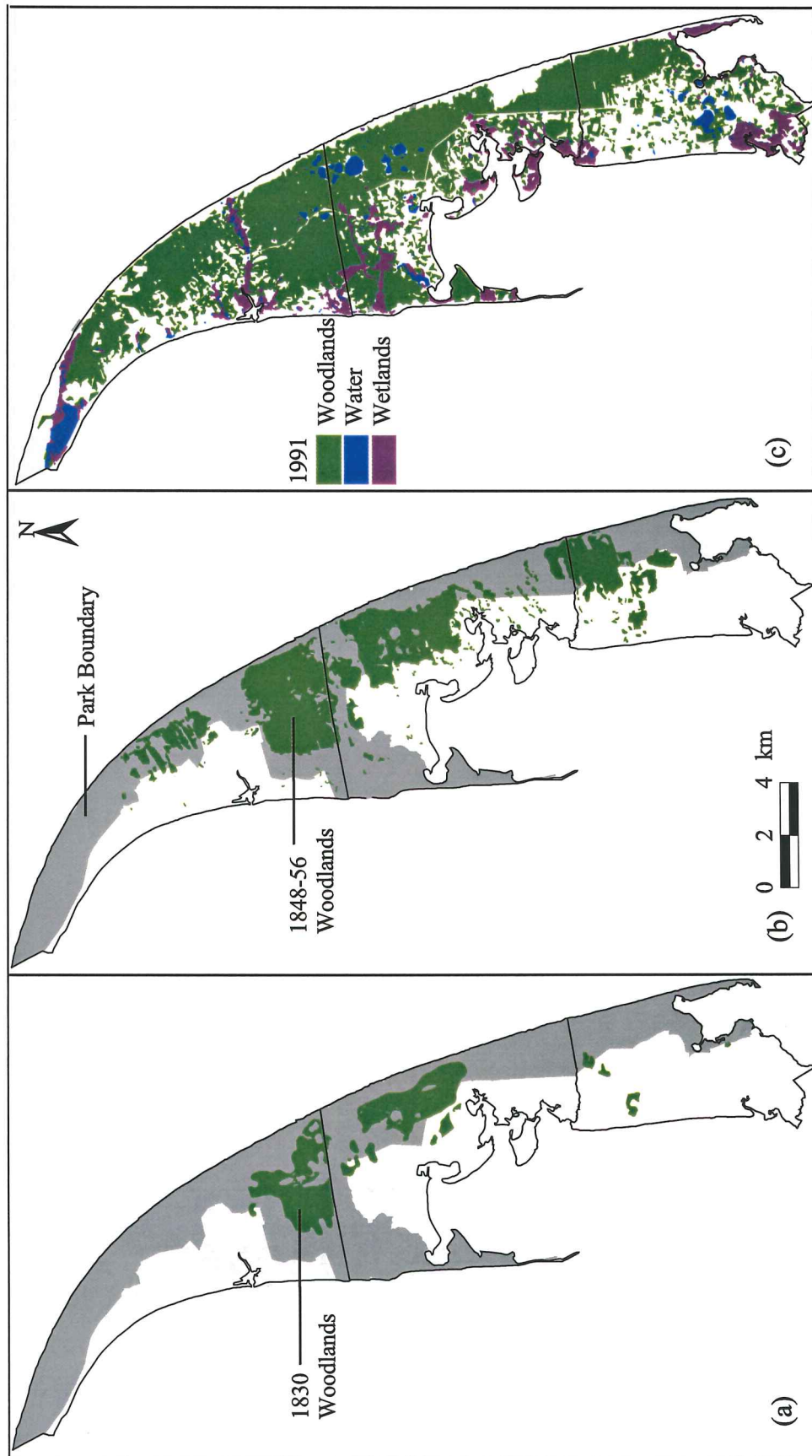
Figure 3. Distribution of woodlands on outwash desposits of eastern Cape Cod for 1830 (a), 1848-56 (b), and 1991 (c). Woodlands are from Massachusetts town maps, US Coast and Geodetic Survey maps, and MassGIS (1991), respectively.

16
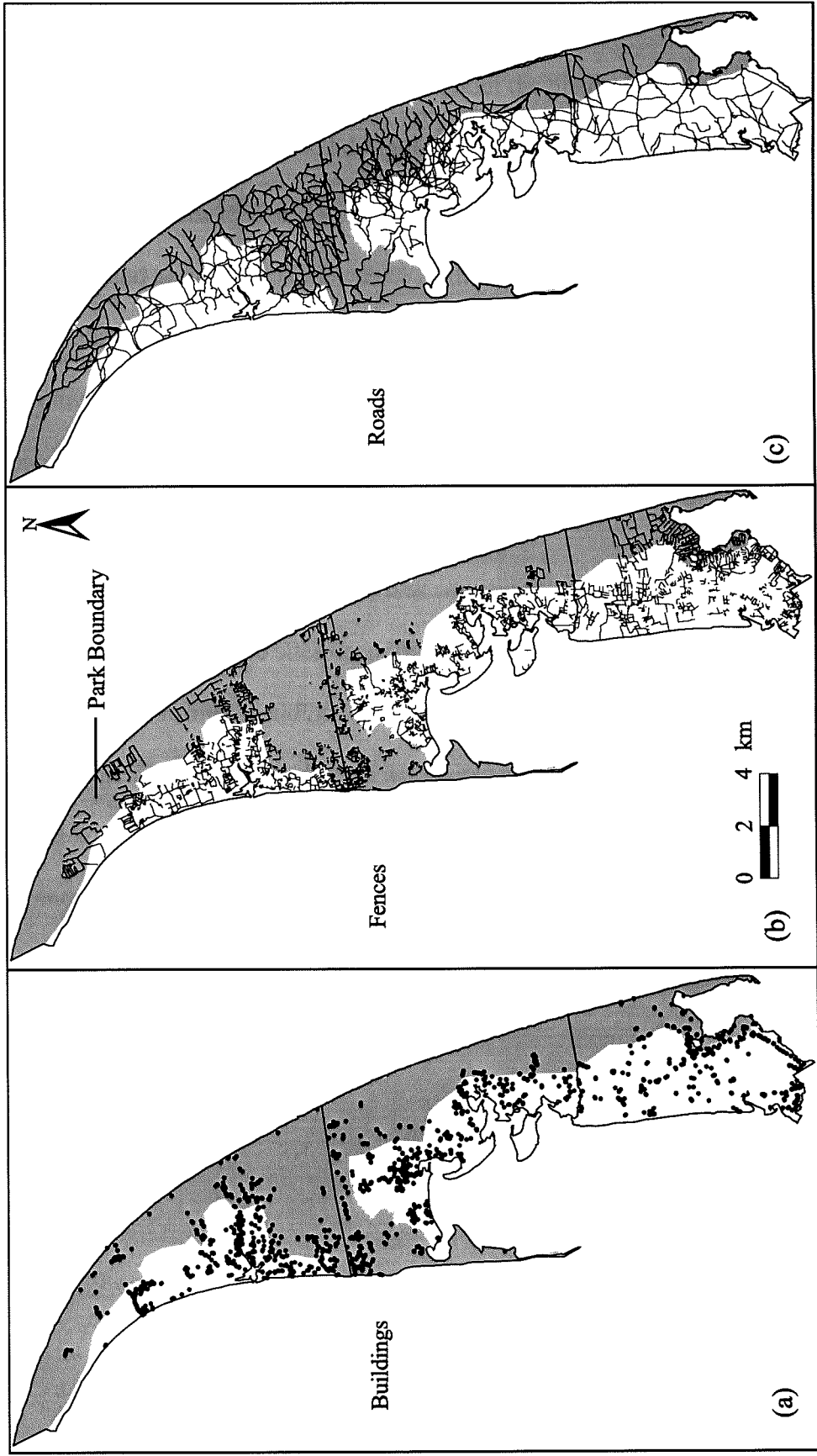
Figure 4. Distribution of buildings (a), fences (b), and roads (c) on maps from 1848-56.

Forty-four percent (n = 38) of the study plots were plowed during the historical period, 42% (n = 37) were woodlots throughout the historical period, and 14% (n = 12) were subjected to other uses and designated "open." Canopy tree stems in plowed or open plots date from 1889 to 1976 with a mean of 1927 ± 21 years (± 1 standard deviation), and aerial photos show 80% of these plots (n = 40) supported woodlands or lower-statured shrublands in 1938, with heathlands or grasslands (n = 7, 14%) and agriculture (n = 3, 6%) occurring in the remaining plots. All woodlot plots (n = 37) supported woodlands or shrublands in 1938, and canopy tree stems date from 1820 to 1949 with a mean of 1915 ± 28 years.

Relationships between past land-use and site conditions

Previously plowed sites occur disproportionately on the Eastham and Truro Plains, whereas former woodlots and open sites are concentrated on the Wellfleet Pitted Plain (Figure 5). Relative to former woodlots and open sites, previously plowed sites also are significantly flatter and have finer-textured, slightly less acidic soils with higher concentrations of phosphorus, total nitrogen, and potassium (Table 2).
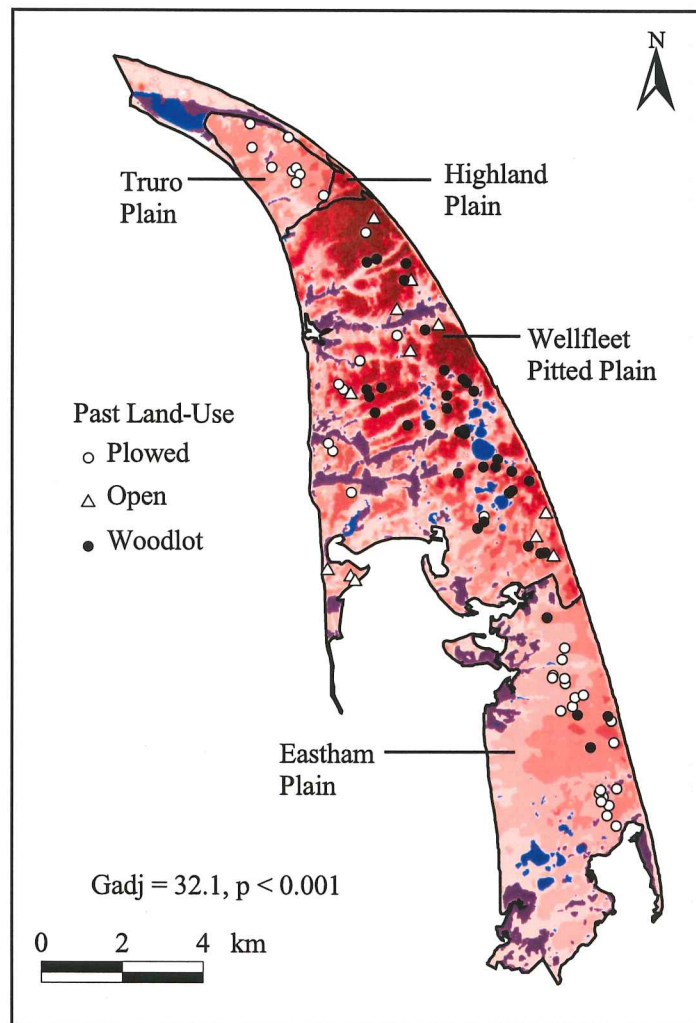
Figure 5. Distribution of categories of past land-use on topographically distinct outwash plains of Cape Cod National Seashore. The G-test determines whether past land-use types occur disproportionately on distinct outwash plains.

Table 2. Median values of site factors for categories of historic land-use on Cape Cod National Seashore, with Kruskal-Wallis statistic (H) and p-values for tests that site factors do not differ among vegetation types. Tests with p ≤ 0.01 are significant at α = 0.05 after accounting for multiple comparisons. Similar letters within rows indicate that post-hoc tests show no significant difference between a pair of vegetation types

| SITE FACTOR | HISTORIC LAND USE | | | | |
	PLOWED n = 38	OPEN n = 12	WOODLOT n = 37	H	P
% Silt + Clay	8.0^a	4.9^c	6.0^b	14.2	0.001
Slope	2.3^a	9.3^{ab}	6.5^b	10.8	0.004
pH	4.4^a	4.3^b	4.2^b	16.1	0.000
N (%)	0.046^a	0.038^b	0.036^b	14.2	0.000
P (mg/kg)	14^a	7^b	7^b	30.7	0.000
K (mg/kg)	13^a	9^{ab}	8^b	13.3	0.001
Ca (mg/kg)	50	26	31	6.8	0.034
Mg (mg/kg)	13	10	11	7.2	0.027
TEC (mequ/100 g)	9.4	5.6	5.7	6.8	0.033
% Organic Matter	1.4	1.2	1.2	7.7	0.021
C:N	24.1	29.1	27.5	5.5	0.063
C (%)	1.1	1.0	1.0	1.6	0.454
TSI (x100)	0.4	0.9	0.2	0.8	0.681

Fire history

There is little information on specific fires that occurred on eastern Cape Cod before the twentieth century. Written historical documents indicate, however, that railroads ignited numerous fires across Cape Cod beginning in the mid-nineteenth century (Collins 1909; Cahoon 1915; Cook 1921; Massachusetts Forestry Association 1928). At least 31 upland fires are known to have occurred in these towns between 1897 and 1962, and several fires larger than 30 ha occurred within CACO boundaries, primarily on the Wellfleet Pitted Plain (Table 3). Some such fires occurred in woodlands, resulted in extensive canopy mortality, and initiated the development of modern canopy stems through seedling establishment or sprouting (Table 3). Other fires occurred in open habitats including grasslands and "moors" (Table 3). Despite numerous ignitions, no large fires have burned on eastern Cape Cod since the establishment of Cape Cod National Seashore in 1961 (Patterson et al. 1984; Dunwiddie and Adams 1995).

Table 3. Documented upland fires within the towns of Eastham, Wellfleet, and Truro (1897-1962). Date, location, size and any other information are taken from written descriptions or 1938 aerial photos. When possible location was summarized by determining (1) whether fires occurred within the present-day boundaries of Cape Cod National Seashore (CACO); and (2) the outwash plain (see Figure 1) where each fire burned.

Date	Size (ha)	CACO?	Outwash Plain	Notes	Source
1897	?	?	Eastham	Old orchard fire	Dunwiddie and Adams (1995)
5/2/1900	80+	?	Eastham		Dunwiddie and Adams (1995)
8/20/1908	200	Yes	Wellfleet / Highland	Woodland and pasture fire	Dunwiddie and Adams (1995)
ca. 1914	80-120	Yes	Wellfleet		Dunwiddie and Adams (1995)
4/5/1915	?	?	Truro	Fire in "moors" and pines. Flames 15 m tall.	Dunwiddie and Adams (1995)
6/7/1917	?	?	Truro		Dunwiddie and Adams (1995)
ca. 1920	?	?	Wellfleet	"Abundant [P. rigida] sprout reproduction…, on a burn near Wellfleet."	R.C. Hall, unpublished photos and notes
1926	?	?	Wellfleet	Severe spring burn south of Truro. "Note patches of exposed mineral soil."	R.C. Hall, unpublished photos and notes
4/19-21/1927	800	Yes	Wellfleet	"This area was covered with pitch pine and oak, but the fire killed practically the whole stand (Parmenter 1928)."	Dunwiddie and Adams (1995)
4/24/1933	6	Yes	Wellfleet	Railroad fire, P. rigida established in 1934	Dunwiddie and Adams (1995)
5/19-21/1933	33	Yes	Wellfleet		Dunwiddie and Adams (1995), 1938 aerial photos, and canopy age estimates
ca. 1935	?	Yes	Wellfleet		Dunwiddie and Adams (1995)
1937	?	?	Wellfleet / Truro	More than 9 grass and woodland fires in Truro set by arsonist.	Dunwiddie and Adams (1995)
4/5/1938	1000	Yes	Wellfleet		Dunwiddie and Adams (1995)
4/19/1938	20	Yes	Wellfleet	Grass fire	Dunwiddie and Adams (1995)
4/21/1938	?	Yes	Wellfleet	Fire in cemetery	Dunwiddie and Adams (1995)
1938	800	Yes	Wellfleet		Dunwiddie and Adams (1995)
5/20/1940	2	Yes	Wellfleet		Dunwiddie and Adams (1995)
8/22/1940	2 total	No	Wellfleet / Truro	Numerous small arson fires in Truro	Dunwiddie and Adams (1995)
7/14/1942	?	?	Eastham	Railroad fire	Dunwiddie and Adams (1995)
1951	10	?	Eastham		Dunwiddie and Adams (1995)
ca. 1960	?	?	Eastham		Dunwiddie and Adams (1995)
1962	1	?	Eastham		Dunwiddie and Adams (1995)

Vegetation variation

Six woodland types were identified by classification and are closely clustered in ordination space (Table 4, Figure 6). All include *Pinus rigida* and *Quercus ilicifolia* but otherwise are distinct in species composition and abundance:

(1) The Pine-Bearberry type is an open-canopy *P. rigida* woodland type characterized by abundant *A. uva-ursi* with frequent *Deschampsia flexuosa*, *G. baccata*, *Schizachyrium scoparium*, and *Q. velutina* or *Q. alba* as seedlings or saplings.

(2) The Pine-Hairgrass type is characterized by abundant *P. rigida* and *D. flexuosa*, with *A. uva-ursi*, *Q. velutina*, and *Trientalis borealis* as common associates

(3) The Pine-Oak-Sedge type includes abundant canopy or subcanopy *Quercus velutina* in addition to *P. rigida* and abundant *Carex pensylvanica* in the herb layer. Other common understory species are *Deschampsia flexuosa*, *Q. alba*, *Prunus serotina*, *G. baccata*, and *Amelanchier* spp.

(4) The Pine-Scrub Oak-Crowberry type is characterized by an open canopy of *P. rigida* and abundant *Quercus ilicifolia*, *Corema conradii*, and *Vaccinium pallidum*. Other common understory species include *Arctostaphylos uva-ursi*, *Gaylussacia baccata*, *Comptonia peregrina*, *Quercus velutina* and *Quercus alba*.

(5) The Pine-Oak-Huckleberry type has abundant canopy *Q. alba*, *P. rigida* and *Q. velutina* and a continuous low shrub layer dominated by *G. baccata* and *Vaccinium angustifolium*. Other common associates include the ericaceous shrubs *V. pallidum*, *Gaultheria procumbens*, *Epigaea repens*, and *A. uva-ursi*.

Table 4. Species composition/abundance of six woodland types on outwash deposits of Cape Cod National Seashore identified by classification. For each species, % = frequency of occurrence and X = mean percent cover when present. Data for species present in fewer than four plots are not shown. Canopy age varies significantly among vegetation types (Kruskal-Wallis H = 15.6, p = 0.008).

	VEGETATION TYPE											
	Pine-Bearberry n = 6		Pine-Hairgrass n = 12		Pine-Oak-Sedge n = 21		Pine-Scrub Oak-Crowberry n = 8		Pine-Oak Huckleberry n = 35		Pine-Scrub Oak-Bayberry n = 5	
Mean Canopy Age (years)	41.5 [b]		78.5 [a]		71.0 [a]		76.3 [a]		83.4 [a]		77.6 [ab]	
SPECIES	%	X	%	X	%	X	%	X	%	X	%	X
Arctostaphylos uva-ursi	100	38	92	3	95	2	100	7	60	1		
Schizachyrium scoparium	67	1	42	1	14	1			3	1		
Rubus allegheniensis	17	1			10	1			9	1		
Aronia arbutifolia	17	1			5	1						
Aster patens	17	1			14	1						
Pinus rigida	100	34	100	52	100	31	100	38	97	20	100	20
Deschampsia flexuosa	100	1	100	25	100	11	13	2	26	1	40	1
Toxicodendron radicans	17	1	42	1	19	1						
Lichen	67	2	75	4	57	1	50	1	17	1	20	1
Trientalis borealis	33	1	75	1	24	1			3	1	60	1
Moss	33	1	75	1	90	1	25	1	46	1	60	4
Chimaphila maculata	17	1	17	1	48	1			11	1		
Melampyrum lineare	17	1	25	1	29	1	13	1	11	1		
Vaccinium corymbosum	17	1	17	7	29	1	13	2	29	1		
Rubus flagellaris/hispidus	33	1			38	1			6	1	40	1
Prunus maritima			25	1	14	1			9	1		
Chimaphila umbellata			25	1	5	1			3	2		
Dryopteris intermedia			8	1	10	1			9	1		
Monotropa uniflora			25	1	38	1			9	1		
Robinia pseudoacacia			8	1	14	1			9	1		

24

Table 4. Continued

SPECIES	VEGETATION TYPE											
	Pine-Bearberry		Pine-Hairgrass		Pine-Oak-Sedge		Pine-Scrub Oak-Crowberry		Pine-Oak Huckleberry		Pine-Scrub Oak-Bayberry	
	%	X	%	X	%	X	%	X	%	X	%	X
Quercus coccinea	67	1	42	2	33	7	25	2	23	6		
Carex pensylvanica	100	10	92	4	71	6	100	40	66	1	60	1
Quercus ilicifolia	17	2	8	1	100	11	75	17	100	5	80	43
Corema conradii	17	1			5	1			3	1		
Vaccinium pallidum			8	1	14	1	100	7	91	4	100	2
Comptonia peregrina	83	1			10	1	50	1	17	1		
Quercus velutina	83	1	92	7	100	24	75	3	100	29	80	6
Quercus alba	83	23	67	1	100	5	75	1	100	18	100	6
Gaylussacia baccata	67	4	33	3	76	4	100	18	100	41	80	11
Vaccinium angustifolia			58	5	57	2	25	2	94	10	80	10
Gaultheria procumbens					5	1	63	4	100	4	100	11
Epigaea repens	17	1	42	1	10	1	13	1	63	1	80	3
Prunus serotina	33	1			81	1			31	1	80	3
Aralia nudicaulis	17	1			19	1			26	1	60	3
Myrica pensylvanica	50	4	42	1	52	2	13	4	57	1	100	1
Parthenocissus quinquefolia			17	1	5	1	13	1	3	1	20	1
Cypripedium acaule	17	1	17	1	10	1	13	1	3	1	20	1
Viburnum dentatum	17	1	8	1	14	1					20	1
Smilax rotundifolia	33	1	8	1	29	1			23	5	80	1
Amelanchier spp.			25	1	62	1			40	1	80	1
Smilax glauca			17	1	5	1			6	1	40	1
Maianthemum canadense					14	1			6	1	60	1
Quercus prinoides					10	1			9	1	20	4
Viburnum nudum var. *cassinoides*					5	1			11	1	40	5
Sassafras albidum									6	2	40	
Pteridium aquilinum									20	2	60	1
Acer rubrum									6	1	40	12

25

Legend:
- ● Pine-Bearberry
- ○ Pine-Hairgrass
- ▼ Pine-Oak-Sedge
- ▽ Pine-Scrub Oak-Crowberry
- ■ Pine-Oak-Huckleberry
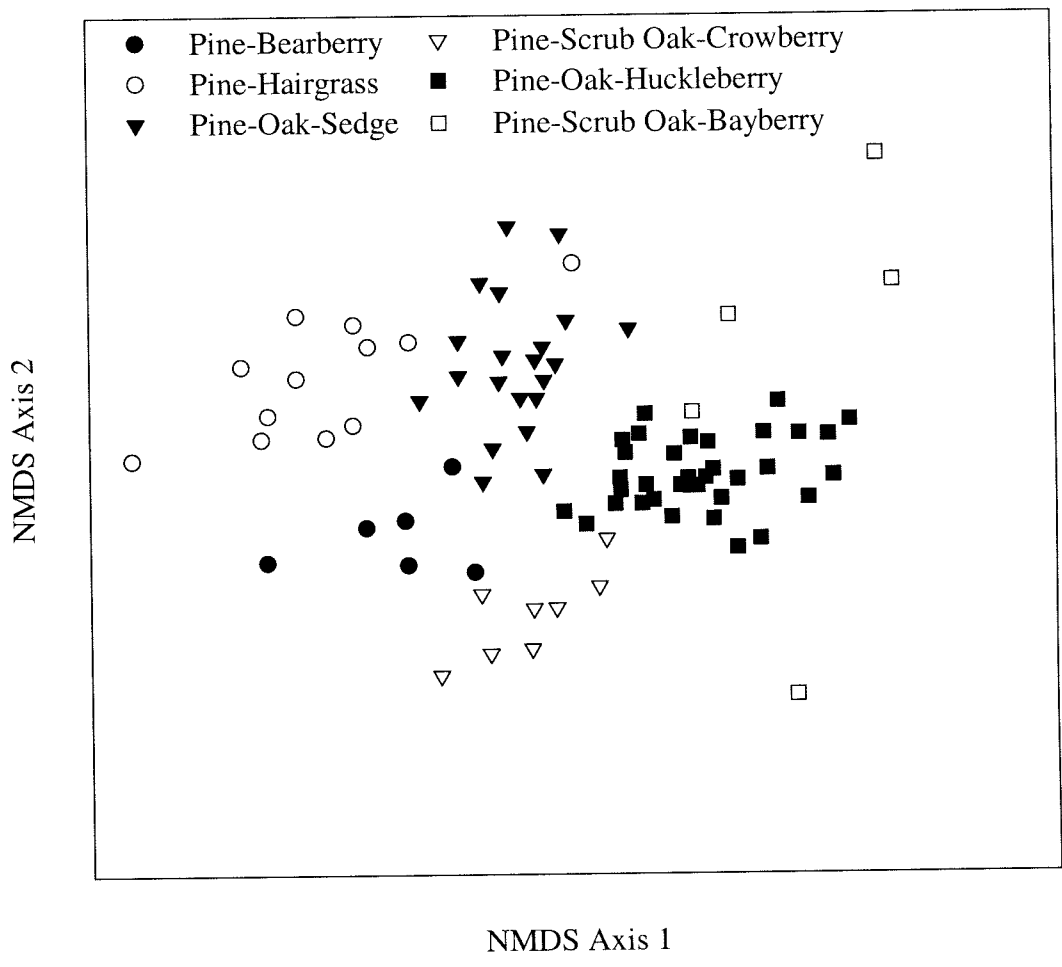- □ Pine-Scrub Oak-Bayberry

NMDS Axis 2

NMDS Axis 1

Figure 6. Ordination of species cover-abundance data from the woodlands of Cape Cod National Seashore. Symbols indicate vegetation types identified by classification.

(6) The Pine-Scrub Oak-Bayberry type is characterized by abundant *Q. ilicifolia*, *V. angustifolium*, *G. procumbens*, *E. repens*, *Aralia nudicaulis* and *Prunus serotina*. Other common species include *Myrica pensylvanica*, *Smilax rotundifolia*, *Acer rubrum*, *Pteridium aquilinum*, *Maianthemum canadense* and *Sassafras albidum*. This type is more variable in composition than other groups and may have been separated into mesic woodlands and *Q. ilicifolia* thickets if more stands of those types were sampled.

Relationships among vegetation and land-use history

Compositional and structural variation is strongly related to differences in past land-use. The Pine-Bearberry, Pine-Hairgrass and Pine-Oak-Sedge types have open understories of *Arctostaphylos uva-ursi*, graminoids, and herbs, and occur preferentially in previously plowed sites (Table 5; Figure 7a). In contrast, the Pine-Oak-Huckleberry, Pine-Scrub Oak-Crowberry and Pine-Scrub Oak-Bayberry types have dense shrub understories, lack abundant herbs and grasses, and occur more frequently in former woodlots (Table 5; Figure 7a).

Although vegetation patterns do not closely track differences in soil texture, several other site variables do differ among sites supporting different vegetation types (Table 5). In addition to having relatively steep slopes, sites supporting the Pine-Scrub-Oak-Bayberry type have soil concentrations of total N, P, K, TEC, % organic matter, and total C that are similar to sites supporting the Pine-Oak-Sedge type (Table 5). These two groups of sites in turn have higher concentrations of total N, TEC, and % organic matter than sites that support the Pine-Hairgrass, Pine-Scrub Oak-Crowberry, Pine-Oak-Huckleberry types (Table 5). Soil pH is relatively high in sites that support the Pine-Bearberry, Pine-Hairgrass, and Pine-Oak-Sedge types (Table 5).

Table 5. Differences in disturbance history and site conditions among the woodland vegetation types of Cape Cod National Seashore. Categories of past disturbance are shown if they occur in >33% of the plots of that vegetation type. Past land-use categories: P = plowed, O = open, and W = woodlot; fire categories: Y = field evidence of fire, N = no field evidence of fire. G-tests indicate whether vegetation types show affinity for different categories of past disturbance. Median values are shown for site factors, with Kruskal-Wallis statistic (H) and p-values for tests that site factors do not differ among vegetation types. All tests with p < 0.01 are significant at α = 0.05 after accounting for multiple comparisons. Similar letters within rows indicate that post-hoc tests show no significant difference between a pair of vegetation types.

				VEGETATION TYPE				
	Pine Bearberry	Pine Hairgrass	Pine-Oak Sedge	Pine-Scrub Oak Crowberry	Pine-Oak Huckleberry	Pine-Scrub Oak Bayberry		
DISTURBANCES	n = 6	n = 12	n = 21	n = 8	n = 35	n = 5	G_{adj}	p
Past land-use	P^a	P^a	P^a	W/O^b	W^b	W^{ab}	80.2	<0.001
Evidence of Fire	N^b	N^b	Y/N^{ab}	Y/N^{ab}	Y^a	Y^a	33.9	<0.001
SITE FACTORS							H	p
% Silt + Clay	9.5	6.5	8.0	4.9	6.0	8.0	10.6	0.060
Slope (degrees)	2.0^c	4.5^{bc}	2.0^c	3.0^c	6.5^{ab}	11.0^a	21.3	0.001
TSI (x100)	-0.6	-0.5	0.4	0.6	0.4	3.3	5.3	0.380
N (%)	0.043^{ab}	0.036^{bc}	0.049^a	0.030^c	0.036^{bc}	0.049^{ab}	25.6	0.000
pH	4.5^{ab}	4.4^a	4.4^a	4.2^{bc}	4.2^c	4.0^c	22.5	0.000
P (mg/kg)	8^b	14^a	14^a	6^c	7^{bc}	12^{ab}	40.2	0.000
K (mg/kg)	11^a	11^{ab}	14^a	8^b	8^b	15^{ab}	17.9	0.003
Ca (mg/kg)	47	54	54	28	28	32	10.9	0.054
Mg (mg/kg)	14	12	13	13	10	13	8.4	0.135
TEC (mequ/100 g)	6.3^{bc}	4.7^e	10.6^{ab}	5.7^{cd}	5.7^c	10.8^a	26.4	0.000
Organic Matter (%)	1.2^{ab}	1.1^c	1.5^a	0.8^c	1.3^{bc}	2.1^{ab}	18.6	0.002
C (%)	1.02^{ab}	0.90^b	1.21^a	0.70^b	1.04^a	1.45^a	16.2	0.006
C:N	23.2	23.9	25.0	23.0	28.3	29.5	13.5	0.019
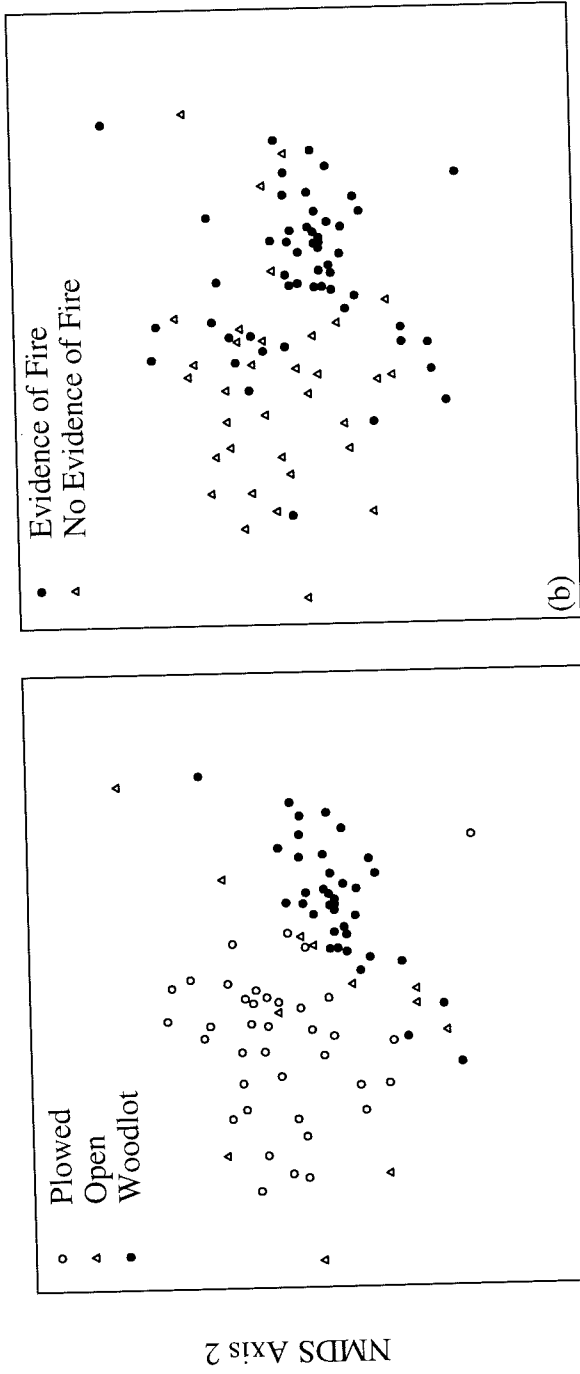
Figure 7. Distribution of past land-use categories (a) and evidence of fire (b) shown in ordination space derived from species cover-abundance data from woodlands of Cape Cod National Seashore.

Field evidence of fire was found infrequently in the Pine-Hairgrass and Pine-Bearberry types relative to the Pine-Oak-Huckleberry and Pine-Scrub Oak-Bayberry types (Table 5; Figure 7b). The Pine-Oak-Sedge and Pine-Scrub Oak-Crowberry types show intermediate frequencies of charcoal or scaring (Table 5; Figure 7b)

Individual species distributions

Ten of the 20 common but not ubiquitous species occur disproportionately in distinct categories of past land-use: *Deschampsia flexuosa*, *Schizachyrium scoparium*, *Chimaphila maculata*, *Trientalis borealis*, *Prunus serotina*, and *Arctostaphylos uva-ursi* occur significantly more frequently in previously plowed woodlands, whereas the ericaceous shrubs *Gaultheria procumbens*, *Vaccinium pallidum*, *Epigaea repens*, and *Gaylussacia baccata* occur significantly more frequently in former woodlots (Figure 8).
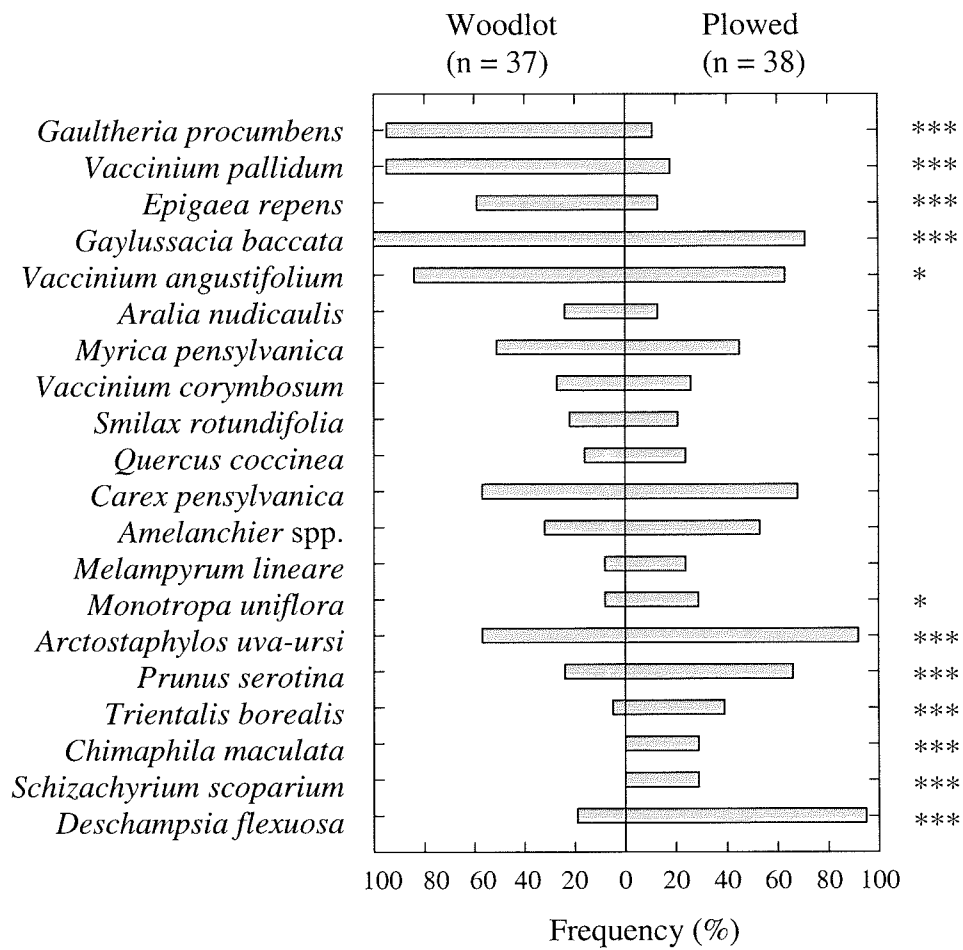
Figure 8. Distribution of common but not ubiquitous species in woodlands with different land-use histories on Cape Cod National Seashore. G-tests results: *** = p < 0.001, * = p < 0.05. Tests with p < 0.01 are significant at α = 0.05 after accounting for multiple comparisons.

DISCUSSION

I estimate that over half of the uplands of Cape Cod National Seashore had been cleared by the mid-nineteenth century for agriculture, and more than 100 years after abandonment, past land-use activities continue to influence modern vegetation patterns independent of the effects of current site conditions. The persistent impact of past land-use can be explained by differences in land-use intensity, notably the extent that native vegetation was locally eradicated and biological constraints on plant species dispersal and establishment back onto sites following agricultural abandonment. Although fire has strongly influenced overstory composition and structure in areas that remained wooded throughout the historical period, it is not responsible for generating the dominant compositional and structural differences documented across the study area. An understanding of the long-term impacts of past land-use is critical to understanding this important biological reserve and may inform management of uncommon heathland and grassland habitats.

Land-cover and land-use change

Palynological evidence and written descriptions suggest that pine-oak woodlands were predominant on eastern Cape Cod at the time of European settlement, perhaps with lesser amounts of mesophytic taxa including *Fagus*, *Carya*, and *Tsuga* occurring in moister, low-lying areas or on fine-textured soils (Altpeter 1937; Ruberstone 1985; Winkler 1985; Dunwiddie and Adams 1995). However Samuel de Champlain's maps and written accounts from 1605 also indicate that open, treeless areas were present in the vicinity of aboriginal settlements, in isolated areas immediately adjacent to the coast, and

in the Provincelands, a 3500 ha late-Holocene dune field located north of the outwash

plains (Winship 1905; Holmes et al. 1998).

European settlement of eastern Cape Cod in the seventeenth century initiated 150-

200 years of land-use that included forest clearance, cultivation, livestock grazing,

burning, and forest cutting. The 1848-56 maps underscore the dramatic impact of

European land-use by the mid-nineteenth century, when the landscape was settled,

predominately open, and crossed by an extensive road network. Woodland occurred in

large intact blocks in the eastern portions of the towns yet still covered only 20% of the

land, which was less than New England as a whole and comparable to heavily agrarian

sections of central Massachusetts (Foster 1992; Foster 1995; Foster et al. 1998).

In the mid-nineteenth century population and farming activity declined due to

opening of the western United States, urban industrialization, and a local decline

maritime industries (Raup and Carlson 1941; Raup 1966; Foster 1995; Holmes et al.

1998). The timing and geographic pattern of agricultural abandonment between 1856

and 1937 are uncertain, however, because no maps from the late-nineteenth century

indicate land cover. Continued grazing, particularly in Truro, may have prevented tree

establishment following the abandonment of arable land (state agricultural census data,

1865-1905). Canopy stem ages are consistent with contemporary observations of

extensive pitch pine establishment in formerly plowed fields in the late-nineteenth to

early-twentieth century (Collins 1909). In continuously wooded stands most canopy

stems appear to have been initiated by severe fires that occurred after 1900 (see below).

Aerial photos further indicate that most modern woodland canopies had established by

1938, although they show some formerly plowed or open sites supporting treeless heathland or grassland habitats.

The current extent of woodland obscures the extent of past agricultural activity. Based on historical sources and field studies modern woodlands and their associated vegetational characteristics can be ascribed to three broad categories of past land-use: approximately 44% was plowed during the historical period, 42% was cut but never cleared completely, and the remaining 14% was subjected to other uses. These different types of past land-uses are highly aggregated across the landscape in relation to site conditions. Previously plowed sites occur in relatively flat areas with fine-textured soils on the Eastham and Truro Plains, where plowing was easier and soils were more fertile. In contrast areas used as woodlots or subjected to other uses are concentrated in areas with more variable topography and coarse-textured soils on the Wellfleet Pitted Plain. The presence of navigable harbors in Wellfleet and Truro also may have discouraged intensive upland management such as plowing by providing opportunities for individuals to engage in maritime activities such as shipping, whaling, and fishing (Rockmore 1979; Ruberstone 1985).

Relationships among vegetation, past land-use, and site conditions

The differences in past land-use across Cape Cod National Seashore correspond with striking differences in current species composition and abundance that persist despite the 100+ years that have followed agricultural abandonment. Former woodlots typically support relatively abundant canopy *Quercus velutina* and *Q. alba* and dense understories of low shrub species such as *Gaylussacia baccata, Vaccinium pallidum, Gaultheria procumbens*, and *Epigaea repens*. In contrast sites that were plowed during

34

the historical period typically lack canopy *Q. alba* or abundant ericaceous shrubs; instead, they have understories dominated by *Deschampsia flexuosa, Arctostaphylos uva-ursi, Prunus serotina, Trientalis borealis, Schizachyrium scoparium*, and *Chimaphila maculata*.

An examination of environmental variables confirms that eastern Cape Cod is less heterogeneous than inland landscapes where compositional variation may be explained by a combination of differences in past land-use and associated environmental gradients (Glitzenstein et al. 1990; Motzkin et al. 1999b). Soil texture in the study area is weakly correlated with vegetation patterns, and the direct effects of slope are seen primarily in the Pine-Scrub Oak-Bayberry type. The occurrence of this association on steep lower slopes indicates that proximity to the water table and cool air drainage may influence its composition and structure (Aizen and Patterson 1993). Other aspects of the environmental variation indicate that vegetation/land-use relationships are not spurious correlations between past land-use and site conditions. The edaphic characterisitcs of sites supporting the Pine-Oak-Huckleberry, Pine-Scrub Oak-Crowberry and Pine-Hairgrass are quite similar, although the only the latter group of sites has been plowed frequently. Differences in land-use history between the Pine-Scrub Oak–Bayberry and Pine-Oak-Sedge types also do not coincide with differences in site conditions. In fact, soil pH is the only edaphic variable that varies with compositional variation in a way that is strongly confounded with past land-use. It is likely, however, that the differences in pH were generated by land-use practices, since land clearance and cultivation are known to cause persistent reductions in forest soil acidity (Richter et al. 1994; Koerner 1997; Verheyen et al. 1999).

It is possible to hypothesize about the mechanisms by which past land-use exerts persistent impacts on woodland vegetation patterns. In general past land-use can impact vegetation patterns by physically-eliminating species or by altering environmental conditions, and these impacts may persist because of limitations on dispersal or restrictions to establishment (Peterken and Game 1984; Matlack 1994; Honnay et al. 1999; Donahue et al. 2000). Similar to patterns documented in this study, *Gaultheria procumbens*, *Vaccinium pallidum*, and *Gaylussacia baccata* are characteristic of former woodlots on xeric sand plains in central Massachusetts, yet they occur only infrequently on previously plowed sites (Motzkin et al. 1996, 1999a). These species apparently were eradicated locally by repeated plowing and may fail to re-colonize for decades or centuries because of limitations on dispersal and more importantly constraints on establishment (Motzkin et al. 1996; Donahue et al. 2000). This scenario likely applies on eastern Cape Cod and is consistent with the observation that *G. procumbens*, *V. pallidum*, and *G. baccata* occur infrequently both at previously plowed sites and at unplowed sites on Great Island in Wellfleet where the original vegetation was eradicated by forest clearance, intensive grazing, and erosion (Friedman 1993).

Historical land-use also has influenced the modern distribution of several species that are absent or uncommon on inland sand plains. For instance *Epigaea repens* is an ericaceous shrub species that is largely restricted to former woodlots, perhaps as a result of limitations on dispersal since its seeds are ant-dispersed and myrmecochores often are slow to colonize areas that were cleared in the past for crop cultivation or pasture land (Clay 1983; Matlack 1994; Brunet and Oheimb 1998; Bossuyt et al. 1999). Among the species that occur more frequently in previously plowed woodlands, *Arctostaphylos uva-*

ursi is well-known to colonize open, xeric sites, where rapid seed establishment and clonal growth rates allow it to become relatively abundant (Hobbs et al. 1984). *Schizachyrium scoparium* behaves similarly as a frequent colonist of abandoned fields (e.g. Niering and Dreyer 1989). However both species are shade intolerant and persist only in low abundance following the establishment of woody vegetation. In contrast *Deschampsia flexuosa*, *Prunus serotina*, *Trientalis borealis*, and *Chimaphila maculata* have effectively colonized areas that were plowed yet appear able to persist under woodland canopies.

Despite the relative abundance of historical information for eastern Cape Cod, the spatial and temporal patterns of European land-use practices were extremely complex and largely undocumented. Prior to the establishment of Cape Cod National Seashore in 1961, parcels of land in this large, topographically heterogeneous study area were owned privately for 200-300 years by numerous people whose sustenance and economic prosperity depended directly on the management of local natural resources. Many of their individual management activities never will be known and yet almost undoubtedly continue to influence vegetation composition and ecosystem function (Foster et al. 1992; Verheyen et al. 1999). The available historical information provides a particularly incomplete description of historical impacts in the "open" category of past land-use. Surprisingly, however, the most conspicuous differences in vegetation result simply from differences in the extent to which native vegetation was eliminated from individual sites. Since these differences in past land-use intensity can be characterized effectively with available historical sources and soils descriptions, it has been possible to document the major persistent influences of past land-use on vegetation patterns.

Relationship among past land-use, fire history, and vegetation

Fires have occurred throughout the Holocene on eastern Cape Cod, and most common plant species have traits both that encourage fire spread and allow for regeneration following fire (Patterson et al. 1984; Winkler 1985; Matlack et al. 1992). Although documentary evidence of fires before 1900 is almost wholly absent, fires almost definitely occurred in woodlands and cleared areas throughout the historical period due to the inflammability of the vegetation and the extensive use of fire to improve agricultural land in New England (Russell 1976; Cronon 1983). There is some indication, however, that fire frequency increased in the late-nineteenth century when the initiation of railroad service introduced a new source of ignitions. There are historical records from the early twentieth century of fires occurring in areas ultimately included within CACO boundaries both in woodlands and open habitats including heathlands ("moors") and grasslands. Fire size and severity declined dramatically in the second half of the twentieth century with the onset of effective fire suppression (Patterson et al. 1984; Dunwiddie and Adams 1995).

Some of the larger woodland fires in the early twentieth century resulted in canopy mortality and allowed for the establishment and/or sprouting of *Pinus ridga, Quercus alba* and *Q. velutina.* These fires occurred primarily on the Wellfleet Pitted Plain where woodlots were concentrated during the historical period and modern vegetation is dominated by the Pine-Oak-Huckleberry, Pine-Scrub Oak-Crowberry, and Pine-Scrub Oak-Bearberry types. Canopy ages and the frequent occurrence of charcoal

and fire scars further corroborates the interpretation that these fires strongly influenced modern overstory composition and structure in many stands of these types.

At sites that were plowed during the historical period, land-use activities greatly altered fuel characteristics by eradicating understory shrubs and allowing for the establishment of grasses, forbs, and shade-intolerant shrub species following agricultural abandonment. These treeless habitats occurred primarily on the Eastham and Truro Plains, where few large fires are known to have burned and field evidence of fire is uncommon. The lack of direct evidence for fires to some extent reflects the under-reporting of grassland fires (Massachusetts Forestry Association 1928) and the low levels of charcoal and fire scars produced in treeless habitats. However following tree re-establishment large fires would have been noted in the historical record and would have left field evidence of their occurrence. The available information indicates, therefore, that woodland fires have occurred relatively infrequently in former agricultural areas currently supporting the Pine-Oak-Sedge, Pine-Hairgrass, and Pine-Bearberry types. Overstory composition and structure in these assemblages principally reflect the initial establishment of *Pinus rigida* into old fields followed in many cases by *Quercus velutina* and *Q. alba* (Stevens 1940; Little 1979).

Major compositional distinctions documented in this study reflect variation in the distribution and abundance of understory species, and it is possible that fire influenced understory compositional patterns. However these impacts are not readily apparent in the modern landscape and appear primarily to have modified pre-existing compositional differences related to past land-use. The potential impacts of past fires on understory composition were determined by differences in local fuel characteristics stemming from

past agricultural activity. In areas that remained wooded throughout the historical period, low severity fires likely resulted in few compositional changes because of the exceptional sprouting ability of ericaceous shrubs (Matlack et al. 1992). This high degree of compositional stability contrasts with the potential effects of high severity fires that may have killed canopy stems, exposed mineral soil, and increased the relative abundance of shade intolerant species including *Quercus ilicifolia* and *Arctostaphylos uva-ursi*. In previously plowed areas compositional changes that occurred following fire in treeless habitats would have depended strongly on initial species composition, fire season, and time since the last fire (Niering and Dreyer 1989; Vickory and Dunwiddie 1997). In both former woodlots and agricultural areas, however, effective fire suppression has led to woodland canopy closure and the accumulation of organic matter, which appears to have altered or eliminated many of the compositional effects of past fires. This is similar to the scenario documented in xeric pine-oak forests in the southern Appalachians (Harrod et al. 2000). In contrast limitations on shrub re-colonization have resulted in persistent compositional differences stemming from past agricultural activity, and overall variation in species composition and abundance strongly reflect differences in past land-use.

Implications for natural resource management

When reserves and conservation areas like CACO initially were established relatively little regard was paid to incorporating a dynamic perspective into the interpretation of current conditions and the development of management guidelines for sand plain ecosystems. However with time there has been a progressive decline in heathland and grassland habitat and their associated biota, and an understanding of sand plain vegetation dynamics has emerged that emphasizes the role of disturbances, notably

fire, in maintaining treeless areas and determining landscape-level patterns of vegetation. The results of this study argue for a major re-thinking of current models of vegetation dynamics by indicating that past land-use is primarily responsible for modern compositional differences and possibly the origin of uncommon heathland and grassland communities.

In particular the results document that large portions of the currently wooded landscape were plowed during the historical period. Pre-existing vegetation was largely eradicated by plowing, and following agricultural abandonment species began to re-establish in former agricultural lands. The composition and structure of treeless old-field habitats is not well-documented, but they differed substantially from the understory assemblages of former woodlots because of constraints on woodland shrub re-establishment. Furthermore the composition of these open old-field communities was undoubtedly highly dynamic in response to fire, grazing, and the modification of site conditions that followed the establishment of woody vegetation.

Three lines of evidence suggest, however, that at least some treeless old-field communities in CACO would have been classified as heathlands and grasslands. (1) Written descriptions from the early twentieth century indicate that heathland and grassland species occurred in what may have been recently abandoned fields or pastures. For instance Blankinship (1903) describes a "Sand Barren Formation" occurring on Cape Cod on "dry sand hills, drifting sands, and open sandy fields and plains" that includes the heathland and grassland species *Arctostaphylos uva-ursi, Corema conradii, Hudsonia tomentosa, H. ericoides, Chrysopsis falcata,* and *Aster linariifolius.* Collins (1909) also notes that *A. uva-ursi, C. conradii, H. tomentosa, H. ericoides,* and *C. falcata* were

41

"species of general distribution" in Eastham, and that *A. uva-ursi* was "very abundant, the shining leaves carpeting large stretches of sand." (2) From the 1938 aerial photos, heathlands and grasslands are known to have occurred in the few plowed or open areas in the study area that remained treeless into the mid-twentieth century. (3) The modern understory composition of many previously plowed areas includes the common heathland and grassland species *Deschampsia flexuosa*, *A. uva-ursi*, and *S. scoparium*, which presumably occurred prior to tree establishment and have persisted in woodland habitats (Dunwiddie et al. 1996).

Heathlands and grasslands therefore appear to have developed in many agricultural areas and have become much less common over the past 150 years because of old-field succession. The decline of these habitats, which are globally uncommon and can support a number of rare plant and animal species (Appendix B in Christensen et al. 1996; Dunwiddie et al. 1996; Vickery and Dunwiddie 1997), has mobilized conservation organizations and government agencies throughout the region to adopt active management strategies. The situation closely parallels conservation and management priorities in Europe, where many uncommon habitats shaped by centuries of land-use activity are threatened by declines in traditional agricultural practices (Kirby and Watkins 1998).

No active heathland and grassland management currently occurs within CACO, but management efforts elsewhere in the region have focused almost exclusively on the use of prescribed fire to maintain open conditions. The use of fire has been justified based on (1) the role fire may have played in maintaining hypothesized presettlement occurrences of treeless habitats (Vickory and Dunwiddie 1997); and (2) the perception

that effective fire suppression in the mid-twentieth century directly resulted in the decline of heathland and grasslands (Dunwiddie and Adams 1995). It is possible that treeless habitats were uncommon components of presettlement vegetation mosaics on eastern Cape Cod. However the current study indicates that heathlands and grasslands became much more extensive across the region following European settlement in areas that were most intensively impacted by agricultural activity (Dunwiddie 1989). Furthermore the historical record for CACO indicates that trees established in these areas during the early twentieth century before fire suppression became effective. I suggest, therefore, that heathland and grassland management strategies would be better rooted in a more comprehensive understanding of past land-use, fire, and associated vegetation dynamics that have led to current conditions. Rather than manage exclusively with prescribed fire, a careful consideration of disturbance history might lead conservation organizations and government agencies to adopt management approaches that mimic the full range of past agricultural practices (e.g. Tiffney 1997; Dunwiddie 1997).

CONCLUSIONS

Much of the ecological research pertaining to the management of biological reserves addresses the impacts of modern human activity or the human disruption of natural processes. Examples include recreational activity, atmospheric pollution, climate change, and fire suppression (Forman and Boerner 1981; Baker 1992; Cole and Landres 1996; Bartlein et al. 1997). The results from this study point to the need for ecologists and natural resource managers to broaden conceptions of human impacts to include the long-term legacies of past land-use. Although the specific impacts of past agriculture on

Cape Cod National Seashore depend greatly on the cultural and ecological setting of eastern Cape Cod, the geographical pervasiveness of past land-use makes it almost certain that analogous patterns are present throughout the northeastern United States and other regions with comparable histories (e.g. Matlack 1994; Koerner et al. 1997; Foster et al. 1999). Ecologists and natural resource managers working in such regions should consider explicitly the possibility that past land-use has played a dominant role in shaping current conditions, and when necessary they should incorporate past land-use into the "sound ecological models and understanding" that ultimately form the scientific basis of ecosystem management (Christensen et al. 1996).

LITERATURE CITED

Aizen, M.A. and W.A. Patterson III. 1995. Leaf phenology and herbivory along a temperature gradient: a spatial test of the phenological window hypothesis. Journal of Vegetation Science **6**: 543-550.

Allen, D.Y. 1997. Long Island Maps and Their Makers. Amereon House. Mattituck, New York, U.S.A.

Altpeter, L.S. 1937. A history of the forests of Cape Cod. Master's Thesis, Harvard University. Petersham, Massachusetts, U.S.A.

Baker, W.L. 1992. Effects of settlement and fire suppression on landscape structure. Ecology **73**: 1879-1887.

Bartlein, P.J., C. Whitlock, and S.L. Shafer. 1997. Future climate in the Yellowstone National Park region and its potential impact on vegetation. Conservation Biology **11**: 782-792.

Blackmore, A.C., M.T. Mentis, and R.J. Scholes. 1990. The origin and extent of nutrient-enriched patches within a nutrient-poor savanna in South Africa. Journal of Biogeography **17**: 463-470.

Blankinship, J.W. 1903. The plant formations of eastern Massachusetts. Rhodora **5**: 124-137.

Bragdon, K.J. 1996. Native People of Southern New England, 1500-1650. University of Oklahoma Press. Norman, Oklahoma, U.S.A.

Bratton, S.P. and S.G. Miller. 1994. Historic field systems and the structure of maritime oak forests, Cumberland Island National Seashore, Georgia. Bulletin of the Torrey Botanical Club **121**: 1-12.

Bussuyt, B., M. Hermy, and J. Deckers. 1999. Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. Journal of Ecology **87**: 628-638.

Brunet, J. and G. von Oheimb. 1998. Migration of vascular plants to secondary woodlands in southern Sweden. Journal of Ecology **86**: 429-438.

Cahoon, R.H. 1915. Forest fires on the Cape. Cape Cod Magazine **1**(3): 17-18.

Cook, H.O. 1921. Forest fire risk in Massachusetts. Journal of Forestry **19**: 762-766.

Christenson, N.L., A.M. Bartuska, J.R. Brown, S. Carpenter, C. D'Antonio, R. Francis, J.F. Franklin, J.A. MacMahon, R.F. Noss, D.J. Parsons, C.H. Peterson, M.G. Turner, and R.G. Woodmansee. 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecological Applications **6**: 665-691.

Clark, J.S. 1986. Coastal forest populations in a changing environment, southeastern Long Island, New York. Ecological Monographs **56**: 259-277.

Clark, J.S. 1990. Fire and climate change during the last 750 years in northwestern Minnesota. Ecological Monographs **60**: 135-159.

Clay, K. 1983. Myrmecochory in the trail arbutus (*Epigaea repens* L.). Bulletin of the Torrey Botanical Club **110**: 166-9.

Coffin, D.P., W.K. Lauenroth, and I.C. Burke. 1996. Recovery of vegetation in a semiarid grassland 53 years after disturbance. Ecological Applications **6**: 538-555.

Cole, D.N. and P.B. Landres. 1996. Threats to wilderness ecosystems: impacts and research needs. Ecological Applications **6**: 168-184.

Collins, F.S. 1909. Notes on the flora of lower Cape Cod. Rhodora **11**: 125-133.

Conover, W.J. 1980. Practical Nonparametric Statistics. John Wiley & Sons. New York, New York, U.S.A.

Cronon, W. 1983. Changes in the Land. Hill and Wang. New York, New York, U.S.A.

Donahue, K., D.R. Foster, and G. Motzkin. 2000. Effects of the past and present on species distributions: land-use history and demography of wintergreen. Journal of Ecology **88**: 303-316.

Dunwiddie, P.W. 1989. Forest and heath: the shaping of the vegetation on Nantucket Island. Journal of Forest History **33**: 126-133.

Dunwiddie, P.W. 1997. Long-term effects of sheep grazing on coastal sandplain vegetation. Natural Areas Journal **17**: 261-264.

Dunwiddie, P.W. and M.B. Adams. 1995. Fire suppression and landscape change on Outer Cape Cod 1600-1994. US Department of Interior Technical Report NPS/NESO-RNR/NRTR/96-08. Washington, D.C., U.S.A.

Dunwiddie, P.W., R.E. Zaremba, and K.A. Harper. 1996. A classification of coastal heathlands and sand plain grasslands in Massachusetts. Rhodora **98**: 117-145.

Dwight, T. 1969. Travels in New England and New York. Harvard University Press. Cambridge, Massachusetts, U.S.A.

Fletcher, P.C. 1993. Soil Survey of Barnstable County, Massachusetts. United States Department of Agriculture Soil Conservation Service. Washington, DC, U.S.A.

Forman, R.T.T. and R.E. Boerner. 1981. Fire frequency and the Pine Barrens of New Jersey. Bulletin of the Torrey Botanical Club **108**: 34-50

Foster, D.R. 1992. Land-use history (1730-1990) and vegetation dynamics in central New England, USA. Journal of Ecology **80**: 753-772.

Foster, D.R. 1995. Land-use history and four hundred years of vegetation change in New England. Pages 253-319 *in* B.L. Turner II, A.G. Sal, F.G. Bernaldez, and F. di Castri, editors. Global Land Use Change. A Perspective from the Columbian Encounter. Consejo Superior de Investigaciones Cientificas. Madrid, Spain.

Foster, D.R. 1999. Thoreau's Country. Harvard University Press. Cambridge, Massachusetts, U.S.A.

Foster, D.R. and G. Motzkin. 1999. Historical influences on the landscape of Martha's Vinyard: perspectives on the management of the Manuel F. Correllus State Forest. Harvard Forest Paper No. 23. Petersham, Massachusetts, U.S.A.

Foster, D.R., T. Zebryk, P. Schoonmaker, and A. Lezberg. 1992. Post-settlement history of human land-use and vegetation dynamics of a *Tsuga canadensis* (hemlock) woodlot in central New England. Journal of Ecology **80**: 773-786.

Foster, D.R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in central New England. Ecosystems **1**: 96-119.

Foster, D.R., M. Fluet, and E.R. Boose. 1999. Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. Ecological Applications **9**: 555-572.

Friedman, R.L. 1992. Governing the Land: An Environmental History of Cape Cod, Massachusetts, 1600-1861. Ph.D. Dissertation, Brandeis University. Waltham, Massachusetts, U.S.A.

Gleason, H.A. and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. The New York Botanical Garden. New York, New York, U.S.A.

Grieg-Smith, P. 1983. Quantitative Plant Ecology. University of California Press. Berkeley, California, U.S.A.

Glitzenstein, J.S., C.D. Canham, M.J. McDonnell and D.R. Streng. 1990. Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. Bulletin of the Torrey Botanical Club. **117**: 106-122.

Grossman, D.H., D. Faber-Langendoen, A.S. Weakly, M. Anderson, P. Bourgeron, R. Crawford, K. Goodin, S. Landaal, K. Metzler, K.D. Patterson, M. Pyne, M. Reid, and L. Sneddon. 1998. International classification of ecological communities: terrestrial vegetation of the United States. Volume 1: The National Vegetation Classification System: development, status and applications. The Nature Conservancy. Arlington, Virginia, U.S.A.

Harrod, J.C., M.E. Harmon, and P.S. White. 2000. Post-fire succession and 20th century reduction in fire frequency on xeric southern Appalachian sites. Journal of Vegetation Science **11**: 465-472.

Heinselman, M. 1996. The Boundary Waters Wilderness Ecosystem. University of Minnesota Press, Minneapolis, MN, U.S.A.

Holmes, R.D., C.D. Hertz, and M.T.Mulholland. 1998. Historical cultural land use study of lower Cape Cod. Cultural Resource Center, Northeast Region, National Park Service, U.S. Department of the Interior. Lowell, Masschusetts, U.S.A.

Honnay, O., M. Hermy, and P. Coppin. 1999. Impact of habitat quality on forest plant species colonization. Forest Ecology and Management **115**: 157-170.

Hobbs, R.J., A.U. Mallik, and C.H. Grimingham. 1984. Studies on fire in Scottish heathland communities III. Vital attributes of the species. Journal of Ecology **72**: 963-976.

Kirby, K.J. and C. Watkins, editors. 1998. The Ecological History of European Forests. CAB International. New York, New York, U.S.A.

Koerner, W., J.L. Dupouey, E. Dambrine, and M. Benoît. 1997. Influence of past land use on the vegetation and soils of the present day forest in the Vosges mountains, France. Journal of Ecology **85**: 351-358.

Little, S. 1979. Fire and plant succession in the New Jersey Pine Barrens. Pages 297-314 *in* R.T.T. Forman, editor. Pine Barrens: Ecosystem and Landscape. Academic Press. New York, New York, U.S.A.

Little, S. and E.B. Moore. 1949. The ecological role of prescribed burning in the pine-oak forests of southern New Jersey. Ecology **30**: 223-233.

MacConnell, W.P., N.A. Pywell, D. Robertson, and W. Niedzwiedz. 1974. Remote sensing 20 years of change in Barnstable, Dukes, and Nantucket Counties, Massachusetts, 1951-1971. Massachusetts Agricultural Experiment Station Bulletin No. 623. Amherst, Massachusetts, U.S.A.

Massachusetts Forestry Association. 1928. The Cape Cod Forest Fire Prevention Experiment. Boston, Massachusetts, U.S.A.

Massachusetts Historical Society. 1802. A description and history of Eastham, in the county of Barnstable. Pages 154-163 *in* Collections of Massachusetts Historical Society Volume VIII. Monroe and Francis. Boston, Massachusetts, U.S.A.

MassGIS. 1991. MassGIS datalayer descriptions and a guide to user services. Boston: Executive Office of Environmental Affairs, Environmental Data Center. Boston, Massachusetts, U.S.A.

Matlack, G.R., D.J. Gibson, and R.E. Good. 1992. Clonal propagation, local disturbance, and the structure of vegetation: ericaceous shrubs in the pine barrens of New Jersey. Biological Conservation **63**: 1-7.

Matlack, G.R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology **75**: 1491-1502.

Massachusetts Archives. 1830. 1830 Map Series. Boston, Massachusetts, U.S.A.

McCune, B. and M.J. Mefford. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design. Gleneden Beach, Oregon, U.S.A.

McDonnell, M.J. and S.T.A. Pickett, editors. 1993. Human as Components of Ecosystems. Springer-Verlag. New York, New York, U.S.A.

McLachlan, J.S., D.R. Foster, and F. Menalled. 2000. Anthropogenic ties to late-successional structure and composition in four New England hemlock stands. Ecology **81**: 717-733.

McManamon, F.P. 1984. Ecological niche theory, cultural adaptation, and current interpretations of prehistoric cultural adaptations of the southen New England coast. Pages 117-160 *in* F.P. McManamon, editor. Chapters in the archeology of Cape Cod. Cultural Resources Management Study No. 8. Division of Cultural Resources, North Atlantic Regional Office, National Park Service. Boston, Massachusetts, U.S.A.

McNab, W.H. 1989. Terrain slope index: quantifying effect of minor landforms on tree height. Forest Science **35**: 91-104.

Mehlich, A. 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. Communications in Soil Science and Plant Analysis **15**: 1409-1416.

Meier, A.J., S.P. Bratton, and D.C. Duffy. 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. Ecological Applications **5**: 935-946.

Motzkin, G., W.A. Patterson III, and N.E.R. Drake. 1993. Fire history and vegetation dynamics of a *Chamaecyparis thyoides* wetland on Cape Cod, Massachusetts. Journal of Ecology **81**: 391-402.

Motzkin, G., D. Foster, A. Allen, J. Harrod, and R. Boone. 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. Ecological Monographs **66**: 345-365.

Motzkin, G. W.A. Patterson III, and D.R. Foster. 1999a. A historical perspective on pitch pine-scrub oak communities in the Connecticut Valley of Massachusetts. Ecosystems **2**: 255-273.

Motzkin, G., P. Wilson, D.R. Foster, and A. Allen. 1999b. Vegetation patterns in heterogeneous landscapes: the importance of history and environment. Journal of Vegetation Science **10**: 903-920.

Niering, W.A. and G.D. Dreyer. 1989. Effects of prescribed burning on *Andropogon scoparius* in postagricultural grasslands in Connecticut. American Midland Naturalist **122**: 88-102.

Oldale, R.N. and R.A. Barlow. 1986. Geologic map of Cape Cod and the Islands, Massachusetts. Map I-1763. US Geological Survey Miscellaneous Investigations Series. Reston, Virginia, U.S.A. 1:100,000.

Parmenter, R.B. 1928. The forests of Barnstable county. Massachusetts Department of Forestry, Division of Forestry. Harvard Forest Archives. Petersham, Massachusetts, U.S.A.

Parsons, D.J., T.W. Swetnam, and N.L. Chistensen, editors. 1999. Uses and limitations of historical variability concepts in managing ecosystems. Ecological Applications **9**: 1177-1277.

Patterson, W.A. III, K.E. Saunders, and L.J. Horton. 1984. Fire regimes of Cape Cod National Seashore. U.S.D.I. National Park Service Office of Scientific Programs, Report OSS 83-1. Boston, Massachusetts, U.S.A.

Patterson, W.A. III and K.E. Sassman. 1988. Indian fires in the prehistory of New England. Pages 107-135 *in* G.P. Nicholas, editor. Holocene Human Ecology in Northeastern North America. Plenum Publishing Corporation. New York, New York, U.S.A.

Peterken, G.P. and M. Game. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. Journal of Ecology **72**: 155-182.

Pickett, S.T.A., editor. 1997. The Ecological Basis of Conservation. Chapman & Hall. New York, New York, U.S.A.

Pickett, S.T.A. and P.S. White, editors. 1985. The Ecology of Natural Disturbances and Patch Dynamics. Academic Press. Orlando, Florida, U.S.A.

Raup, H.M. 1966. The view from John Sanderson's farm. Forest History **10**: 2-11.

Raup, H.M. and R.E. Carlson. 1941. The history of land use in the Harvard Forest. Harvard Forest Bulletin Number 20. Petersham, Massachusetts, U.S.A.

Rice, W.R. 1989. Analyzing tables of statistical tests. Evolution **43**: 223-225.

Richter, D.D., D. Markewitz, C.G. Wells, H.L. Allen, R. April, P.R. Heine, and B. Urrego. 1994. Soil chemical change during three decades in an old-field loblolly pine (*Pinus taeda* L.) ecosystem. Ecology **75**: 1463-1473.

Rockmore, M. 1979. Documentary review of the historical archeology of the Cape Cod National Seashore. Division of Cultural Resources, North Atlantic Regional Office, National Park Service. Lowell, Masschusetts, U.S.A.

Romme, W.H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs **52**: 199-221.

Ruberstone, P.A. 1985. Changes in the coastal wilderness: historical land-use patterns on outer Cape Cod, 17-19th centuries. Pages 17-124 *in* McManamon, F.P., P.E. Rubertone and S. Terry Childs, editors. Chapters in the archeology of Cape Cod, III: the historic period and historic period archeology. Cultural Resources Management Study No. 13. Division of Cultural Resources, North Atlantic Regional Office, National Park Service. Lowell, Masschusetts, U.S.A.

Russell, H. 1976. A Long Deep Furrow. University Press of New England. Hanover, New Hampshire, U.S.A.

Russell, E.W.B., R.B. Davis, R.S. Anderson, T.E. Rhodes, and D.S. Anderson. 1993. Recent centuries of vegetational change in the glaciated north-eastern United States. Journal of Ecology **81**: 647-664.

Shalowitz, A.L. 1964. Shore and Sea Boundaries. U.S. Department of Commerce Coast and Geodetic Survey Publication 10-1. Washington, D.C., U.S.A.

Sokal, R.R. and F.J. Rohlf. 1995. <u>Biometry</u>. W.H. Freeman and Company. New York, New York, U.S.A.

Stevens, T.D. 1940. Forest succession on upland soils in the New Jersey Pine Barrens. Ph.D. Dissertation. Yale University. New Haven, Connecticut, U.S.A.

Stone, T.A. 1999. The land cover and land use of Cape Cod, 1951 to 1990. Environment Cape Cod **1**: 35-49.

Storer, D.A. 1984. A simple high volume ashing procedure for determination of soil organic matter. Communications in Soil Science and Plant Analysis **15**: 759-772.

Thoreau, H.D. 1989. <u>Cape Cod</u>. Penguin Books. New York, New York, U.S.A.

Tiffney, W.N. 1997. The role of nutrient-level control in maintaining and restoring lowland heaths: British and northern European techniques of potential application in northeastern North America. Pages 69-78 *in* Vickory, P.D. and P.W. Dunwiddie, editors. 1997. <u>Grasslands of Northeastern North America</u>. Massachusetts Audubon Society. Lincoln, Massachusetts, U.S.A.

U.S. Department of Agriculture. 1993. <u>Soil Survey Manual</u>. USDA Handbook Number 18. U.S. Government Printing Office, Washington, D.C., U.S.A.

Verheyen, K., B. Bossuyt, M. Hermy, and G. Tack. 1999. The land use history (1278-1990) of a mixed hardwood forest in western Belgium and relationship with soil chemical characteristics. Journal of Biogeography **26**: 1115-1128.

Vickory, P.D. and P.W. Dunwiddie, eds. 1997. <u>Grasslands of Northeastern North America</u>. Massachusetts Audubon Society. Lincoln, Massachusetts, U.S.A.

Westveld, M. 1956. Natural forest vegetation zones of New England. Journal of Forestry **54**: 332-338.

Whitney, G.G. 1994. <u>From Coastal Wilderness to Fruited Plain</u>. Cambridge University Press. New York, New York, U.S.A.

Winkler, M.G. 1985. A 12,000-year old history of vegetation and climate for Cape Cod, Massachusetts. Quaternary Research **23**: 301-12.

Winship, G.P., ed. 1905. <u>Sailors Narratives of Voyages along the New England Coast, 1524-1624</u>. Research Source Works Series #188, American Classics in History and Social Science # 30. Burt Franklin. Boston, Massachusetts, U.S.A.

WPA. 1937. Land-use maps for the Towns of Eastham, Wellfleet, and Truro. Massachusetts State Planning Board, Works Progress Administration, Boston, Massachusetts, U.S.A.