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CONSERVATION OF CHANGING LANDSCAPES: VEGETATION AND LAND-USE HISTORY OF CAPE COD NATIONAL SEASHORE

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Abstract. The pervasive impact of historical land use is often underappreciated in the management and restoration of conservation areas and natural resources. We used historical and ecological approaches to determine the relative influences of past land use, fire, and site conditions on woodland vegetation patterns in Cape Cod National Seashore (CACO), the largest protected coastal landscape and area of sand-plain vegetation in New England. Coastal sand plains are the focus of intense conservation activity because they support uncommon plant and animal assemblages that are dynamic as a result of past disturbance and ongoing human impacts.

CACO was predominantly wooded prior to extensive land clearance for historical agriculture. Historical maps and modern soil profiles indicate that by the mid-19th century, ~44% of the area supporting sand-plain woodlands in CACO was plowed for crops or pasture, 42% was logged repeatedly but never cleared, and 14% was open and subjected to diverse uses. Relationships between modern vegetation and 19th-century land use are striking and largely independent of site conditions. Continuously wooded areas support pine–oak woodlands with abundant ericaceous shrubs, whereas previously plowed sites have less canopy oak, more pine, few ericaceous shrubs, and a distinct understory including the grass *Deschampsia flexuosa* and the shade-intolerant shrub *Arctostaphylos uva-ursi*. Current composition and historical sources suggest that past agriculture generated extensive heathland and grassland habitats, much of which has subsequently reforested. In contrast to many interpretations and management guidelines, the persistent influence of fire is principally on the canopy composition and structure of former woodlots. The results highlight a need (1) to integrate an understanding of past land use into ecological models underlying the management of biological reserves; and (2) to consider the use of management approaches that mimic past agricultural practices in order to maintain and restore important sand-plain habitats.

Key words: Cape Cod National Seashore, Massachusetts (USA); fire; grasslands; heathlands; landscape conservation; land-use history; New England; pine barrens; pitch pine; sand plains.

INTRODUCTION

Based on substantial evidence that climate change and natural disturbance are important drivers of ecological change, an understanding of the natural variability of ecosystems is increasingly considered in natural area management (Romme 1982, Pickett and White 1985, Clark 1990, Heinselman 1996, Pickett 1997, Swanson et al. 1998, Parsons et al. 1999). Although historical land-use practices also exert profound impacts on natural systems, ecologists and conservationists have not fully embraced the notion that prior activities such as cultivation, grazing, and forest cutting may determine ecosystem structure, composition, and function and might be included in future management plans (Peterken and Game 1984, Blackmore et al. 1990, Meier et al. 1995, Coffin et al. 1996, Kirby and Watkins 1998, Foster et al. 1999, 2003). Land-use history may be particularly important in regions such as eastern North America that have been shaped by centuries of Euro-American activity (Russell et al. 1993, Whitney 1994, Foster et al. 1998, Foster 1999, 2000, McLachlan et al. 2000). In these areas, there is need to consider both natural and human processes and to integrate an understanding of past land use and natural variability into management policies for biological reserves (Motzkin et al. 1993, Bratton and Miller 1994, Foster and Motzkin 1999).

In the northeastern United States, "sand plains," distinctive ecosystems on deposits of glacial outwash primarily in coastal areas, are major centers of biodiversity and rarity and focal points for conservation activity. On the Massachusetts and New York coast, private, state, and federal effort has sought acquisition, protection, and management of these unusual habitats and biotic assemblages. In addition to woodlands and shrublands dominated by pitch pine (*Pinus rigida*) and oak (*Quercus* spp.), these drought-prone sites support globally uncommon grasslands and heathlands (Christensen et al. 1996, Dunwiddie et al. 1996). Past research on sand plains and related ecosystems has emphasized

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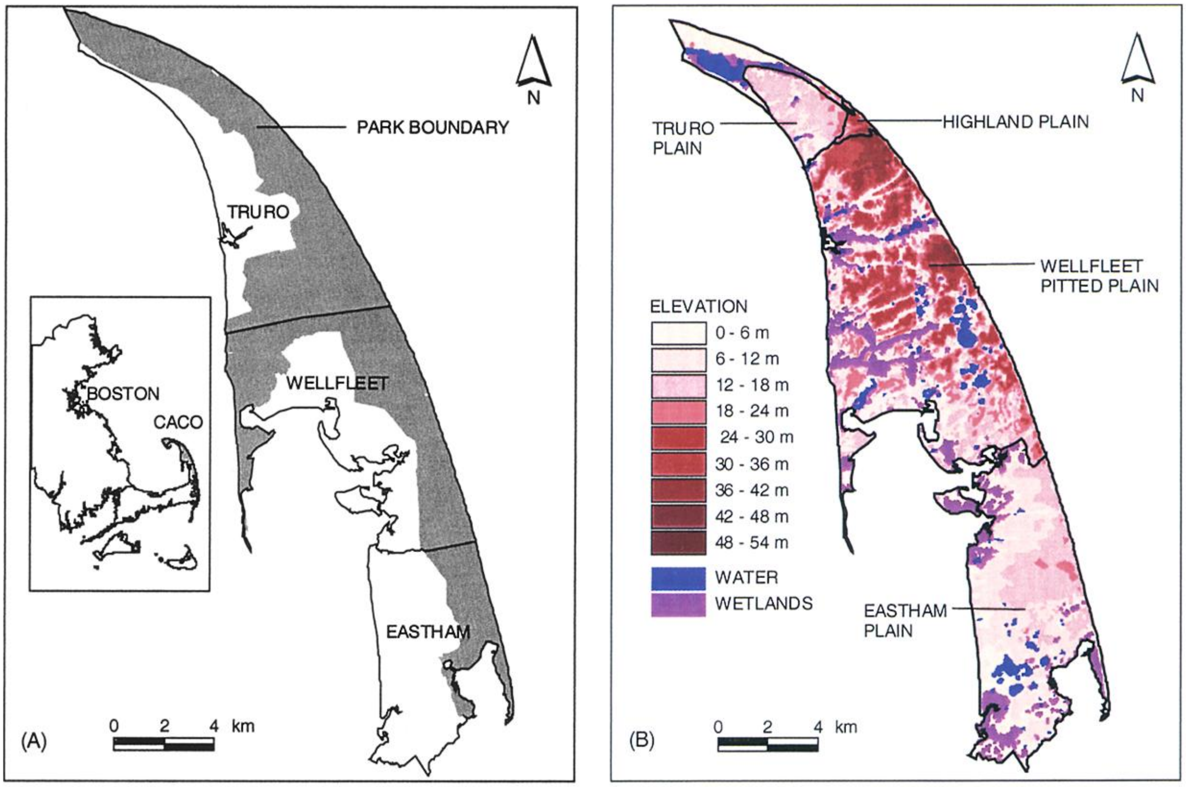

FIG. 1. (A) Location of Cape Cod National Seashore (CACO) in southeastern Massachusetts and study area showing town and park boundaries. (B) Topography of major sand plains, adapted from Oldale and Barlow (1986), with water and wetlands from MassGIS (1991).

the effects of fire on vegetation dynamics, structure, and composition and the negative consequences of fire suppression on habitat quality (Little and Moore 1949, Forman and Boerner 1981, Patterson et al. 1984, Vickery and Dunwiddie 1997). It has been hypothesized that fire was largely responsible for controlling the landscape pattern of forests of pitch pine, oak, and ericaceous plants and for maintaining coastal woodlands, heathlands, and grasslands before European settlement (Vickery and Dunwiddie 1997). The emphasis on fire has led conservation groups and government agencies to adopt management policies centered on the use of prescribed fire to perpetuate or restore vegetation patterns and plant assemblages. However most sand plains have a long history of human impacts, and no systematic attempt has been made to evaluate the occurrence and relative importance of past land use, fire, and site conditions on vegetation composition, structure, and landscape pattern.

Identifying the role of past human activity often is difficult because land use is poorly documented and may be correlated with the physical environment (Glitzenstein et al. 1990, Motzkin et al. 1999*b*). Motzkin et al. (1996, 1999*a*) identified land-use history as the primary determinant of modern vegetation patterns across edaphically homogeneous sand plains in central Massachusetts. The current study evaluates patterns of species composition and abundance across a more heterogeneous coastal landscape, focusing on Cape Cod National Seashore (CACO), the largest conservation area in the region. The research evaluates the relative importance of edaphic factors, land-use history, and fire in controlling modern vegetation patterns and addresses the following questions: (1) What have been the spatial and temporal patterns of land cover, land use, and fire on eastern Cape Cod since European settlement? (2) How was land use distributed in relation to site conditions? (3) How important are past land use and fire in explaining modern vegetation patterns relative to environmental factors? (4) What are the implications of these results for the conservation and management of sand-plain habitats?

STUDY AREA

Cape Cod National Seashore (CACO; 42°30′ N, 70°00′ W) is a 10 900-ha area managed by the National Park Service that spans eastern Cape Cod, Massachusetts on the Atlantic Coastal Plain (Fig. 1A). The park includes large tracts in the towns of Provincetown, Truro, Wellfleet, and Eastham, as well as smaller areas in Orleans and Chatham. Surficial deposits are largely Wisconsinan outwash plains and postglacial dunes but also include ice-contact, marsh, swamp, and beach deposits (Oldale and Barlow 1986). Mean January and

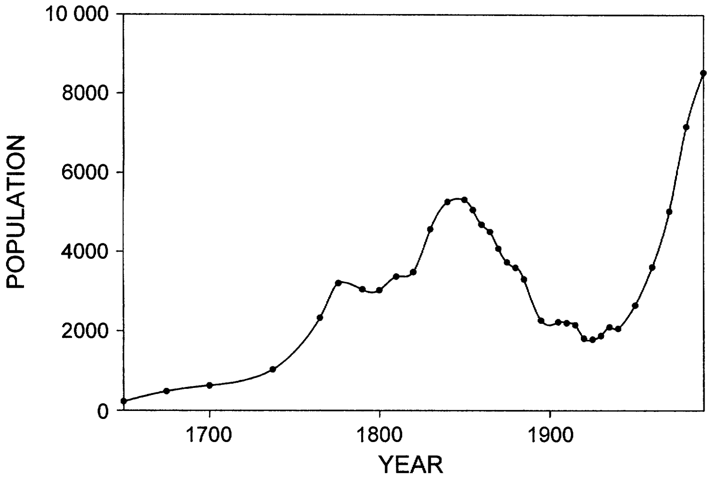

FIG. 2. European population trends in Eastham, Wellfleet, and Truro (1650–1990). Data for 1650–1765 are from Altpeter (1937), and state and federal census data are used for later time periods. Aboriginal populations are estimated to have been 450–500 as late as 1698 (Ruberstone 1985).

July temperatures (1900–1980 from Provincetown) are 0.4°C and 20.3°C, respectively; annual precipitation averages 102 cm and is evenly distributed throughout the year (Patterson et al. 1984).

The study focuses on the CACO sand plains in Truro, Wellfleet, and Eastham (Fig. 1A), which support ~5000 ha of pine–oak woodlands. Pitch pine (*Pinus rigida*; nomenclature follows Gleason and Cronquist 1991) and oaks (*Quercus* spp.) have been important taxa in the study area since 9000 yr BP (Winkler 1985). Although elevation only reaches 54 m above sea level (a.s.l.) on the westerly sloping plains, kame and kettle formations and east–west-trending valleys provide local relief, particularly on the Wellfleet Pitted Plain (Fig. 1B; Oldale and Barlow 1986). Ponds and streams occupy depressions that 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 (Fletcher 1993).

Native Americans occupied eastern Cape Cod throughout the Holocene, with subsistence centered on hunting, the exploitation of marine resources, and limited horticulture (McManamon 1984, Bragdon 1996). Although local aboriginal clearing and fire likely affected the composition and structure of vegetation, palynological evidence and written descriptions indicate that the area was mostly wooded at the time of European settlement (Altpeter 1937, Ruberstone 1985, Winkler 1985, Dunwiddie and Adams 1995, Parshall et al., *in press*). English colonists settled present-day Wellfleet and Eastham in 1644 and Truro by 1700, and local geography influenced the contribution of agriculture and maritime activities to each town's economy. Favorable soils in Eastham encouraged crop and livestock production, a good harbor in Wellfleet supported maritime activities, and Truro developed a mixed economy (Rockmore 1979, Ruberstone 1985). Land use in the 17th through mid-19th centuries dramatically altered the uplands; forests were cut for wood products and fuel, broad areas were cleared and plowed for crops, and pastures and woodlands were grazed (Altpeter 1937, Ruberstone 1985, Friedman 1992, Dunwiddie and Adams 1995). Regional economic decline, widespread emigration (Fig. 2), and farm abandonment characterized the mid- to late 19th century, and further agricultural decline and increased tourism and development occurred throughout the 20th century (Holmes et al. 1998, Stone 1999).

CACO was established in 1961 to protect natural and cultural resources and to provide recreational opportunities for the public. Upland vegetation management is primarily restricted to complete fire suppression and maintenance of open areas in the vicinity of administrative buildings and historic sites.

METHODS

We used historical maps and documents, aerial photographs, and field sampling of vegetation and soils to determine patterns of land-cover and land-use change, species composition and abundance, site conditions, and fire history. Analysis focused on identifying relationships among past land-use, fire, site conditions, and vegetation.

Land-cover/land-use change and fire history

U.S. Coast and Geodetic Survey maps (1848–1856; Shalowitz 1964) were used to identify the extent and location of woodlands and cultural features near the peak of historic forest clearance. These detailed maps (1:10 000) depict woodlands, open areas, wetlands, topography, buildings, roads, and fences and were digitized into a geographic information system using ArcView (version 3.1a) and the Data Automation Kit (Environmental Systems Research Institute, Redlands, California). In grid format in ArcView (40-m pixel resolution), woodland area from 1848–1856 was calculated for Eastham, Wellfleet, and Truro and, separately,

TABLE 1. (A) Number of study plots in woodlands within Cape Cod National Seashore (CACO) sampled in each combination of town and 1848–1856 land-cover category. (B,C) Area of woodland shown on 1848–1856 maps for the entire towns of Eastham, Wellfleet, Truro (B), and for the portion of those towns currently wooded and within CACO (C).

	A) Study plots		B) Woodlands in entire town		C) Woodlands in CACO	
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

Note: Percentages are relative to total town area (B; MacConnell et al. 1974) and modern woodland area within CACO (C; MassGIS 1991).

for the part of each town currently wooded and within CACO boundaries (MassGIS 1991).

Land cover at each vegetation plot (see *Methods*: *Modern vegetation*) in the late 1930s was determined from three sources: black and white aerial photos (1:24 000; November 1938, Harvard Forest Archives) examined under a mirror stereoscope, town maps from the Works Progress Administration (WPA 1937), and minimum stand age estimates (see *Methods*: *Modern vegetation*).

Fire history on eastern Cape Cod (1897–1961) came from town reports, newspaper articles, and personal interviews (Dunwiddie and Adams 1995), unpublished notes by R. C. Hall, U.S. Forest Service (Harvard Forest Archives), 1938 aerial photos, and historical sources. Where possible the location and area were estimated for each fire.

Modern vegetation, disturbance history, and site conditions

Modern woodland vegetation and site conditions were sampled during summer 1999 at 89 20 × 20 m plots stratified by town and 1848–1856 land cover (open or wooded). With the exception of historically wooded areas in Eastham, which were uncommon, at least 10 plots were sampled in former open and wooded areas in each town (Table 1). Plots were established in areas with >25% tree cover, no evidence of a seasonally high water table, and no recent disturbance. Plot locations were chosen randomly in ArcView and located 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 (dbh) was recorded for all living (>2.5 cm dbh) and dead (>10 cm dbh) tree stems, and sprouting patterns (e.g., multiple stems) 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 × 15 cm cylindrical steel corer. The two samples were air-dried and combined, and carbon and nitrogen content was determined using a Fisons CN analyzer (Fisons Instruments, Beverly, Massachusetts). Aggregated 0–30 cm samples were analyzed by Brookside Labs (New Knoxville, Ohio) for texture, pH (1:1 in water), extractable nutrients (Mehlich 1984), and percentage organic matter (Storer 1984). Analysis included: pH, percentage silt + clay, percentage organic matter, percentage total nitrogen, percentage total carbon, C:N, total exchange capacity (TEC; millimole per 100 g soil), and extractable concentrations (milligram per kilogram) of phosphorus (as P_2O_5), calcium, magnesium, and potassium.

To categorize physiography, each plot was assigned to one of three outwash plains (i.e., Eastham Plain, Wellfleet Pitted Plain, or Truro Plain; Oldale and Barlow 1986), with the single plot sampled on the Highland Plain grouped with the adjacent, edaphically similar Truro Plain. Mean slope and terrain shape index (TSI; McNab 1989) were used to quantify local topography. Slope was measured from each plot center at 45-degree increments starting in the aspect direction. TSI is calculated as the arithmetic mean of slope measurements and describes land surface shape; negative values indicate 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). Minimum stand age was estimated by coring 1–3 of the largest trees as close to the bases as possible. Cores were mounted and sanded, and annual rings were counted under 10–30× magnification. Soil profiles and wood were examined for macroscopic charcoal or fire scars.

Field evidence was combined with information from the 1848–1856 maps to assign plots to 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 crops or pasture. Plots lacking Ap horizons and mapped as wooded on the 1848–1856 maps were considered "woodlots," continually wooded areas where trees were cut but the vegetation was never com-

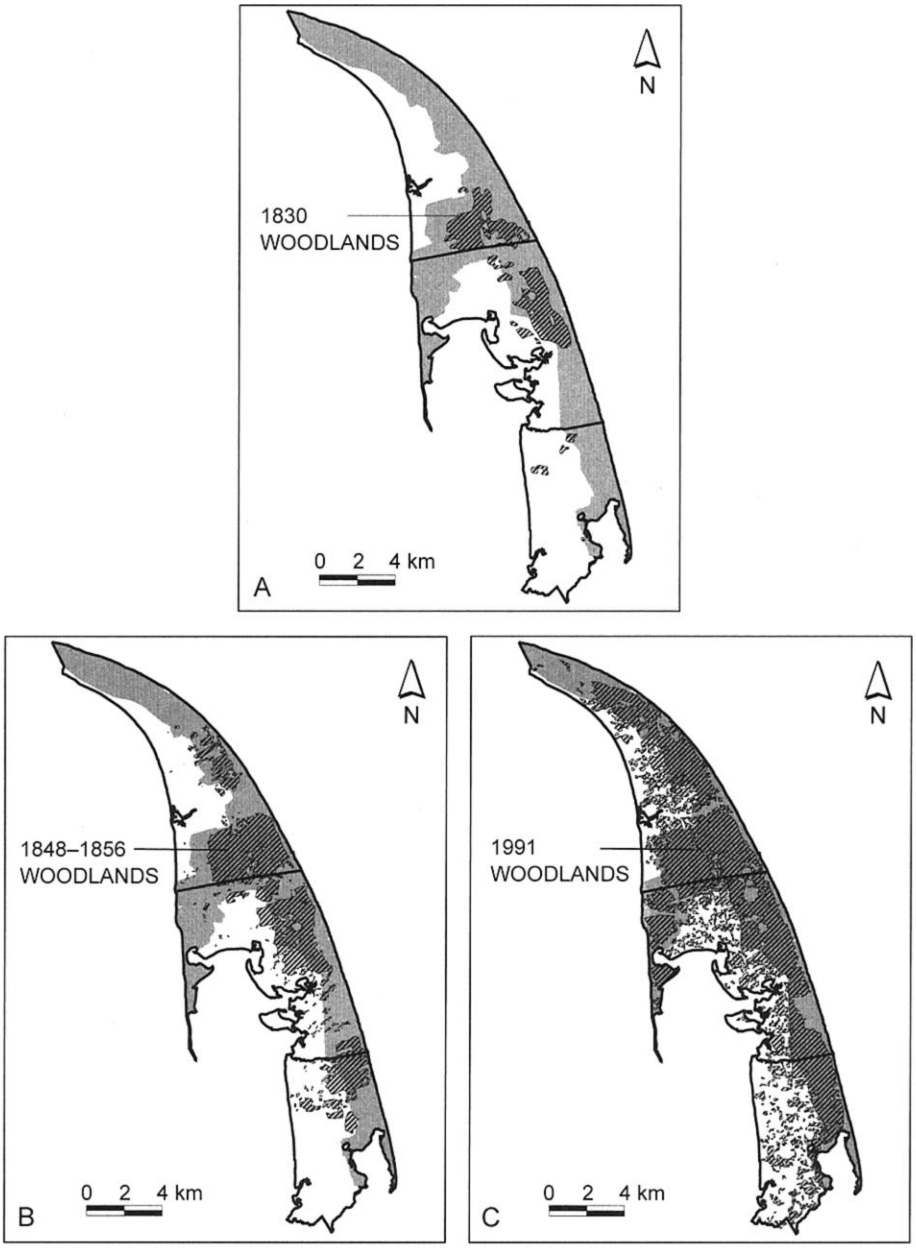

FIG. 3. Distribution of woodlands on sand plains of eastern Cape Cod in (A) 1830, (B) 1848–1856, and (C) 1991 from town maps (Massachusetts Archives 1830), U.S. Coast and Geodetic Survey maps (Shalowitz 1964), and MassGIS (1991), respectively.

pletely eliminated. Plots lacking Ap horizons but open on the 1848–1856 maps have varied histories and were designated "open." Some open plots in coastal settings or topographic depressions have disturbed soils resulting from erosion or overwash. Other open plots have no visible soil disturbance but may have been used as pastures. Three plots are considered woodlots despite being mapped as open in 1848–1856, as each occurs within 100 m of a former woodland border and contains large oak sprouts that 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 past land use varied among the three Plains (Sokal and Rohlf 1995). Kruskal-Wallis tests (with post hoc comparisons; cf. Conover [1980]) were used to determine whether soil texture, topography, and other soil prop-

FIG. 4. Distribution of (A) buildings, (B) fences, and (C) roads on 1848–1856 maps.

erties differed among land uses. 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 with 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 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.

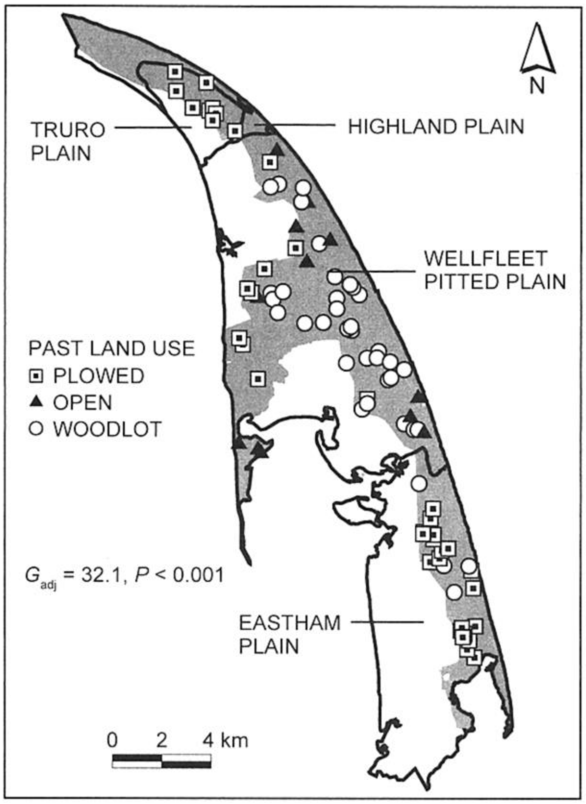

FIG. 5. Distribution of categories of past land use of woodlands of Cape Cod National Seashore on topographically distinct sand plains. The G test determines whether past land-use types occur disproportionately on distinct sand plains.

G tests of independence were used to determine whether the vegetation types identified by classification occurred disproportionately at sites of specific past land use or fire. Kruskal-Wallis tests were used to determine whether the vegetation types had different minimum stand ages or topographic or edaphic characteristics. The experimentwise error rate for this group of tests was adjusted to $\alpha = 0.05$.

Analyses of overall vegetation variation showed strong relationships between species composition and abundance and past land use (see *Results*). To further explore the influences of past land use on individual species distributions, presence/absence data for species occurring in 13–87% of plowed and woodlot plots were analyzed using G tests. The small number of open plots were excluded from this analysis. The experimentwise error rate for these tests was adjusted to $\alpha = 0.05$.

RESULTS

Land-cover and land-use change

In 1848–1856 eastern Cape Cod was extensively settled and deforested, with ~20% of Eastham, Wellfleet, and Truro remaining wooded (Table 1B; Fig. 3B). Only 44% of current woodlands in CACO were wooded between 1848 and 1856 (Table 1C). Buildings and fences occurred throughout open areas, and roads crossed open and wooded areas (Fig. 4). Field evidence and historical sources confirm the accuracy of these mid-19th century land-cover depictions. All but one of 38 plots with an Ap horizon are mapped as open on 1848–1856 maps, and woodland on the 1848–1856 maps coincides with historical descriptions of pine–oak woodland in north Eastham on the Wellfleet border (Fig. 3A; Massachusetts Historical Society 1802, Dwight 1969, Thoreau 1989).

Forty-four percent of plots were plowed historically and open in the mid-19th century, 42% were wooded in 1848–1856, and 14% were open and subject to other uses. Minimum stand ages in plowed or open plots range from 26 to 113 yr, with a mean of 72 ± 21 yr

TABLE 2. Median values of site factors for categories of historical 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.

	Historical land use				
Site factor	Plowed n = 38	Open n = 12	Woodlot n = 37	H	P
Percentage 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 (mmol/100 g)	9.4	5.6	5.7	6.8	0.033
Percentage 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 (×100)	0.4	0.9	0.2	0.8	0.681

Notes: Tests with $P = 0.01$ are significant at $\alpha = 0.05$ after accounting for multiple comparisons. Similar letters within rows indicate that post hoc tests show no significant difference between a pair of vegetation types. Abbreviations are: TEC, total exchange capacity; TSI, terrain shape index.

(1 SD). Aerial photos indicate that 80% of plots supported woodlands or shrublands in 1938, with the remainder in heathland or grassland (14%) and agriculture (6%). All woodlot plots were woodland or shrubland in 1938 with stands ranging from 51 to 180 yr old with a mean of 85 ± 28 yr.

Past land use and site conditions

Plowed sites occur disproportionately on the Eastham and Truro Plains, whereas former woodlots and open sites are concentrated on the Wellfleet Plain (Fig. 5). Among land uses, previously plowed sites are flatter and have finer textured, less acidic soils with higher concentrations of phosphorus, total nitrogen, and potassium (Table 2).

Fire history

Little detailed information is available for fires that predate the 20th century. However historical sources indicate that locomotives caused many ignitions across Cape Cod beginning in the mid-19th century (Collins 1909, Cahoon 1915, Cook 1921, Massachusetts Forestry Association 1928). At least 31 fires occurred from 1897–1962, and several fires exceeding 30 ha occurred within CACO boundaries, primarily on the Wellfleet Pitted Plain (Table 3). Some woodland fires generated extensive mortality and the establishment of the current canopy (Table 3). Other fires burned open habitats including grasslands and "moors" (Table 3). No large fires have occurred since the establishment of CACO in 1961 (Patterson et al. 1984, Dunwiddie and Adams 1995).

Vegetation variation

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

1) Pine–bearberry includes open-canopy *P. rigida* woodland with abundant *Arctostaphylos uva-ursi*, frequent *Deschampsia flexuosa*, *Gaylussacia baccata*, *Schizachyrium scoparium*, and *Q. velutina* or *Q. alba* seedlings or saplings.
2) Pine–hairgrass is characterized by abundant *P. rigida* and *D. flexuosa*, with *A. uva-ursi*, *Q. velutina*, and *Trientalis borealis* common.
3) Pine–oak–sedge has *Q. velutina* and *P. rigida* in the canopy or subcanopy with a ground cover of *Carex pensylvanica*. Common understory species are *D. flexuosa*, *Q. alba*, *Prunus serotina*, *G. baccata*, and *Amelanchier* spp.
4) Pine–scrub oak–crowberry has an open canopy of *P. rigida* and abundant *Q. ilicifolia*, *Corema conradii*, and *Vaccinium pallidum*. Common understory species include *A. uva-ursi*, *G. baccata*, *Comptonia peregrina*, *Q. velutina*, and *Q. alba*.
5) Pine–oak–huckleberry has a canopy of *Q. alba*, *P. rigida*, and *Q. velutina* and continuous low shrub layer of *G. baccata* and *Vaccinium angustifolium*. Common species include the ericaceous shrubs *V. pallidum*, *Gaultheria procumbens*, *Epigaea repens*, and *A. uva-ursi*.
6) Pine–scrub oak–bayberry is characterized by abundant *Q. ilicifolia*, *V. angustifolium*, *G. procumbens*, *E. repens*, *Aralia nudicaulis*, and *Prunus serotina*. Common species include *Myrica pensylvanica*, *Smilax rotundifolia*, *Acer rubrum*, *Pteridium aquilinum*, *Maianthemum canadense*, and *Sassafras albidum*. This type is variable in composition and may have been separated into mesic woodlands and *Q. ilicifolia* thickets if more stands were sampled.

Vegetation and land-use history

Vegetation pattern, composition, and structure are strongly related to past land use at the landscape and stand level. The pine–bearberry, pine–hairgrass, and pine–oak–sedge types have open understories of *Arctostaphylos uva-ursi*, graminoids, and herbs, and occur preferentially in areas previously in agriculture (Table 5; Fig. 6A, B). 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; Fig. 6A, B). The differences in composition and structure are striking (Fig. 7).

Although vegetation patterns do not closely track differences in soil texture, several site variables do differ among the types (Table 5). Sites supporting pine–scrub oak–bayberry and pine–oak–sedge vegetation have similar soil concentrations of total N, P, K, TEC, percentage organic matter, and total C (Table 5). These sites in turn have higher concentrations of total N, TEC, and percentage organic matter than sites supporting pine–hairgrass, pine–scrub oak–crowberry, pine–oak–huckleberry vegetation (Table 5). Soil pH is relatively high in sites with pine–bearberry, pine–hairgrass, and pine–oak–sedge types (Table 5).

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 (Table 5; Fig. 6C). The pine–oak–sedge and pine–scrub oak–crowberry types show intermediate frequencies of charcoal or scarring (Table 5; Fig. 6C).

Individual species distributions and land-use history

Ten of the 20 common but not ubiquitous species occur disproportionately in relation to land-use history. *Deschampsia flexuosa*, *Schizachyrium scoparium*, *Chimaphila maculata*, *Trientalis borealis*, *Prunus serotina*, and *Arctostaphylos uva-ursi* are significantly more frequent in woodlands that were plowed historically, whereas the ericaceous shrubs *Gaultheria procumbens*,

TABLE 3. Documented upland fires within the towns of Eastham, Wellfleet, and Truro (1897–1962).

Date	Size (ha)	CACO?	Plain	Notes	Source
1897	?	?	Eastham	old orchard fire	Dunwiddie and Adams (1995)
2 May 1900	80+	?	Eastham		Dunwiddie and Adams (1995)
20 Aug 1908	200	yes	Wellfleet/Highland	woodland and pasture fire	Dunwiddie and Adams (1995)
~1914	80–120	yes	Wellfleet		Dunwiddie and Adams (1995)
5 Apr 1915	?	?	Truro	fire in "moors" and pines, flames 15 m tall	Dunwiddie and Adams (1995)
7 Jun 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*
19–21 Apr 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)
24 Apr 1933	6	yes	Wellfleet		Dunwiddie and Adams (1995)
19–21 May 1933	33	yes	Wellfleet	railroad fire, *P. rigida* established in 1934	Dunwiddie and Adams (1995), 1938 aerial photos, and canopy age estimates
ca. 1935	?	yes	Wellfleet		Dunwiddie and Adams (1995)
1937	?	?	Wellfleet/Truro	>9 grass and woodland fires in Truro set by arsonist	Dunwiddie and Adams (1995)
5 Apr 1938	1000	yes	Wellfleet		Dunwiddie and Adams (1995)
19 Apr 1938	20	yes	Wellfleet	grass fire	Dunwiddie and Adams (1995)
21 Apr 1938	?	yes	Wellfleet	fire in cemetery	Dunwiddie and Adams (1995)
1938	800	yes	Wellfleet		Dunwiddie and Adams (1995)
20 May 1940	2	yes	Wellfleet		Dunwiddie and Adams (1995)
22 Aug 1940	2 total	no	Wellfleet/Truro	numerous small arson fires in Truro	Dunwiddie and Adams (1995)
14 Jul 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)

Notes: Date, location, size, and 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 Fig. 1) where each fire burned.

Vaccinium pallidum, *Epigaea repens*, and *Gaylussacia baccata* occur more frequently in former woodlots (Fig. 8).

DISCUSSION

Our results document the importance of land-use history in the development of modern vegetation of Cape Cod National Seashore, where most woodlands have established on sites used previously for agriculture, and vegetation patterns principally reflect differences in the intensity of past land use. Historical agricultural activity led to the development of vegetation patterns that are likely unprecedented relative to conditions before

TABLE 4. Species composition/abundance of six woodland types on outwash deposits of Cape Cod National Seashore, identified by classification.

	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)	
Species	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$	%	$\bar{X}$
Arctostaphylos uva-ursi	100	38	92	3	95	2	100	7	60	1		
Schizachyrium scoparium	67	1	42	1	14	1						
Rubus allegheniensis	17	1			10	1			3	1		
Aronia arbutifolia	17	1			5	1			9	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						
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						
Chimaphila umbellata			25	1	5	1			9	1		
Dryopteris intermedia			8	1	10	1			3	2		
Monotropa uniflora			25	1	38	1			9	1		
Robinia pseudoacacia			8	1	14	1			9	1		
Quercus coccinea					33	7			23	6		
Carex pensylvanica	67	1	42	2	71	6	25	2	66	1	60	1
Quercus ilicifolia	100	10	92	4	100	11	100	40	100	5	80	43
Corema conradii	17	2	8	1	5	1	75	17	3	1		
Vaccinium pallidum	17	1			14	1	100	7	91	4	100	2
Comptonia peregrina			8	1	10	1	50	1	17	1		
Quercus velutina	83	1	92	7	100	24	75	3	100	29	80	6
Quercus alba	83	1	67	1	100	5	75	1	100	18	100	6
Gaylussacia baccata	83	23	33	3	76	4	100	18	100	41	80	11
Vaccinium angustifolium	67	4	58	5	57	2	25	2	94	10	80	10
Gaultheria procumbens					5	1	63	4	100	4	100	11
Epigaea repens	17	1			10	1	13	1	63	1	80	3
Prunus serotina	33	1	42	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	10	1	13	1	3	1	20	1
Viburnum dentatum	17	1	8	1	14	1					20	1
Smilax rotundifolia	17	1	8	1	29	1			23	5	80	1
Amelanchier spp.	33	1	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	1
Pteridum aquilinum									20	2	60	1
Acer rubrum									6	1	40	12

Notes: For each species, % = frequency of occurrence, and $\bar{X}$ = mean percent cover when present; n = number of plots. 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). Mean canopy age (yr): pine–bearberry = 41.5^{b}; pine–hairgrass = 78.5^{a}; pine–oak–sedge = 71.0^{a}; pine–scrub oak–crowberry = 76.3^{a}; pine–oak–huckleberry = 83.4^{a}; pine–scrub oak–bayberry = 77.6^{ab}. Superscript letters show results of post hoc tests; different letters indicate significant ($P < 0.05$) differences.

European settlement, when fire appears to have been a dominant disturbance process. In particular, agriculture eradicated low shrub species that, despite having exceptional fire tolerance, have proven to be poor colonizers of abandoned fields. Agricultural abandonment also provided opportunities for the development of extensive heathland and grassland communities, which have declined through the 20th century as a result of widespread reestablishment of trees. Rather than focus exclusively on prescribed fire, effective protection and

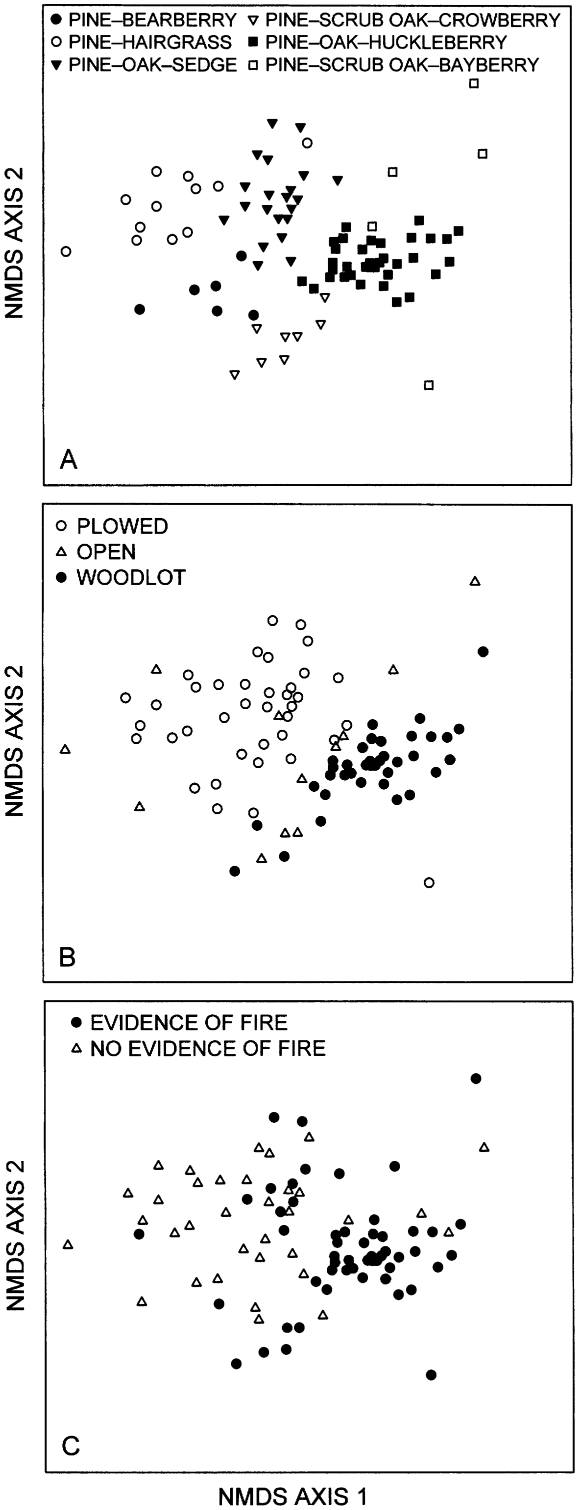

FIG. 6. Ordination of species cover–abundance data from woodlands of Cape Cod National Seashore. Symbols indicate vegetation types identified by (A) classification, (B) categories of past land use, and (C) field evidence of fire. NMDS denotes nonmetric multidimensional scaling.

restoration of these increasingly uncommon open communities may require management regimes that mimic the range of land-use practices that allowed for their historical development.

The development of modern vegetation patterns

For at least 9000 yr before European settlement, woody vegetation dominated by *Pinus rigida* and *Quercus* spp. covered much of eastern Cape Cod's sand plains (Winkler 1985, Parshall et al. 2002). Xeric site conditions, large populations of Native Americans, and flammable vegetation led to high fire frequencies relative to most inland areas in New England (Patterson et al. 1984, Parshall et al. 2002). Despite the prevalence of fire, however, no written or palynological evidence exists for extensive herbaceous communities on sand plains before the arrival of Europeans (Altpeter 1937, Ruberstone 1985, Winkler 1985, Dunwiddie and Adams 1995, Parshall et al. 2002). Any nonwooded upland vegetation likely was restricted to dunes, coastal bluffs, and the immediate vicinity of aboriginal villages (Champlain's accounts in Winship 1905, Holmes et al. 1998).

Following European settlement, more than 200 yr of land use led to the development of an open landscape by the mid-19th century, with the majority of the study area converted to fields that were cleared for crops or pasture. Remaining woodland was concentrated in the eastern portion of the study area and on the topographically variable Wellfleet Pitted Plain, but covered only 20% of the land, much less than in New England as a whole (Foster 1992, 1995, Foster et al. 1998). Although topography and soil fertility may have influenced these land-use patterns, Cape Cod's sand plains are less heterogeneous than other areas of the northeastern United States where past land use is closely tied to the edaphic environment (Glitzenstein et al. 1990, Motzkin et al. 1999*b*). In the coastal region, other factors (e.g., the location of navigable harbors and marine resources) had substantial influence on the patterns of historical land use (Rockmore 1979, Ruberstone 1985).

Historical and paleoecological evidence document continued fire in the postsettlement landscape, and a combination of cutting and fire likely shaped the composition and structure of remnant woodlands (Parshall et al. 2002). Documented fires on the Wellfleet Pitted Plain in the early 20th century led to canopy mortality and exposure of mineral soil. Rapid establishment and sprouting of *Pinus rigida* and *Quercus* spp. initiated modern stands, and sprouting and clonal growth led to the reestablishment of the low shrub layer (Matlack et al. 1992). Shade-intolerant species such as *Quercus ilicifolia* and *Arctostaphylos uva-ursi*, which may have temporarily benefited from fire, likely declined in most stands with canopy closure, forest floor development, or competition from more tolerant shrubs.

In areas used previously for agriculture, evidence of plowing suggests that preexisting vegetation was com-

TABLE 5. Differences in disturbance history and site conditions among the woodland vegetation types of Cape Cod National Seashore.

	Vegetation type							
	Pine–bearberry	Pine–hairgrass	Pine–oak–sedge	Pine–scrub oak–crowberry	Pine–Oak–huck-leberry	Pine–scrub oak–bayberry	All vegetation types	
Disturbance or factor	(n = 6)	(n = 12)	(n = 21)	(n = 8)	(n = 35)	(n = 5)	G_{adj} or H†	P
Disturbances								
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								
Percentage 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 (×100)	−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
Phosphorus (mg/kg)	8^{b}	14^{a}	14^{a}	6^{c}	7^{bc}	12^{ab}	40.2	0.000
Potassium (mg/kg)	11^{a}	11^{ab}	14^{a}	8^{b}	8^{b}	15^{ab}	17.9	0.003
Calcium (mg/kg)	47	54	54	28	28	32	10.9	0.054
Magnesium (mg/kg)	14	12	13	13	10	13	8.4	0.135
TEC (mmol/100 g)	6.3^{bc}	4.7^{c}	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
Carbon (%)	1.02^{ab}	0.90^{b}	1.21^{a}	0.70^{b}	1.04^{a}	1.45^{a}	16.2	0.006
Carbon:Nitrogen	23.2	23.9	25.0	23.0	28.3	29.5	13.5	0.019

Notes: 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 $\alpha = 0.05$ after accounting for multiple comparisons. Similar letters within rows indicate that post hoc tests show no significant difference between a pair of vegetation types.

† G_{adj} for disturbances; H for site factors.

pletely eradicated. As agricultural abandonment began in the 19th century, an abundance of xeric, high-light environments of exposed mineral soil became available for plant colonization. These habitats are favored by heathland and grassland species, which are described in historical accounts as establishing in eastern Cape Cod's abandoned fields (Blankinship 1903, Collins 1909, Hobbs et al. 1984, Niering and Dreyer 1989, Dunwiddie et al. 1996). Fires are known to have occurred on some abandoned agricultural land, although fuel characteristics on these sites differed substantially from remnant woodlots.

By the mid-20th century *Pinus rigida*, often with *Quercus velutina* and *Q. alba*, had established in most old fields, leaving only isolated heathlands and grasslands (Collins 1909, Stevens 1940, Little 1979; L. Carlson et al., *unpublished manuscript*). Populations of heathland and grassland species apparently declined with forest development although species such as *Arctostaphylos uva-ursi*, *Deschampsia flexuosa*, and *Schizachyrium scoparium* continue to persist in many old-field woodlands. Historical accounts and field evidence suggest that severe fires have been relatively uncommon in old-field woodlands since woody species have become dominant.

Although many species have successfully colonized former agricultural areas, the shrubs that dominate the understory of former woodlots have established in old fields infrequently and in low abundance even 100–150 yr after abandonment. Relatively small edaphic differences among sites suggest that past agricultural activities did not render old fields unsuitable for these species by altering environmental conditions; rather, it is likely that life-history traits have restricted recolonization (Peterken and Game 1984, Matlack 1994, Brunet and Oheimb 1998, Bossuyt et al. 1999, Honnay et al. 1999, Donohue et al. 2000). Biotic constraints on colonization appear to vary by species: poor germination and/or early survival may prevent the establishment of *Gaultheria procumbens*, *Vaccinium pallidum*, and *Gaylussacia baccata*, whereas limitations on propagule movement may restrict the ant-dispersed *Epigaea repens* (Clay 1983, Motzkin et al. 1996, 1999*a*, Donohue et al. 2000).

Therefore our results document that modern vegetation patterns reflect a combination of natural and human disturbance processes with differences in historical land use initiating persistent compositional and structural differences. Although fires have occurred occasionally, they have primarily influenced overstory composition and structure in continuously wooded areas and have not eradicated the major patterns of vegetation variation associated with historical land use. Modern vegetation patterns likely do not resemble those from any time before European settlement because of the distinct pattern and ecological impacts of historical agriculture. In particular, the requirement that plants recolonize old fields via propagule dispersal, es-

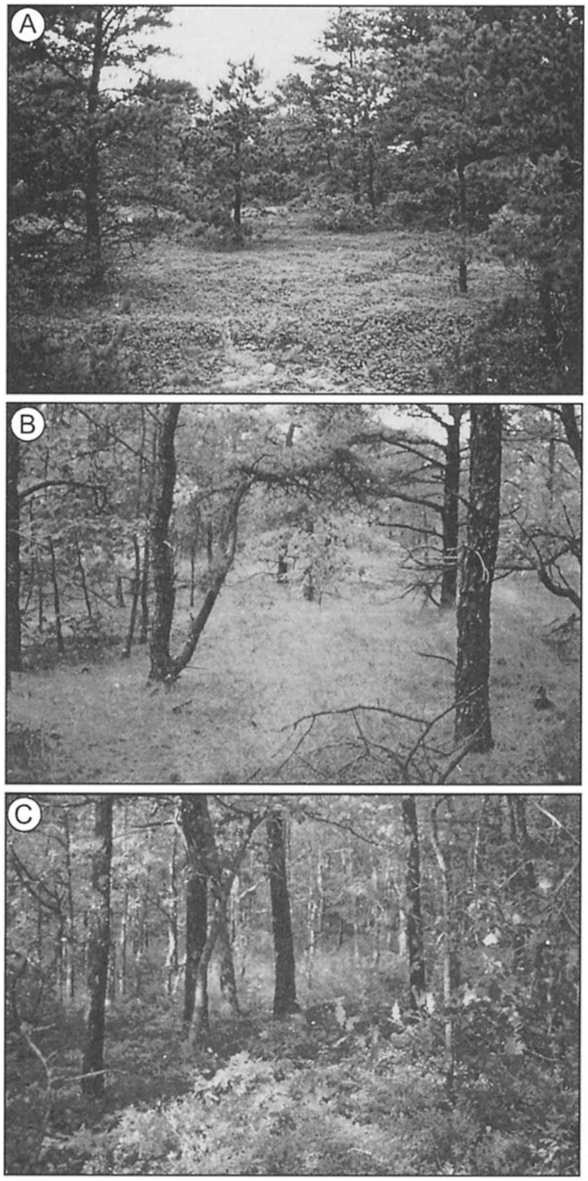

FIG. 7. Examples of selected vegetation types identified by classification: (A) pine–bearberry type, (B) pine–hairgrass type, and (C) pine–oak–huckleberry type. Stands in (A) and (B) were plowed historically, whereas (C) was used as a woodlot.

tablishment, and clonal growth contrasts with the opportunities for individual plants to sprout from the residual stems, rhizomes, and lignotubers that survive most fires. It is notable, however, that severe fire and agriculture may provide similar opportunities for some shade-intolerant species (e.g., *Arctostyphylos uva-ursi*) to establish on exposed mineral soil (Hobbs et al. 1984).

Implications for biodiversity conservation

Since CACO was established in 1961, tree establishment has led to the decline of heathland and grassland communities, prompting recommendations that the National Park Service intervene with active management to protect these uncommon habitats (L. Carlson et al., *unpublished manuscript*). Proposed management strategies have centered around the use of prescribed fire, primarily based on two hypotheses about vegetation dynamics: that heathland and grassland communities were created and maintained before European settlement by fire, and that they have declined as a consequence of 20th-century fire suppression (Dunwiddie and Adams 1995, Dunwiddie et al. 1996, Vickery and Dunwiddie 1997).

This study cannot definitively resolve debates about the disturbance processes responsible for shaping presettlement vegetation patterns. However the exceptional fire tolerance of dominant woodland species potentially explains why presettlement fires do not appear to have generated extensive heathlands and grasslands. It is possible, however, that species that occur in modern heathland and grassland habitats may have occurred in the understory of some regenerating woodlands following severe presettlement fires. Therefore, although the reintroduction of severe fire to woodlands would not likely restore expansive heathlands and grasslands, it could help to perpetuate some characteristic plant species within a largely wooded landscape.

Rather than being caused principally by fire suppression, the recent decline of heathland and grassland appears to result from reforestation that began with agricultural abandonment. Since past agricultural activity created the open, sandy environments that led to the development of heathlands and grasslands, the restoration of these highly uncommon communities will likely require a management regime that mimics past agriculture. Possible treatments include complete removal of woody vegetation (both above and belowground) and mineral soil exposure using a combination of mechanical disturbance, grazing, and fire (e.g., Dunwiddie 1997, Tiffney 1997). The presence of remnant populations, and the potential persistence of viable seed banks, further suggest that heathland and grassland restoration would likely be more successful in old fields than in former woodlots. Such a management approach would parallel examples from Europe, where successional habitats that have declined with recent changes in land use are maintained using techniques that resemble traditional agricultural practices (Kirby and Watkins 1998).

CONCLUSIONS

Our ability to detect the effects of land-use history on the vegetation of Cape Cod National Seashore relies on unusually detailed historical information, and the specific patterns identified strongly reflect the study area's particular physical environment, flora, and history of human activity. However, past land use has likely shaped vegetation in other landscapes in ways that differ from natural processes, and this study illus-

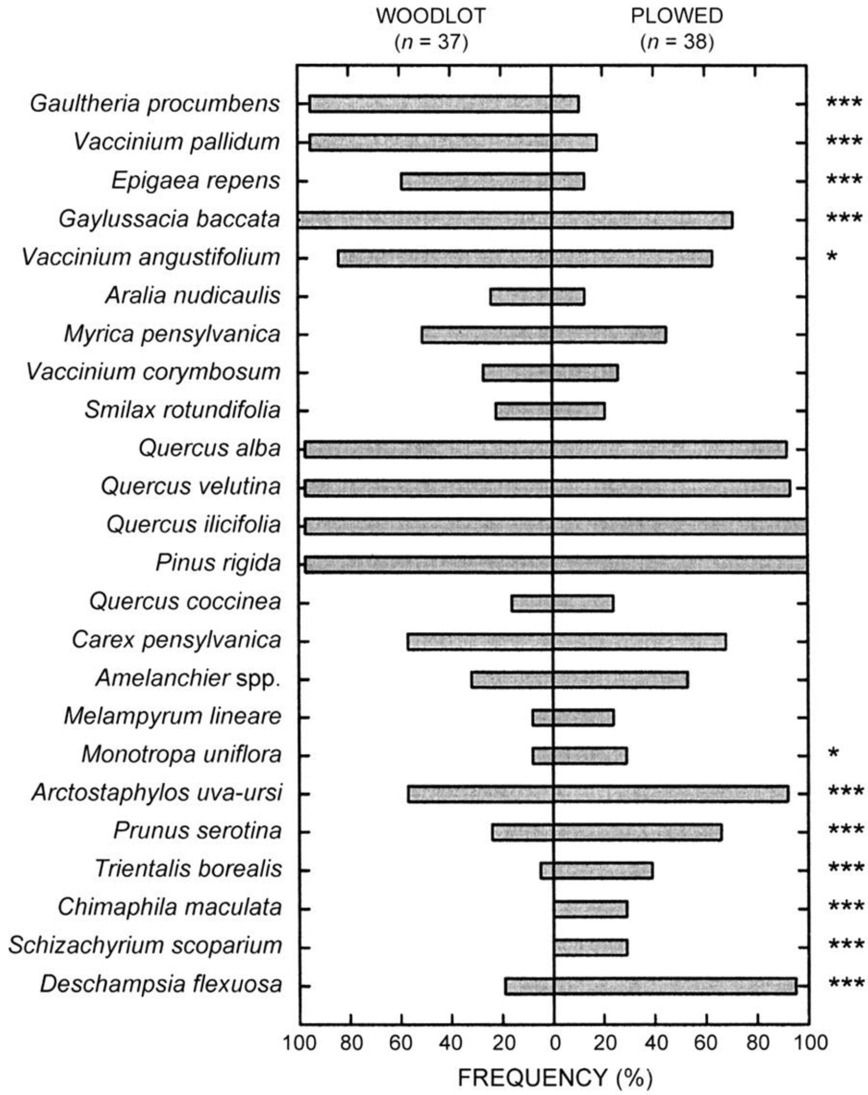

FIG. 8. Distribution of common species in woodlands of Cape Cod National Seashore with different land-use histories. G test results: $*P < 0.05$; $***P < 0.001$. Tests with $P < 0.01$ are significant after accounting for multiple comparisons.

trates that understanding these distinct land use impacts should be a central component of conservation initiatives. The effects of past land use must be given particular attention in efforts to protect and restore successional communities like heathlands and grasslands. If past land use has played a central role in the development of desired vegetation patterns, then land-use practices rather than natural disturbances might represent the best guide for active management intended to perpetuate these communities through time.

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