Journal of Biogeography, **29**, 1439–1454

Vegetation variation across Cape Cod, Massachusetts: environmental and historical determinants

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Abstract

Aim We evaluate environmental and historical determinants of modern species composition for upland vegetation types across Cape Cod, Massachusetts, a region that supports numerous uncommon species assemblages that are conservation priorities.

Location The study area encompasses the entire peninsula of Cape Cod, Massachusetts, USA.

Methods Historical changes in land-use and land-cover across the study region were determined from historical maps and documentary sources. Modern vegetation and soils were sampled and land-use and fire history determined for 352 stratified-random study plots. Ordination and classification were used to assess vegetation variation, and *G*-tests of independence and Kruskal–Wallis tests were used to evaluate relationships among individual species distributions, past land-use, surficial landforms and edaphic conditions.

Results At the scale of this investigation, modern species distributions result from individualistic response to a range of environmental and historical factors, including geography, substrate and disturbance history, especially the pattern of past agricultural activity. The structure or composition of all vegetation types in the region have been shaped by past land-use, fire, or other disturbances, and vegetation patterns will continue to change through time. Conservation efforts aimed at maintaining early successional vegetation types may require intensive management comparable in intensity to the historical disturbances that allowed for their widespread development.

Keywords
Cape Cod, fire, heathlands, land-use, New England, pine–oak woodland, pitch pine, soils, vegetation.

INTRODUCTION

For over a century, ecologists have attempted to determine the factors that control plant species distributions and variation in vegetation composition. Whereas early studies emphasized the importance of edaphic and environmental controls, numerous recent studies have documented the importance of a wide range of natural and anthropogenic disturbances in controlling modern vegetation patterns and dynamics. Such disturbances may influence species distributions and abundances for many centuries (Grimm, 1984; Peterken & Game, 1984; Turner *et al.*, 1997) and may, in some instances, be more important in controlling modern vegetation patterns than current resource variation (Motzkin *et al.*, 1996). In part, resolving the relative influence of resource and environmental conditions vs. historical factors on vegetation patterns is dependent on the scale of inquiry. Across broad geographical regions, steep environmental gradients, or long (e.g. millennial) time-scales, environmental variation is expected to have a strong influence on vegetation patterns (Whittaker & Niering, 1965; Russell & Davis, 2001; Cogbill *et al.*, 2002; Foster *et al.*, 2002a). In contrast, on sites with limited environmental variation, historical factors may be more likely to influence vegetation (Motzkin *et al.*, 1996, 1999a; Bellemare *et al.*, 2002; Gerhardt & Foster, 2002). Determining controls on vegetation variation at intermediate scales of geographical or

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environmental variation is challenging, because both environmental and historical factors may potentially influence species distributions and composition (Motzkin *et al.*, 1999b) and because appropriate historical data may be lacking or difficult to collect.

In previous studies, we determined that the history of past land-use exerts persistent influence on modern vegetation on sand plain ecosystems in the north-eastern US, primarily as a result of biological limitations on species colonization after agriculture or other disturbances (Motzkin *et al.*, 1996, 1999a; Compton *et al.*, 1998; Donohue *et al.*, 2000; Eberhardt *et al.*, 2003). Whereas our earlier studies focused on sites that were relatively homogeneous with respect to edaphic and resource conditions, here we apply similar methodologies to investigate environmental and historical influences on vegetation variation across Cape Cod, MA, a more heterogeneous coastal landscape that includes substantial geographical, topographic and edaphic variation.

The upland vegetation of Cape Cod and nearby coastal areas is characterized by a range of woodlands, barrens, grasslands and heathlands that support numerous uncommon species that are among the highest priorities for conservation in the north-eastern US (Barbour *et al.*, 1998; Beers & Davison, 1999; Motzkin & Foster, 2002; Eberhardt *et al.*, 2003). Understanding environmental and historical variation among these communities and the factors that control changing species abundances over time is critical for determining appropriate conservation objectives and management approaches (Foster & Motzkin, 1998; Motzkin & Foster, 2002). In many regions, attempts to evaluate historical influences on modern vegetation are limited by a lack of information on landscape changes over time. In contrast, considerable information is available about the geological (Oldale, 1992; Uchupi *et al.*, 1996), palaeoecological (Winkler, 1985; Patterson & Backman, 1988; Tzedakis, 1992; Motzkin *et al.*, 1993; Parshall *et al.*, 2003) and human history of Cape Cod (e.g. Kittredge, 1930; McManamon, 1984; MHC, 1987; Friedman, 1993; Dunford & O'Brien, 1997; Holmes *et al.*, 1997), providing critical historical perspectives for our studies. Although the floristics of the region have been well documented (e.g. Collins, 1909; Hinds, 1966; Burk, 1968; Svenson, 1970; Svenson & Pyle, 1979), ecological studies of upland vegetation have been primarily restricted to Cape Cod National Seashore on outer Cape Cod (e.g. McCaffrey, 1973; Patterson *et al.*, 1983; Carlson *et al.*, 1991; Chokkalingham, 1995; Dunwiddie & Adams, 1995; Eberhardt *et al.*, 2003; although see Boyce, 1954) or specific vegetation types (Dunwiddie *et al.*, 1996; Eberhardt *et al.*, 2003), and no previous studies have investigated vegetation variation across the peninsula. By sampling across a wide range of sites in both forested and non-forested vegetation, we were able to evaluate whether the distribution and composition of uncommon species assemblages result from unusual environmental conditions or particular disturbance histories. Specific objectives for the current study include: (1) to document the history of land-use and land-cover change across Cape Cod for the historical period (seventeenth century – present); and (2) to evaluate the influence of environmental conditions and variation in historical disturbance on modern species distributions and vegetation patterns.

STUDY REGION

The study region includes the entire peninsula of Cape Cod, a 107,000 ha region in eastern Massachusetts, US (Fig. 1). The region is largely composed of deep glacial deposits of Wisconsinan origin, primarily extensive pitted and level outwash plains; a series of hilly morainal deposits occurs in the western portion of the peninsula, glacial lake deposits occur in the north-central portion of the region, and extensive dune deposits occur at the outer tip of Cape Cod (Oldale & Barlow, 1986). Upland soils vary from excessively drained sands on outwash and dune deposits, to sandy and loamy soils on moraines, to finer-textured soils that developed in glacial lake deposits (Fletcher, 1993). The climate of the region is characterized by cold winters and warm summers, with average annual precipitation of *c.* 110 cm, nearly 50% of which falls from April to September (Fletcher, 1993). The regional vegetation is characterized as pitch pine–oak (*Pinus rigida–Quercus*; Westveld *et al.*, 1956).

Native Americans are thought to have inhabited Cape Cod continuously from the Palaeo Indian period (9000–12,000 yr BP) onward, although rising sea levels have apparently eliminated most early archaeological remains. At the time of European settlement in the seventeenth century, the largest Native groups occurred on the outer and mid Cape, with numerous smaller groups across the study region

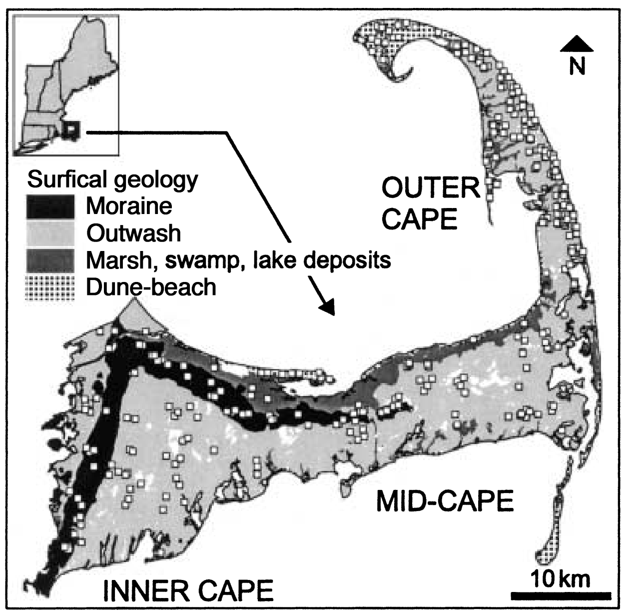

Figure 1 Simplified surficial geological map of Cape Cod, Massachusetts (from Oldale & Barlow, 1986), with 352 vegetation and soils plots sampled in 1999–2000. The inset map indicates the location of the study area in the north-eastern US.

(MHC, 1987). Native Americans on Cape Cod in the Late Woodland Period have been characterized as 'conditionally sedentary', with an emphasis on estuarine resources augmented by hunting, gathering and, after 1300 AD, maize agriculture (Bragdon, 1996).

METHODS

Historical changes in land-use/land-cover

A wide range of primary and secondary sources was used to evaluate changes in historical land-use and land-cover, including witness trees from early land surveys, tax valuation and census data (Hall *et al*., 2002), regional histories and archaeological surveys (e.g. MHS, 1802; Kittredge, 1930; Altpeter, 1937; Ruberstone, 1984; MHC, 1987; Friedman, 1993; Dunwiddie & Adams, 1995; Holmes *et al*., 1997), forestry surveys (Rane, 1907; Parmenter, 1928) and twentieth century maps of land-cover change (MacConnell *et al*., 1974; MassGIS, 1999). Two series of maps were used to determine land-use/land-cover in the mid-nineteenth century. For most of the study region, detailed (1 : 10,000 scale) US Coast and Geodetic Survey maps from 1845 to 1861 were available, indicating woodlands, wetlands, roads, fencelines and buildings (Shalowitz, 1964). For interior portions of inner Cape Cod that were not included on these maps, land-cover was determined from a series of 1830 town maps (*c*. 1 : 20,000 scale; Massachusetts Archives, 1830; Hall *et al*., 2002). Although some maps indicate compositional and structural variation among woodlands, distinctions are inconsistent and all such cover types were combined into a single 'wooded' category; other upland areas were classified as 'open'. All maps were digitized using ArcView and the Data Automation Kit (ESRI, 1996).

Vegetation, soils and disturbance history

In order to evaluate the influence of surficial landforms and historical land-use on modern vegetation, 352 20×20 m plots were established in 1999–2000 (Fig. 1). Plot distribution was stratified by mid-nineteenth century land-cover (open vs. wooded) and landform (e.g. moraine, outwash, dunes and glacial lake deposits; Oldale & Barlow, 1986), with at least four randomly located plots sampled each in formerly open and wooded areas in every town. Plots were restricted to upland sites; wetlands, active agricultural lands, sparsely vegetated beaches, coastal bluffs, and dunes dominated by *Ammophila breviligulata* were excluded.

Within each plot, percentage cover of each vascular plant species was estimated in eight cover-abundance classes. Diameter at breast height (d.b.h.) was recorded for all living (>2.5 cm d.b.h.) and dead (>10 cm d.b.h.) trees, and stems that obviously sprouted from shared rootstocks were noted. Mean slope and terrain shape index (TSI) (McNab, 1989) were used to quantify local topography, and shallow soil pits (30–50 cm) were dug into the B horizon at one to two random locations in each plot and described following standard methods (USDA, 1993). Two samples each of 0–15 and 15–30 cm mineral soils were collected using a 5×15 cm cylindrical steel corer. Aggregated (0–30 cm) samples from each plot were air-dried and analysed by Brookside Labs, Inc. (New Knoxville, OH, USA) for texture, pH (1 : 1 in water), extractable nutrients (calcium, magnesium, phosphorus and potassium concentrations; Mehlich, 1984), and percentage of organic matter (Storer, 1984).

Field evidence of disturbance history was recorded at each plot, including the presence of macroscopic soil charcoal, charred wood, fire scars, barbed wire, cut stumps, windthrow mounds, etc. (Motzkin *et al*., 1996). Particular emphasis was placed on recording evidence of soil disturbance such as plough (Ap) horizons, buried soil horizons and missing surface horizons. Field evidence was then combined with information from the mid-nineteenth century maps to assign plots to broad categories of past land-use. Plots with Ap horizons were considered formerly 'ploughed' for crop production or pasture improvement. Plots that lacked clear Ap horizons but showed other evidence of soil disturbance from human or natural causes (including recently active dunes, areas of storm deposition or erosion and disturbance associated with military or other past uses) were considered 'disturbed'. Plots lacking Ap horizons or other evidence of soil disturbance that were mapped as non-wooded in the mid-nineteenth century were considered 'open', whereas currently wooded plots with undisturbed soils that were mapped as wooded in the nineteenth century were considered 'primary woodlands' (i.e. continuously wooded). All primary woodlands were likely to have been cut or burned during the historical period and none are considered to be 'old-growth'.

Data analyses

Classification and ordination of species abundance data were used to characterize vegetation variation and to evaluate relationships between environmental and historical variables and vegetation composition. An agglomerative clustering algorithm was used to group plots into vegetation assemblages (flexibe $\beta = -0.25$; Greig-Smith, 1983). Species data were also ordinated by non-metric multidimensional scaling (NMDS) of Bray–Curtis distances (Minchin, 1987) using random starting points. The NMDS results were rotated using the varimax procedure to maximize loading on the ordination axes (McCune & Mefford, 1999).

G-tests of independence were used to determine whether: (1) the frequencies of vascular plant species differ among sites with differing land-use histories (ploughed, disturbed, open and primary woodlands); (2) categories of past land-use or surficial landforms (outwash, moraine, beach/dune, and lake-bottom deposits) differ among vegetation types defined by cluster analysis and (3) surficial landforms differ among categories of past land-use. Kruskal–Wallis tests were used to determine whether vegetation types defined by cluster analysis, categories of past land-use, or surficial landforms differ with respect to edaphic conditions. In conducting these analyses, we performed a large number of significance tests and are therefore likely to report a few significant results that are due to chance. We have chosen not to perform a Bonferroni adjustment for multiple tests (Rice, 1989) in these exploratory analyses, realizing that some results reported as statistically significant may result from chance alone, but most of the conclusions should be sound.

RESULTS

Historical changes in land-use and land-cover

Palaeoecological reconstructions (Parshall *et al.*, 2003), early historical descriptions (Knowlton, 1914; Altpeter, 1937; Motzkin & Foster, 2002) and witness tree data from early land surveys (Hall *et al.*, 2002) confirm that the study region was largely forested with pine (*Pinus*) and oak (*Quercus*) woodlands at the time of European settlement, with lesser amounts of hickory (*Carya*), beech (*Fagus*) and other species, particularly on inner Cape Cod (Fig. 2; Hall *et al.*, 2002). Beginning in the mid-seventeenth century, rapid clearing for settlement and agriculture reduced the extent of woodlands across Cape Cod and altered the composition and structure of remaining woodlands through repeated grazing, burning, harvesting and other activities. Frequently, these land-use practices resulted in local wood shortages and severe erosion, prompting passage of numerous acts of legislation through the seventeenth and eighteenth centuries aimed at restricting environmental degradation (McCaffrey, 1973; Friedman, 1993). By the mid-nineteenth century, only *c.* 41% of the region remained wooded (Fig. 3) with primarily small woodlands on outer Cape Cod and extensive woodlands on the inner Cape and in adjacent

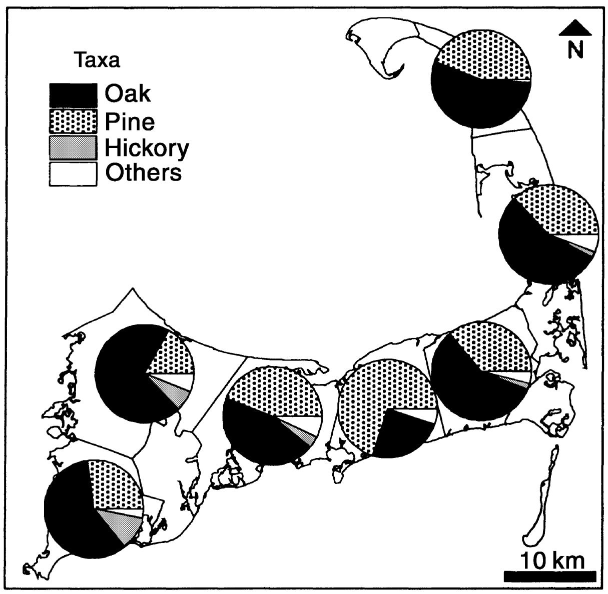

Figure 2 Early historical vegetation composition on Cape Cod, based on 'witness trees' from seventeenth–eighteenth century lotting surveys.

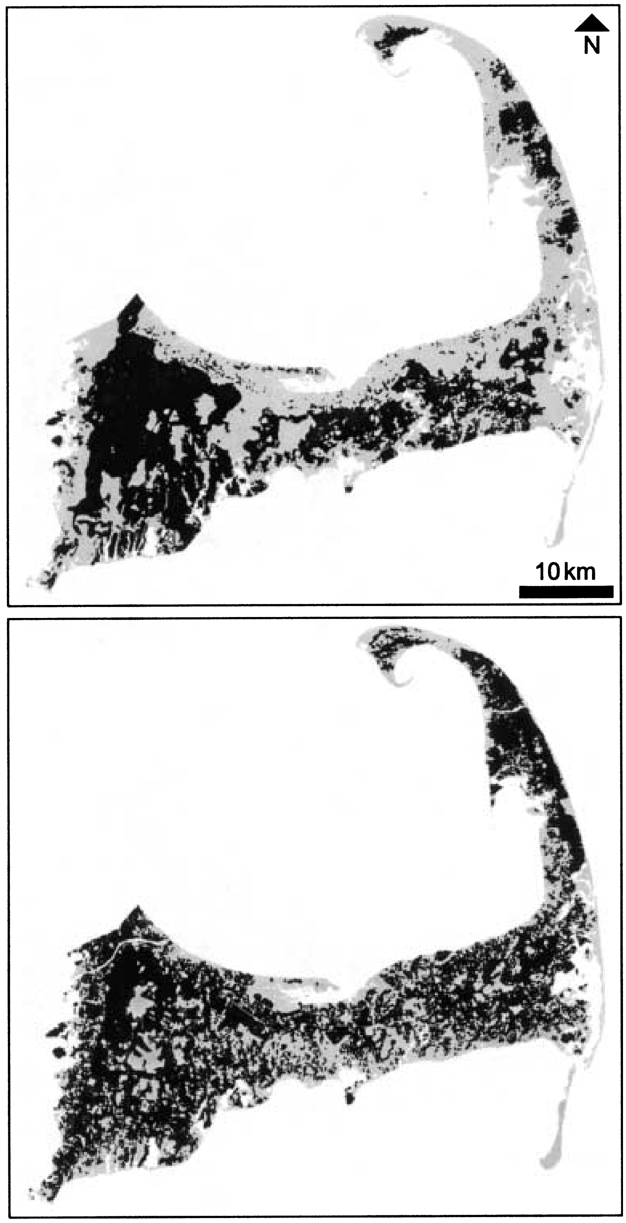

Figure 3 Mid-nineteenth century (top) and modern (bottom) woodlands (black) on Cape Cod, Massachusetts. Based on USCGS (1845–1861), Massachusetts Archives (1830), and MassGIS (1999).

portions of south-eastern Massachusetts (Hall *et al.*, 2002). Remaining woodlands were frequently and heavily cut for wood products; for instance, in 1885, more than 91% of the harvesting operations reported for Barnstable County involved stands <40 years of age, with 44% in stands <25 years old (Anonymous, 1887).

Widespread farm abandonment in the nineteenth and early twentieth centuries allowed for an increase in forest area to 61% by 1951 (Stone, 1999), through both natural re-forestation and extensive planting of native and non-native trees (Thoreau, 1871; Bowditch, 1878; Walsh, 1927; McCaffrey, 1973). However, residential and commercial development once again reduced the area of forests on Cape Cod to *c.* 43% by 1990 (Stone, 1999). The modern pattern of forest distribution differs from that which occurred in the nineteenth century. Whereas woodlands have increased over the past century and a half on outer Cape Cod, particularly in areas that have been incorporated into Cape Cod National Seashore, woodlands on the inner Cape have become increasingly fragmented by development (Fig. 3).

Not all sites became re-forested after the abandonment of agricultural land in the mid-nineteenth century; particularly on heavily disturbed and exposed sites on outer Cape Cod, heathlands with abundant low shrubs (e.g. *Arctostaphylos uva-ursi*, *Corema conradii*, *Hudsonia ericoides*) were quite common in the first half of the twentieth century (Collins, 1909; Hinds, 1966). Heathland vegetation also became established in the twentieth century on heavily disturbed areas such as former military bases (e.g. Camp Wellfleet). However, many heathlands were lost in recent decades to residential development, while others experienced encroachment by taller woody vegetation and a gradual development of woodlands. By 1985, only 271 ha of heathlands remained on Cape Cod National Seashore, representing a 63% decrease from 1962 (Carlson *et al*., 1991). Heathlands continue to decline at a rapid rate as a result of invasion by taller woody vegetation and residential development, and only a few hundred hectares of heathlands currently remain on Cape Cod, primarily in Cape Cod National Seashore and in a few other small sites.

Vegetation and environmental variation

Modern vegetation varies substantially across the uplands of Cape Cod, from closed canopy oak–pine forests, to pitch pine–scrub oak (*P. rigida*–*Q. ilicifolia*) woodlands, to sparsely vegetated dunes, grasslands and heathlands with few trees. Cluster analysis identified nine vegetation associations that differ with respect to species composition, structure, and abundance (Table 1; Fig. 4). Several forested associations [Oak–Briar (*Quercus*–*Smilax*), Oak–Pine–Maple (*Quercus*–*Pinus*–*Acer*), Oak–Pine–Huckleberry (*Quercus*–*Pinus*–*Gaylussacia*), Pine–Oak–Hairgrass (*Pinus*–*Quercus*–*Deschampsia*)] are distinguished on the basis of understory composition and varying amounts of *Q. velutina, Q. alba, Q. coccinea* (inner Cape Cod only), and *P. rigida*, with other tree species (e.g. *Acer rubrum*, *P. strobus*, *Prunus serotina*) frequent or abundant primarily in the Oak–Pine–Maple type (Table 1). *Quercus ilicifolia* and several ericaceous shrubs (e.g. *Gaylussacia baccata* and *Vaccinium* spp.) are common in Oak–Pine–Huckleberry, Pitch Pine–Scrub Oak, and Bearberry–Scrub Oak (*Arctostaphylos*–*Q. ilicifolia*) vegetation, whereas *A. uva-ursi*, *Hudsonia* spp. and *C. conradii* vary in abundance in several primarily non-forested types. Hairgrass (*D. flexuosa*) occurs in several heathland and grassland types and is characteristic of the Pine–Oak–Hairgrass association.

Soil disturbance from historical ploughing or harrowing remains clearly visible in modern soil profiles. On most sites with undisturbed soils across the study area, the generally coarse texture and acidic soils have facilitated podzolization, with well developed light grey, albic horizons overlying distinct spodic horizons. In contrast, on sites that have been ploughed or harrowed, surface horizons have been mixed, resulting in fairly uniform Ap horizons that are light brown and frequently have abundant light-coloured mineral grains from the original albic horizons. On sites that have reforested since agricultural abandonment, a shallow, redeveloping natural A horizon is also frequently visible at the top of the Ap horizon.

Vegetation variation is strongly associated with differences in past land-use, landforms and edaphic characteristics (Table 2). Oak–Pine–Huckleberry and Pitch Pine–Scrub Oak vegetation types occur predominantly in primary woodlands with undisturbed soil profiles, whereas a wide range of forested and non-forested associations have developed on sites that were formerly ploughed or where the soils were otherwise disturbed. Oak–Pine–Maple and Oak–Pine–Huckleberry associations occur disproportionately on moraines, Pitch Pine–Scrub Oak and Pine–Oak–Hairgrass types are characteristic of outwash, whereas Pitch Pine–Hairgrass, Bearberry–Scrub Oak and Poverty Grass–Hairgrass (*Hudsonia tomentosa*–*Deschampsia*) types are characteristic of beach/dune deposits. The Cedar–Bayberry–Honeysuckle (*Juniperus*–*Myrica*–*Lonicera*) association typically occurs on lake-bottom deposits with relatively fine-textured soils and high cation concentrations (Table 2).

Site conditions differ among landforms (Table 3); the moraines have the finest-textured soils and highest organic matter, whereas beach/dune deposits are coarse-textured and have the highest pH and magnesium concentrations. Outwash deposits are characterized by low pH (median = 4.3) and generally sandy soils on outer Cape Cod, but somewhat finer-textured soils (sandy loams) on the inner Cape (Fig. 5).

Species distributions

The modern distributions of numerous species are strongly associated with patterns of historical land-use. In particular, several graminoid, herbaceous and dwarf shrub species occur most frequently on previously cleared sites where soils were formerly ploughed or disturbed, including common heathland and grassland species such as *Deschampsia flexuosa*, *Schizachyrium scoparium*, *Hudsonia* spp. and *A. uva-ursi* (Table 4). In contrast, numerous ericaceous species (e.g. *G. baccata*, *G. frondosa*, *Gaultheria procumbens*, *Epigaea repens*, *Vaccinium* spp., *Kalmia angustifolia*) as well as *Pteridium aquilinum*, *Q. alba*, and *Q. coccinea* occur more frequently on sites with undisturbed soil profiles. In areas with undisturbed soils, several species that are typically found on moist sites in the North-east (e.g. *Nyssa sylvatica*, *Viburnum dentatum*, *V. nudum*) are more frequent in areas that were 'open' in the mid-nineteenth century than in primary woodlands.

Table 1 Frequency (%) and mean abundance of species in nine vegetation types defined by cluster analysis. Bold values indicate species that occur in >75% of plots within a vegetation type

	Oak–Briar $n = 19$		Oak–Pine–Maple $n = 54$		Oak–Pine–Huckleberry $n = 103$		Pitch Pine–Scrub Oak $n = 27$		Pine–Oak–Hairgrass $n = 65$		Pitch Pine–Hairgrass $n = 19$		Bearberry–Scrub Oak $n = 37$		Poverty Grass–Hairgrass $n = 15$		Cedar–Bayberry–Honeysuckle $n = 13$	
Species	% Freq	Abund	% Freq	Abund	% Freq	Abund	% Freq	Abund	% Freq	Abund	% Freq	Abund	% Freq	Abund	% Freq	Abund	% Freq	Abund
Toxicodendron radicans	**84.2**	**2.4**	27.8	0.5	3.9	0.5			46.2	2.5	21.1	0.9	29.7	1.4	46.7	6.2	61.5	1.6
Smilax rotundifolia	**100.0**	**13.9**	**81.5**	**3.8**	35.9	2.7	11.1	0.5	50.8	3.4	10.5	0.5	5.4	0.5				
Viburnum dentatum	**89.5**	**6.5**	59.3	1.4	16.5	0.9	14.8	0.5	33.8	2.7	10.5	0.5	13.5	0.5			46.2	2.3
Parthenocissus quinquefolia	**94.7**	**0.9**	13.0	0.5	1.9	0.5	18.5	0.5	13.8	0.5	15.8	0.5	16.2	0.5	13.3	0.5	53.8	1.6
Rubus allegheniensis	52.6	0.5	16.7	0.5	1.9	0.5	3.7	0.5	6.2	0.5			2.7	0.5			23.1	0.5
Corylus americana	26.3	4.4	9.3	2.4	1.9	0.5			4.6	0.5								
Prunus serotina	**100.0**	**6.4**	**79.6**	**0.8**	46.6	1.5	51.9	2.5	**87.7**	**0.7**	36.8	1.7	64.9	0.9	33.3	1.1	69.2	5.1
Sassafras albidum	52.6	13.7	31.5	5.0	18.4	3.7	7.4	1.3	3.1	0.5								
Rhus copallinum	26.3	0.5	1.9	0.5	1.0	0.5	14.8	0.9	3.1	0.5			2.7	0.5			15.4	0.5
Ilex opaca	31.6	4.3	13.0	0.7	1.9	5.3			12.3	0.7								
Maianthemum canadense	52.6	0.7	46.3	1.7	5.8	0.5			21.5	0.9								
Rubus hispidus	52.6	0.7	48.1	0.5	9.7	0.5	25.9	1.2	18.5	0.5	5.3	2.0	2.7	0.5	6.7	0.5	46.2	0.8
Vaccinium corymbosum	57.9	2.3	51.9	2.7	34.0	1.2	7.4	2.0	38.5	2.8	15.8	2.2	8.1	0.5				
Smilax glauca	52.6	0.7	40.7	1.0	12.6	0.5	14.8	1.6	16.9	0.5	10.5	0.5	8.1	0.5			7.7	0.5
Nyssa sylvatica	31.6	2.6	25.9	5.1					7.7	0.8								
Ilex verticillata	21.1	1.3	14.8	0.9	1.9	0.5			3.1	1.3								
Fagus grandifolia	15.8	19.3	18.5	7.6	2.9	1.0			6.2	2.9								
Acer rubrum	57.9	9.8	**77.8**	**9.8**	17.5	3.0			1.5	0.5	5.3	0.5					7.7	0.5
Amelanchier spp.	52.6	8.0	**77.8**	**1.0**	52.4	0.5	44.4	1.0	64.6	0.5	15.8	0.5	40.5	0.6	6.7	0.5	7.7	4.0
Aralia nudicaulis	47.4	5.8	**81.5**	**1.3**	42.7	1.6	18.5	4.9	32.3	1.0			2.7	0.5			7.7	2.0
Ilex glabra	10.5	0.5	25.9	9.3	2.9	1.5			3.1	1.3	5.3	0.5						
Gaylussacia frondosa	10.5	1.3	29.6	7.1	12.6	4.7			1.5	0.5								
Lycopodium obscurum	10.5	0.5	20.4	0.8	1.9	0.5			4.6	0.5								
Lycopodium complanantum	5.3	0.5	20.4	0.6	1.9	0.5			3.1	1.3								
Vaccinium stamineum	5.3	0.5	13.0	2.3	14.6	3.1			4.6	4.7								
Uvularia sessilifolia	5.3	0.5	24.1	0.5	1.9	0.5	7.4	0.5										
Viburnum nudum	26.3	3.0	**85.2**	**3.6**	35.9	1.1	25.9	2.1	21.5	1.6								
Lyonia ligustrina	5.3	0.5	40.7	1.9	10.7	1.9												
Kalmia angustifolia	5.3	0.5	51.9	1.4	22.3	2.6	25.9	1.6	1.5	0.5	5.3	0.5	2.7	2.0				
Pinus strobus	5.3	0.5	53.7	10.4	16.5	4.5	7.4	0.5	15.4	8.6								
Clethra alnifolia			22.2	28.3	1.0	2.0			1.5	0.5	5.3	0.5						
Cypripedium acaule			55.6	0.5	26.2	0.5	22.2	0.5	21.5	0.5	15.8	0.5	8.1	0.5				
Carex pensylvanica	**78.9**	**6.4**	50.0	1.1	63.1	0.6	59.3	0.9	61.5	4.2	15.8	0.5	81.1	1.3	40.0	4.6	15.4	2.3
Aronia spp.	36.8	0.5	37.0	0.8	30.1	0.5	7.4	0.5	9.2	0.5	5.3	2.0	5.4	0.5				
Quercus coccinea	31.6	7.1	**77.8**	**36.4**	67.0	32.2	25.9	12.3	43.1	4.9			10.8	0.5			23.1	0.5
Quercus alba	**89.5**	**15.8**	**94.4**	**13.1**	**99.0**	**18.6**	74.1	9.2	**92.3**	**6.0**	26.3	0.5	35.1	0.6	13.3	0.5	23.1	0.5
Monotropa uniflora	31.6	0.5	33.3	0.5	29.1	0.5	11.1	0.5	38.5	0.5	15.8	0.5	2.7	0.5				
Gaultheria procumbens	26.3	0.5	**77.8**	**6.0**	**86.4**	**3.9**	74.1	5.3	9.2	0.8			10.8	0.9				
Pteridium aquilinum	26.3	0.8	68.5	1.9	59.2	3.1	33.3	3.6	1.5	0.5							7.7	2.0

Table 1 *continued*

Epigaea repens			33.3	0.6	58.3	0.8	37.0	1.6	13.8	1.9								
Vaccinium pallidum	26.3	1.2	**83.3**	**3.1**	**95.1**	**4.2**	**96.3**	**6.8**	29.2	2.0	5.3	0.5	29.7	1.6	6.7	4.0	7.7	0.5
Vaccinium angustifolium	36.8	3.3	**87.0**	**2.3**	**97.1**	**5.3**	55.6	1.9	61.5	4.5	21.1	0.9	32.4	4.5	6.7	0.5	15.4	1.3
Gaylussacia baccata	63.2	10.0	**100.0**	**18.3**	**100.0**	**42.4**	**100.0**	**14.0**	**78.5**	**9.9**	26.3	3.4	48.6	5.9	6.7	0.5	7.7	2.0
Quercus velutina	**89.5**	**16.9**	**90.7**	**15.6**	**90.3**	**20.1**	51.9	3.6	**98.5**	**22.0**	**89.5**	**2.0**	45.9	1.2	20.0	0.5	7.7	4.0
Quercus ilicifolia	31.6	29.4	29.6	2.0	**78.6**	**3.6**	**100.0**	**36.3**	**81.5**	**7.1**	47.4	4.9	**86.5**	**15.5**	40.0	1.5	38.5	1.5
Pyrola rotundifolia	15.8	0.5	16.7	0.5	6.8	0.5	33.3	0.5										
Comptonia peregrina					6.8	0.7	37.0	0.5	10.8	0.5	5.3	0.5	37.8	0.6	6.7	2.0	7.7	2.0
Quercus prinoides	10.5	0.5	13.0	0.5	16.5	0.8	48.1	2.2	3.1	0.5			13.5	1.1	6.7	2.0		
Melampyrum lineare			9.3	0.5	18.4	0.5	25.9	0.5	29.2	0.5	10.5	0.5	21.6	0.5			7.7	0.5
Chimaphila umbellata			5.6	0.5	8.7	0.5	3.7	0.5	1.5	0.5	15.8	0.5	2.7	0.5				
Pinus rigida	42.1	10.1	**87.0**	**16.9**	**97.1**	**20.7**	**88.9**	**21.4**	**100.0**	**29.5**	**100.0**	**35.3**	**94.6**	**11.4**	46.7	1.1	38.5	3.1
Chimaphila maculata	31.6	0.5	16.7	0.5	3.9	0.5			44.6	0.5	10.5	0.5	2.7	0.5				
Trientalis borealis	42.1	0.5	59.3	0.5	12.6	0.5	25.9	0.5	46.2	0.7	68.4	0.8	21.6	0.5				
Deschampsia flexuosa	68.4	2.1	25.9	0.6	23.3	0.6	22.2	0.8	**98.5**	**7.2**	**100.0**	**17.9**	**86.5**	**1.9**	**93.3**	**2.0**	46.2	3.9
Aster patens	15.8	0.5					7.4	0.5	6.2	0.5			13.5	0.5	13.3	0.5	7.7	0.5
Aster paternus							11.1	0.5	4.6	0.5	5.3	0.5	21.6	0.7	6.7	0.5	7.7	0.5
Corema conradii							29.6	12.6	4.6	0.5			45.9	9.9	13.3	0.5		
Hudsonia ericoides													59.5	1.1	20.0	1.7		
Arctostaphylos uva-ursi	5.3	2.0	5.6	7.0	25.2	0.6	63.0	4.5	63.1	2.7	68.4	3.6	**100.0**	**36.0**	66.7	10.7		
Prunus maritima	10.5	0.5							6.2	0.5	52.6	0.7	40.5	0.6	60.0	4.2	23.1	8.7
Aster linariifolius									1.5	0.5			40.5	0.6	46.7	0.7		
Lechea spp.							3.7	0.5					21.6	0.5	60.0	0.5	7.7	0.5
Hudsonia tomentosa									1.5	2.0	26.3	0.8	32.4	0.9	**80.0**	**13.5**	7.7	0.5
Ammophila breviligulata	5.3	0.5							1.5	0.5	15.8	0.5	10.8	0.5	**86.7**	**0.7**	7.7	0.5
Polygonella articulata									4.6	0.5	21.1	0.5	2.7	0.5	53.3	0.5	7.7	0.5
Solidago sempervirens	15.8	0.5					7.4	0.5			5.3	0.5	5.4	0.5	53.3	0.5	7.7	0.5
Carex rugosperma									1.5	0.5			18.9	0.5	46.7	0.5	7.7	0.5
Schizachyrium scoparium	15.8	1.0							20.0	0.6	31.6	0.5	54.1	0.7	46.7	1.1	38.5	27.2
Solidago odora			5.6	0.5	2.9	0.5	7.4	0.5	3.1	0.5	10.5	0.5	16.2	0.5	26.7	0.5		
Robinia pseudoacacia	15.8	4.7	9.3	4.1	2.9	1.0			13.8	2.1							15.4	23.8
Achillea millefolium	15.8	0.5					3.7	0.5					8.1	0.5	20.0	0.5	46.2	0.5
Baptisia tinctoria					4.9	0.5	14.8	1.4	6.2	0.5					6.7	0.5	30.8	1.3
Danthonia spicata	15.8	1.0	3.7	0.5			3.7	0.5	1.5	0.5			18.9	0.5	13.3	0.5	23.1	0.5
Solidago rugosa	47.4	0.7	3.7	0.5			3.7	0.5					10.8	0.5			69.2	1.7
Rubus flagellaris	26.3	0.5	3.7	0.5	2.9	0.5	18.5	1.1	4.6	0.5	5.3	0.5	21.6	0.5	6.7	0.5	53.8	3.9
Rosa virginiana	21.1	0.5							4.6	0.5	5.3	0.5	5.4	0.5			38.5	8.2
Myrica pensylvanica	42.1	1.5	40.7	1.8	47.6	3.3	33.3	1.1	60.0	2.3	36.8	1.2	67.6	1.7	73.3	3.8	69.2	1.6
Lonicera morrowii	57.9	3.7							3.1	0.5			2.7	0.5			69.2	1.8
Juniperus virginiana	31.6	20.0	3.7	0.5			3.7	0.5	12.3	1.5			16.2	1.0	20.0	2.2	69.2	28.1
Rumex acetosella													13.5	0.5	20.0	1.7	53.8	0.5

Species such as *G. baccata* and *P. rigida* are widely distributed across Cape Cod, whereas the distributions of several other species show strong geographical patterns across the study region (Fig. 5). *Arctostaphylos uva-ursi* and *D. flexuosa* are most common on dune or outwash deposits on outer Cape Cod, whereas *Lycopodium/Diphasiastrum* spp., *Ilex opaca*, *Uvularia sessilifolia*, *P. strobus*, *Carya glabra/ovalis*, and *G. frondosa* occur most frequently on moraine or outwash deposits on the inner Cape. *Quercus coccinea* is most common across the inner- and mid-Cape regions, and *Q. stellata* is largely restricted to the mid-Cape, where it apparently reaches its northern limit of distribution (Stransky, 1990). *Vaccinium stamineum* was also largely found in the mid-Cape, where it also occurred in the mid-nineteenth century (Torrey & Allen, 1962). *Corema conradii* is most abundant on outer Cape Cod within the town of Wellfleet.

Fire history

Palaeoecological reconstructions provide information on the long-term fire history of Cape Cod (Backman, 1984; Winkler, 1985; Motzkin *et al.*, 1993; Parshall *et al.*, 2003). In the *c.* 1000 years before European settlement, fires were more common on Cape Cod than in much of New England (Patterson & Sassaman, 1988; Parshall *et al.*, 2003). Fires were particularly important in pine woodlands on outwash soils on inner Cape Cod, and were less important on hardwood-dominated moraines; outer Cape Cod apparently experienced the lowest fire occurrence (Parshall *et al.*, 2003).

Fire generally increased in the historical period in association with widespread land clearing (Parshall *et al.*, 2003; although see Motzkin *et al.*, 1993). However, little documentary evidence is available for fires prior to the mid-nineteenth century, as is the case across much of New England, even in areas that apparently burned frequently (Motzkin *et al.*, 1996; Foster & Motzkin, 1999). From the mid-nineteenth to the early twentieth centuries, fires were common across Cape Cod, primarily as a result of ignitions by railroads (Anonymous, 1887, 1899; Collins, 1909; Rane, 1910; Cahoon, 1915; Cook, 1921). Fire detection and suppression improved dramatically in the twentieth century (Rane, 1910; Massachusetts Forestry Association, 1928; Patterson *et al.*, 1983), although occasional large fires continued to occur through the 1930s (Dunwiddie & Adams, 1995; Eberhardt, 2001). No large fires have occurred on Cape Cod National Seashore or other portions of outer Cape Cod in recent decades, despite numerous ignitions. In contrast, large wildfires and extensive prescribed fires have occurred occasionally on inner Cape Cod, especially on or near the Massachusetts Military Reservation.

Fire scars or macroscopic charcoal were observed in 52% of our plots, including greater than 70% of plots in Pitch

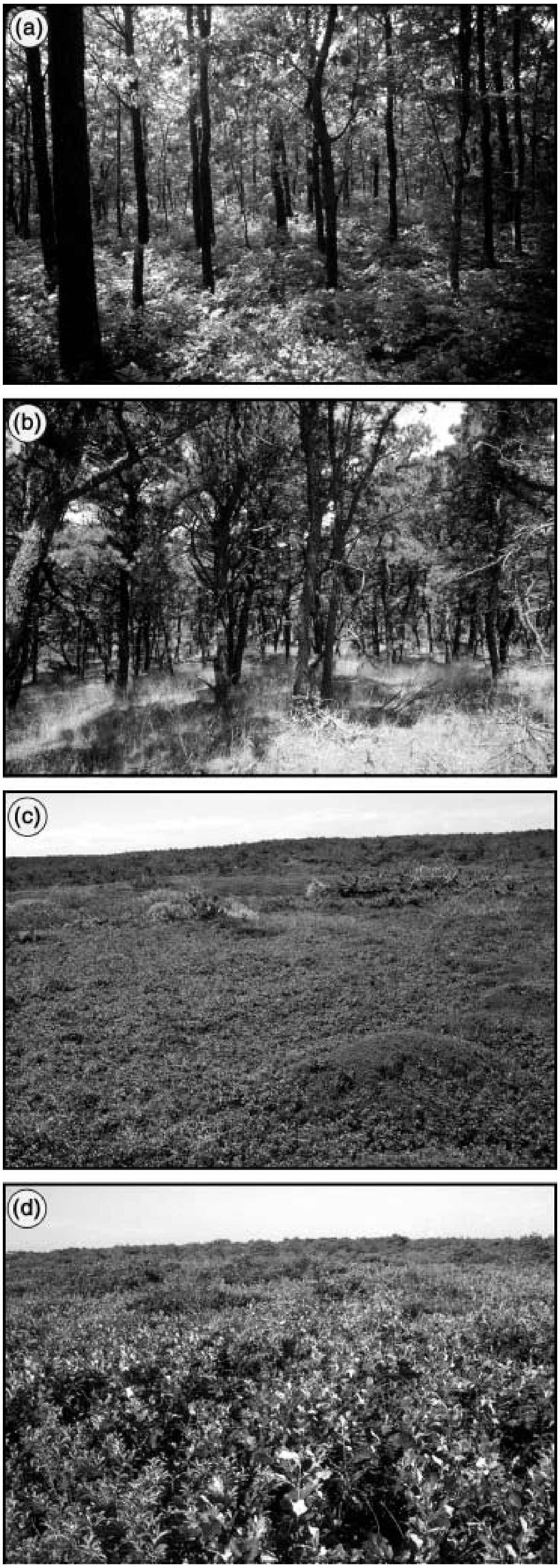

Figure 4 Photographs of common vegetation associations on Cape Cod, MA, including (a) Oak–Pine–Huckleberry, (b) Pine–Oak–Hairgrass, (c) Bearberry–Scrub Oak and (d) Pitch Pine–Scrub Oak.

Table 2 Differences in disturbance history and site conditions among upland vegetation types on Cape Cod, Massachusetts. Categories of past land-use and parent material are shown if a vegetation type occurs disproportionately on sites in that category; similar letters within rows indicate no significant difference. Categories of land-use history: P = ploughed, D = other soil disturbance, O = open, W = woodlot. Categories of parent material: O = outwash, M = moraine, D = beach/dune deposits, L = lake deposits. Median values are shown for other site factors, with Kruskal–Wallis statistic (*H*). All variables except TSI differ among types

	Oak–Briar $n = 19$	Oak–Pine–Maple $n = 54$	Oak–Pine–Huckleberry $n = 103$	Pitch Pine–Scrub Oak $n = 27$	Pine–Oak–Hairgrass $n = 65$	Pitch Pine–Hairgrass $n = 19$	Bearberry–Scrub Oak $n = 37$	Poverty Grass–Hairgrass $n = 15$	Cedar–Bayberry–Honeysuckle $n = 13$	*G*	*P*
Past land-use	P^{a}	O^{b}	W^{c}	W^{c}	P/O^{d}	P/D^{a}	P/D^{a}	D^{a}	P/D^{a}	317.1	<0.001
Parent material	D/L^{a}	M^{b}	M^{b}	O^{a}	O^{c}	D^{a}	D^{a}	D^{a}	L^{a}	166.0	<0.001
Evidence of fire (%)	21.1^{a}	48.1^{a}	72.5^{b}	77.8^{b}	37.5^{a}	31.6^{a}	48.6^{a}	13.3^{a}	38.5^{a}	52.2	<0.001
										H	*P*
Slope (°)	5.0^{abc}	7.0^{bc}	5.5^{bcd}	4.0^{e}	3.5^{ae}	3.5^{ae}	4.0^{ade}	3.4^{ae}	3.0^{ae}	31.4	0.000
TSI (×100)	−0.4	0.7	−0.2	0.0	0.2	0.2	−0.9	−1.3	0.0	13.0	0.111
Silt + clay (%)	6.0^{ab}	16.5^{c}	10.0^{ad}	8.4^{ad}	8.0^{a}	2.0^{e}	6.0^{be}	3.0^{e}	19.4^{cd}	71.003	0.000
TEC (mequ 100 g^{-1})	11.73^{ab}	13.04^{b}	10.54^{ac}	6.09^{d}	10.46^{cd}	1.46^{e}	2.33^{e}	0.71^{e}	8.99^{acd}	140.954	0.000
pH	4.4^{a}	4.3^{b}	4.3^{b}	4.3^{ab}	4.4^{a}	4.7^{c}	4.8^{cd}	5.3^{e}	5.0^{de}	132.080	0.000
Organic matter (%)	2.12^{ab}	2.32^{a}	1.85^{b}	1.66^{c}	1.46^{c}	0.53^{d}	1.15^{e}	0.48^{de}	2.90^{a}	113.029	0.000
Ca (mg kg^{-1})	70^{a}	33^{ab}	30^{b}	84^{abc}	29^{ab}	66^{abc}	89^{c}	75^{c}	434^{d}	51.720	0.000
Mg (mg kg^{-1})	21^{ab}	11^{c}	10^{c}	18^{ad}	12^{e}	14de	28^{bf}	24^{bf}	51^{f}	131.073	0.000
K (mg kg^{-1})	22^{a}	18^{b}	13^{cd}	18^{be}	13^{ce}	10^{df}	14^{bc}	8^{cef}	28^{a}	46.984	0.000

Sample sizes for past land-use analyses: Oak–Briar, $n = 19$; Oak–Pine–Maple, $n = 52$; Oak–Pine–Huckleberry, $n = 98$; Pitch Pine–Scrub Oak, $n = 27$; Pine–Oak–Hairgrass, $n = 64$; Pitch Pine–Hairgrass, $n = 19$; Bearberry–Scrub Oak, $n = 37$; Poverty Grass–Hairgrass, $n = 15$; Cedar–Bayberry–Honeysuckle, $n = 13$.

	Outwash $n = 219$	Moraine $n = 60$	Beach/dune $n = 54$	Lake $n = 19$	G	P
Evidence of fire (%)	54.6	54.2	38.9	42.1	5.1	>0.05
					H	P
Slope	4.0^{a}	7.0^{b}	5.3^{ab}	5.0^{ab}	13.8	0.003
TSI	0.0	−0.4	−0.3	−0.8	2.8	0.421
Silt + clay (%)	9.00^{a}	20.85^{b}	2.50^{c}	5.00^{d}	112.9	0.000
TEC (mequ 100 g^{-1})	8.94^{a}	11.73^{b}	1.03^{c}	6.28^{d}	78.8	0.000
pH	4.3^{a}	4.4^{a}	4.9^{b}	4.6^{a}	33.8	0.000
Organic matter (%)	1.56^{a}	2.17^{b}	0.83^{c}	1.27^{a}	85.1	0.000
Ca (mg kg^{-1})	54	29	71	90	6.2	0.104
Mg (mg kg^{-1})	13^{a}	10^{b}	24^{c}	23^{c}	61.4	0.000
K (mg kg^{-1})	14	18	17	14	8.6	0.035

Table 3 Environmental characteristics and evidence of fire on different landforms on Cape Cod, Massachusetts. Median values are shown, with Kruskal–Wallis statistic (H) and *post hoc* comparisons for variables that differ among landforms; similar letters within rows indicate no significant difference

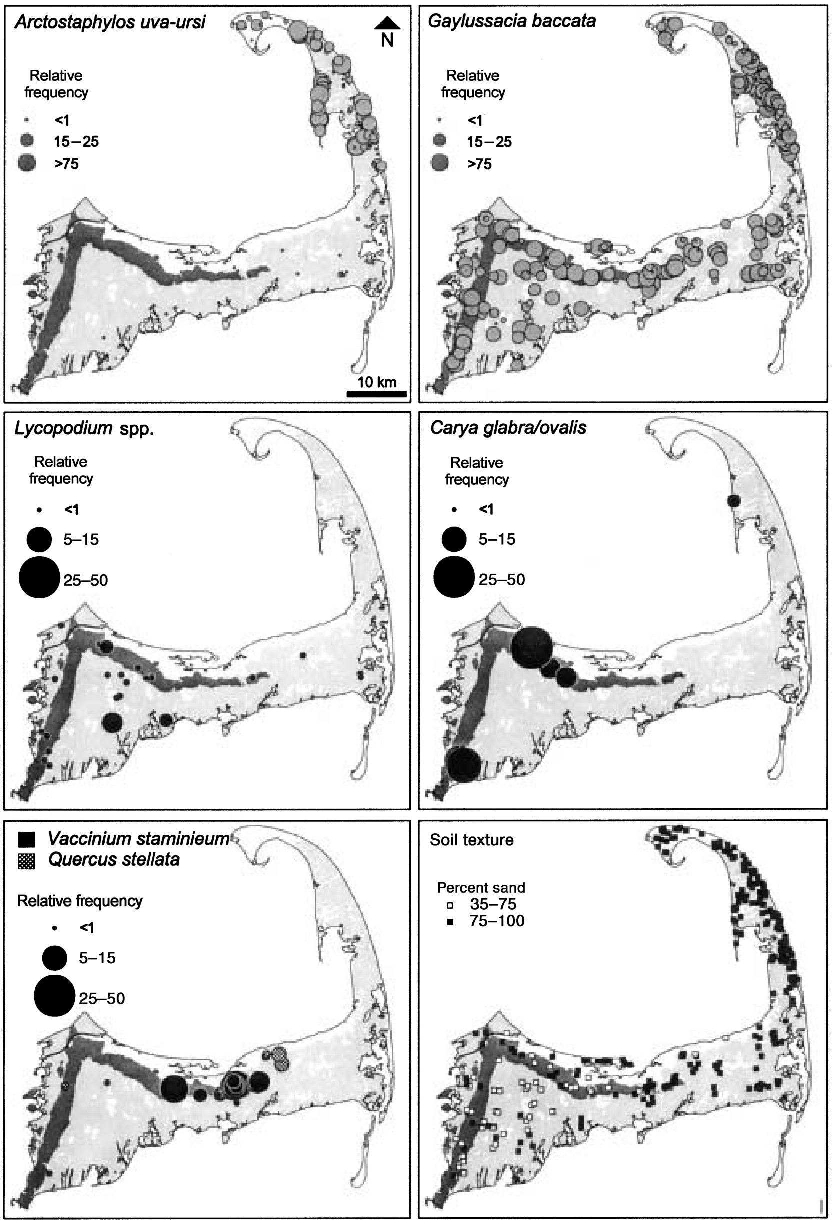

Figure 5 Distribution and abundance of vascular plant species and soil texture (bottom right) in 352 plots on Cape Cod, Massachusetts. Relative species abundance is indicated by the size of the dark circles. Plot distribution is indicated in the map of soil texture. The map of *Lycopodium* species includes *Diphasiastrum*.

Table 4 Frequency of occurrence of vascular plant species on sites of differing past land-use on Cape Cod, Massachusetts. Data are shown only for species that were present in >5% of the plots. Bold values indicate species affinities for different land-use categories, based on *G*-tests with *post hoc* comparisons. Similar letters within rows indicate no significant difference

Species	Ploughed $n = 106$ %	Disturbed $n = 68$ %	Open $n = 60$ %	Woodlot $n = 110$ %	Overall $n = 344$ %	*G*	*P*
Deschampsia flexuosa	**76.4**^{a}	**85.3**^{a}	45^{b}	20^{c}	54.7	108.0	<0.001
Schizachyrium scoparium	**31.1**^{a}	**27.9**^{a}	3.3^{b}	0^{b}	15.7	68.6	<0.001
Prunus maritima	**17.9**^{a}	**33.8**^{a}	0^{b}	0.9^{b}	12.5	60.2	<0.001
Arctostaphylos uva-ursi	**58.5**^{a}	**64.7**^{a}	25^{b}	20^{b}	41.6	57.0	<0.001
Hudsonia ericoides	**9.4**^{a}	**22.1**^{a}	0^{b}	0^{b}	7.3	40.1	<0.001
Aster linariifolius	**10.4**^{a}	**17.6**^{a}	0^{b}	0^{b}	6.7	33.8	<0.001
Rubus flagellaris	**16**^{a}	**17.6**^{a}	6.7^{b}	1.8^{b}	10.2	19.8	<0.001
Juniperus virginiana	**16**^{a}	**17.6**^{a}	6.7^{b}	1.8^{b}	10.2	19.8	<0.001
Toxicodendron radicans	**35.8**^{a}	**42.6**^{a}	**28.3**^{a}	9.1^{b}	27.3	33.5	<0.001
Chimaphila maculata	**26.4**^{a}	5.9^{b}	**23.3**^{a}	3.6^{b}	14.5	32.4	<0.001
Prunus serotina	**79.2**^{a}	55.9^{b}	**76.7**^{a}	47.3^{b}	64.0	30.6	<0.001
Hudsonia tomentosa	6.6^{a}	**35.3**^{b}	0^{c}	0^{c}	9.0	67.0	<0.001
Lechea spp.	4.7^{a}	**20.6**^{b}	0^{a}	0^{a}	5.5	36.2	<0.001
Ammophila breviligulata	3.8^{a}	**27.9**^{b}	0^{a}	0^{a}	6.7	54.2	<0.001
Lonicera morrowii	13.2	7.4	0.0	3.6	6.7	15.6	<0.005
Parthenocissus quinquefolia	23.6	25.0	10.0	10.0	17.2	12.3	<0.05
Danthonia spicata	9.4	8.8	3.3	0.9	5.5	10.8	<0.05
Myrica pensylvanica	53.8	64.7	45.0	41.8	50.6	10.0	<0.05
Solidago rugosa	12.3	8.8	1.7	4.5	7.3	8.7	>0.05
Solidago odora	8.5	10.3	5.0	1.8	6.1	7.4	>0.05
Carex pensylvanica	60.4	57.4	55.0	55.5	57.3	0.7	>0.05
Corema conradii	8.5	20.6	3.3	4.5	8.7	14.4	<0.01
Comptonia peregrina	9.4	20.6	10.0	9.1	11.6	5.8	>0.05
Baptisia tinctoria	4.7	5.9	5.0	5.5	5.2	0.1	>0.05
Maianthemum canadense	17.0	16.2	20.0	10.0	15.1	3.8	>0.05
Rubus hispidus	26.4	10.3	33.3	16.4	21.2	13.6	<0.01
Trientalis borealis	40.6	27.9	38.3	20.9	31.4	11.6	<0.05
Amelanchier spp.	53.8	36.8	63.3	49.1	50.6	9.7	<0.05
Smilax glauca	20.8	8.8	28.3	18.2	18.9	8.7	>0.05
Rubus allegheniensis	14.2	5.9	10.0	4.5	8.7	7.0	>0.05
Lycopodium obscurum	8.5	2.9	6.7	2.7	5.2	4.5	>0.05
Robinia pseudoacacia	9.4	5.9	6.7	2.7	6.1	4.4	>0.05
Vaccinium corymbosum	32.1	16.2	38.3	33.6	30.5	9.6	<0.05
Pinus rigida	88.7	77.9	93.3	90.0	87.8	7.6	>0.05
Pyrola rotundifolia	11.3	1.5	8.3	9.1	8.1	7.2	>0.05
Quercus ilicifolia	74.5	57.4	63.3	68.2	67.2	6.0	>0.05
Chimaphila umbellata	5.7	2.9	5.0	6.4	5.2	1.1	>0.05
Ilex glabra	0.9	8.8	8.3	8.2	6.1	9.2	>0.05
Ilex opaca	5.7	4.4	11.7	5.5	6.4	2.9	>0.05
Fagus grandifolia	3.8	2.9	13.3	5.5	5.8	6.6	>0.05
Melampyrum lineare	17.0	14.7	20.0	18.2	17.4	0.7	>0.05
Vaccinium stamineum	3.8	1.5	13.3	9.1	6.7	9.9	<0.05
Uvularia sessilifolia	1.9	0.0	13.3	7.3	34.6	17.3	<0.005
Quercus prinoides	8.5	13.2	8.3	20.9	13.4	8.5	>0.05
Monotropa uniflora	**31.1**^{a}	5.9^{b}	**28.3**^{a}	**26.4**^{a}	24.1	19.7	<0.001
Quercus velutina	77.4^{a}	55.9^{b}	**90**^{a}	**84.5**^{a}	77.6	25.1	<0.001
Lyonia ligustrina	5.7^{a}	1.5^{a}	**23.3**^{b}	10.9^{a}	9.6	19.5	<0.001
Nyssa sylvatica	6.6^{a}	1.5^{a}	**21.7**^{b}	3.6^{a}	7.3	19.6	<0.001
Viburnum dentatum	36.8^{a}	20.6^{a}	**48.3**^{b}	20^{a}	30.2	19.7	<0.001
Smilax rotundifolia	40.6^{a}	23.5^{a}	**63.3**^{b}	36.4^{a}	39.8	22.0	<0.001
Pinus strobus	14.2^{a}	2.9^{a}	**41.7**^{b}	15.5^{a}	17.2	34.2	<0.001
Cypripedium acaule	20.8^{a}	5.9^{b}	**50**^{c}	23.6^{a}	23.8	35.4	<0.001
Viburnum nudum	26.4^{a}	7.4^{b}	**58.3**^{c}	35.5^{a}	31.1	43.5	<0.001
Acer rubrum	14.2^{a}	7.4^{a}	**35**^{b}	**27.3**^{b}	20.6	21.3	<0.001

Table 4 *continued*

Species	Ploughed $n = 106$ %	Disturbed $n = 68$ %	Open $n = 60$ %	Woodlot $n = 110$ %	Overall $n = 344$ %	G	P
Aronia spp.	12.3^{a}	7.4^{a}	**36.7^{b}**	**25.5^{b}**	19.8	23.5	<0.001
Gaylussacia frondosa	2.8^{a}	0^{a}	**23.3^{b}**	**12.7^{b}**	9.0	31.3	<0.001
Sassafras albidum	4.7^{a}	5.9^{a}	**20^{b}**	**26.4^{b}**	14.5	27.2	<0.001
Quercus coccinea	37.7^{a}	8.8^{b}	**71.7^{c}**	**59.1^{c}**	44.8	71.2	<0.001
Epigaea repens	15.1^{a}	7.4^{a}	**38.3^{b}**	**45.5^{b}**	27.3	46.0	<0.001
Kalmia angustifolia	5.7^{a}	1.5^{a}	**31.7^{b}**	**31.8^{b}**	17.7	51.9	<0.001
Vaccinium angustifolium	57.5^{a}	20.6^{b}	**81.7^{c}**	**88.2^{c}**	64.2	97.2	<0.001
Gaylussacia baccata	60.4^{a}	50^{a}	**98.3^{b}**	**97.3^{b}**	76.7	97.9	<0.001
Quercus alba	75.5^{a}	35.3^{b}	**95^{c}**	**96.4^{c}**	77.6	100.3	<0.001
Pteridium aquilinum	9.4^{a}	5.9^{a}	**41.7^{b}**	**65.5^{b}**	32.3	111.9	<0.001
Vaccinium pallidum	32.1^{a}	27.9^{a}	**85^{b}**	**89.1^{b}**	58.7	125.5	<0.001
Gaultheria procumbens	18.9^{a}	8.8^{a}	**58.3^{b}**	**89.1^{c}**	46.2	173.3	<0.001

Table 5 Environmental characteristics and evidence of fire among categories of past land-use on Cape Cod, Massachusetts. Categories of parent material are shown if past land-use occurred disproportionately on sites of a given category; similar letters within rows indicate no significant difference. Categories of parent material: O = outwash, M = moraine, D = beach/dune deposits, L = lake deposits. Median values are shown for variables other than fire, with Kruskal–Wallis statistic (H)

	Ploughed $n = 106$	Disturbed $n = 68$	Open $n = 60$	Woodlot $n = 110$	G	P
Parent material	O/L^{a}	D^{b}	O/M^{c}	O^{c}	27.9	<0.001
Evidence of fire (%)	37.9^{a}	44.1^{a}	45.0^{a}	73.6^{b}	32.5	<0.001
					H	P
Slope	3.2^{a}	4.0^{a}	7.3^{b}	5.5^{b}	34.5	0.000
TSI	−0.2	−0.3	0.3	0.0	3.8	0.285
Silt + clay (%)	9.0^{ab}	4.0^{c}	12.1^{a}	9.0^{b}	48.3	0.000
TEC (mequ 100 g^{-1})	8.0^{a}	1.4^{b}	11.2^{c}	10.5^{c}	67.5	0.000
pH	4.6^{a}	4.8^{b}	4.3^{c}	4.2^{d}	112.2	0.000
Organic matter (%)	1.6^{a}	1.1^{b}	1.9^{c}	1.8^{ac}	40.7	0.000
Ca (mg kg^{-1})	75.0^{a}	76.0^{a}	32.0^{b}	33.0^{b}	16.4	0.001
Mg (mg kg^{-1})	17.0^{a}	24.5^{b}	10.0^{c}	10.0^{c}	80.7	0.000
K (mg kg^{-1})	15.5	18.0	15.5	14.5	8.1	0.044

Pine–Scrub Oak and Oak–Pine–Huckleberry vegetation (Table 2). Evidence of fire was observed in only 13% of plots characterized by the Poverty Grass–Hairgrass association, and 21% of plots supporting the Oak–Briar type. Evidence of fire was recorded more frequently in areas that were continuously wooded (74%) than in 'ploughed' (38%), 'disturbed' (44%), or 'open' (45%) land-use categories (Table 5). Field evidence of fire did not vary among landforms across the study region (Table 3).

DISCUSSION

The influence of past land-use on modern species richness and composition is increasingly recognized for a wide range of ecosystems and several studies have identified specific biological or edaphic factors that may contribute to the persistence of these patterns for centuries (e.g. Peterken & Game, 1984; Matlack, 1994; Wulf, 1997; Brunet & Von Oheimb, 1998a,b; Donohue *et al.*, 2000; Verheyen & Hermy, 2001; Bellemare *et al.*, 2002; Eberhardt *et al.*, 2003; Foster *et al.*, 2003). In particular, comparisons of primary and secondary woodlands have identified a suite of 'ancient forest plant species' that are restricted in their abilities to colonize recent woodlands as a result of dispersal or recruitment limitations (Verheyen & Hermy, 2001). In regions such as the north-eastern US with long histories of widespread and intensive disturbance by human activity, it is likely that the modern distributions and abundances of nearly all species are highly altered from those that occurred prior to human settlement. However, the degree to which past human activity, natural disturbance, or modern environmental gradients influence vegetation variation on any particular landscape differs in part in response to the nature and intensity of past disturbances, the degree of variation in environmental and resource conditions, and the life-history characteristics of the species involved. Our results from Cape Cod document the influence of historical, environmental and geographical factors on vegetation variation and species distributions across the region. Importantly, despite substantial environmental variation and a century or more since widespread abandonment of agriculture, historical land-use continues to influence the distributions and abundances of numerous species, including many that are high priorities for conservation.

Relationships among vegetation, environment, fire and past land-use

Substantial variation in geography, environment and site history has influenced vegetation composition and structure across the study region. Several vegetation associations are more or less restricted to sites with particular histories and are often restricted to specific geographical or environmental conditions. For instance, heathlands that support Bearberry–Scrub Oak vegetation occur most frequently on sandy soils of outer Cape Cod, where they developed almost exclusively on dunes or on sites that were formerly ploughed, grazed, or experienced other severe soil disturbance such as military activity; in contrast, Oak–Pine–Huckleberry and Pitch Pine–Scrub Oak vegetation occurs predominantly on sites that were continuously wooded, and the structure of many of these stands has been strongly influenced by fire (Eberhardt *et al.*, 2003). Pitch Pine–Scrub Oak vegetation also commonly occurs on outer Cape Cod in a narrow band that parallels the coast between the coastal bluff and taller stature forests, suggesting the possibility that salt spray may influence the composition and structure of this vegetation type (Boyce, 1954). Woody vegetation on peninsulas in coastal Maine is also strongly influenced by environmental variation that is related to distance to the coast (Milne & Forman, 1986); however, the irregular shape of Cape Cod and the high degree of variation in environmental conditions and disturbance histories precluded a direct analysis of potential peninsular effects on vegetation (independent of environmental variation) in our study region (Milne & Forman, 1986).

Fire was common in the past across the study area, although the importance of fire apparently varies spatially and temporally. Several potential sources of error in our field observations indicate that caution is necessary in interpreting fire history. Because we relied exclusively on field observations of macroscopic charcoal and fire scars, our data almost certainly underestimate the actual distribution of fire (Motzkin *et al.*, 2002). The occurrence of macroscopic charcoal and fire scars is strongly related to vegetation composition, structure and fire intensity, and fires undoubtedly occurred in some areas that we recorded as having no field evidence of fire. In particular, fires that occurred in grassland or other non-forested vegetation would generate little or no persistent macroscopic charcoal and no fire scars, and would be most likely be to overlooked in our field observations. In addition, because charcoal is highly recalcitrant, charcoal found in undisturbed soils of continuously wooded areas may result from fires over a broad time-scale (i.e. millennia), whereas on former agricultural lands with disturbed soils, macroscopic charcoal is typically derived from fires that have occurred in the recent past (i.e. since agricultural abandonment). Despite these inconsistencies in our estimates of the occurrence of past fire, we suspect that the pattern of greater importance of fire in Oak–Pine–Huckleberry and Pitch Pine–Scrub Oak vegetation on continuously wooded areas than in Poverty Grass–Hairgrass or Oak–Briar types on disturbed sites is likely to represent a real trend. For instance, on outer Cape Cod, Eberhardt (2001) found that several twentieth century fires occurred in continuously wooded sites rather than in woodlands on former agricultural lands. Our field observations suggest that on continuously wooded sites, modern canopy age-structure and composition frequently developed as a result of past fire and perhaps cutting. In contrast, even on those former agricultural sites that have burned, fire appears to have primarily modified vegetation patterns that largely result from past agriculture. Chokkalingham (1995) has also documented the influence of insect defoliation on forest stand dynamics on Cape Cod, noting a reduced rate of succession from pine to oak-dominated stands as a result of selective herbivory on hardwoods; such effects may be particularly important as a result of increased fire suppression in recent decades.

Conservation implications

Relationships between modern vegetation and site history similar to those observed on Cape Cod are found across coastal New England, although the extent and intensity of historical disturbances vary substantially in different portions of the region (Dunwiddie & Adams, 1995; Foster & Motzkin, 1999; Foster *et al.*, 2002b; Motzkin & Foster, 2002; Eberhardt *et al.*, 2003). Although little is known of the pre or early historical distributions of plant species that are uncommon today on Cape Cod, the modern distributions of several species are primarily restricted to early successional habitats such as dunes, heathlands, or grasslands, nearly all of which have been severely disturbed by historical land-use practices (McCaffrey, 1973; Dunwiddie *et al.*, 1996; Motzkin & Foster, 2002). As a result, it is unlikely that the modern distributions of these species closely approximate those that occurred prior to European arrival. Maintenance of these species and assemblages on sites other than dunes or highly exposed coastal locations may require intensive management that is comparable in intensity with the historical disturbances that gave rise to their current abundance and distribution. Although we suspect that the dominant vegetation on sites that have been wooded continuously is more similar to that which occurred prior to European settlement, additional studies are necessary to evaluate the effects of ongoing human disturbances, especially forest fragmentation resulting from suburbanization, on the composition and dynamics of these woodlands.

ACKNOWLEDGMENTS

We thank E. Largay, L. Miskimins, S. Sabin, S. Sekinger and G. Yorgey for field assistance, A. Allen, W. Patterson III and T. Rawinski for informative discussions, and N. Finley,

M. Adams and D. Crary from Cape Cod National Seashore for logistical support. Thanks to Pat Swain of the Massachusetts Natural Heritage and Endangered Species Program for helpful comments on the manuscript. Thanks also to Massachusetts Audubon Society, The Trustees of Reservations, MA Department of Environmental Management, MA Division of Fisheries and Wildlife, and numerous town officials for permission to sample the lands that they administer. Support for this study was provided by The Nature Conservancy's Ecological Research Program, National Science Foundation and Andrew Mellon Foundation. This paper is a contribution of the Harvard Forest Long Term Ecological Research Program.

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