Distribution and Dynamics of American Beech in Coastal Southern New England

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Abstract - *Fagus grandifolia* (American Beech) is uncommon along the coast of southern New England, but occasionally forms unusual monodominant stands with higher beech abundance than is typical for inland areas. This study documents the distribution of beech on Cape Cod and nearby coastal islands, and evaluates environmental and historical factors that are likely to influence its distribution. Tree-ring data from six beech forests in the study region were used to determine age structure and to assess the importance of disturbance history for beech forest development.

Beech is irregularly distributed across the coastal region. It is most common and abundant on moraines and in areas that are close to water bodies, presumably as a result of reduced drought stress and increased protection from wildfire. The largest monodominant beech forest (approximately 1000 ha) known from the eastern US occurs on Naushon Island, but few stands elsewhere in the region exceed 5 ha. In the six intensively studied forests, the relative importance of beech has increased in recent decades. Decreased establishment of oaks and other associated species in the 20th century has presumably resulted from regional declines in forest harvesting and fire. Increased beech dominance in the 20th century corresponds with episodic beech establishment and growth release after several hurricanes in the 1920s–1950s. Thus, unlike the small-scale gap dynamics characteristic of beech in the extensive northern hardwood forests of northern New England and New York, large-scale wind disturbances apparently contribute to local beech dominance in coastal New England where beech is otherwise uncommon.

Introduction

Fagus grandifolia Ehrh. (American Beech) is widespread throughout temperate forests of eastern North America, occurring in a wide range of forest types under varied site conditions (Braun 1950). Beech is common in the extensive northern hardwood forests of the northeastern United States and adjacent portions of southeastern Canada, extending south along the Appalachian Mountains through the southeastern US. A few isolated populations of a distinct variety (*Fagus grandifolia* Ehrh. var. *mexicana* (Martinez) Little) occur in cloud forests of eastern Mexico (Williams-Linera et al. 2003). While the western and southern limits of the range of American Beech are related to moisture availability, cold hardiness may restrict its northern limit (Cogbill 2005).

In the northern portion of its range, beech occurs from sea level to approximately 1000 m above sea level, where it is most commonly found on

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mesic soils derived from glacial till (Tubbs and Houston 1990). In northern hardwood forests in the Northeast, beech is co-dominant with *Acer saccharum* Marsh. (Sugar Maple), *Betula alleghaniensis* Britton (Yellow Birch), *Picea rubens* Sarg. (Red Spruce), and other species. Despite a history of intensive investigation of beech in northern New England and New York (e.g., Canham 1990, Cogbill 2005), its distribution, abundance, and dynamics along the coast of southern New England are poorly documented. In particular, although beech has long been known from a few locations on Cape Cod and nearby coastal islands (e.g., Archer 1602, Fogg 1930, Hinds 1966), considerable uncertainty exists about its historical and modern distributions and dynamics in the region. While beech is uncommon along the coast, it is occasionally locally abundant, attaining levels of dominance that are rare in inland areas (Busby 2006).

Variation in beech-stand dynamics between coastal and inland stands is likely caused by differences in regional disturbance regimes. Beech is extremely shade-tolerant and, in northern hardwood forests, is considered a late-successional species. In these forests, beech typically establishes in the forest understory, eventually emerging to the canopy in gaps created by the loss of individual trees or small groups of trees (Canham 1990, Runkle 1981). Major wind disturbances that create large canopy gaps are uncommon in such forests, in contrast to coastal areas where hurricanes are more frequent and severe (Boose et al. 2001) and may strongly influence beech forest development (Busby et al. 2009). Fire, which has the potential to eliminate or limit beech, has historically been more frequent in the coastal region than in inland portions of New England (Parshall et al. 2003). Beech bark disease, a scale-fungus complex, has led to substantial changes in northern hardwood forest structure and dynamics in recent decades (Morin et al. 2006, Twery and Patterson 1984). However, beech bark disease has not significantly altered forest structure or composition in most sites along the coast of southern New England (Busby 2006; D. Houston, Danville, VT, pers. comm.).

Our aim in this study was to document the distribution of American Beech on Cape Cod and nearby coastal islands, evaluate the factors that control its distribution, and determine how beech-dominated stands develop and persist in the coastal region where beech is otherwise uncommon. The specific objectives of this study are: (1) to describe patterns of beech distribution and abundance relative to geographic, environmental, and historical conditions in the coastal region; and (2) characterize the influence of disturbance history on beech forest development using data on tree growth and establishment.

Study Area

The study area includes Cape Cod, MA and nearby coastal islands (Fig. 1). A single putative old-growth site on Aquidneck Island, RI, approximately 50 km west of Cape Cod, was included as one of our six intensive-study sites for age structure and dendroecological analyses (see below). Cape Cod and the nearby islands were largely formed during the Wisconsinan glaciation, and are characterized by extensive glacial outwash deposits, a series of moraines, smaller areas of glacial lake sediments, and areas of more recent dune deposits (Oldale 1992). Soils on outwash and dune deposits are typically excessively drained sands while soils on moraines are rocky and variable in texture (Fletcher and Roffinoli 1986). Substrate and landscape position exert strong control on regional vegetation composition and natural disturbance regimes (Motzkin et al. 2002, Parshall et al. 2003). *Pinus rigida* Mill. (Pitch Pine), several *Quercus* tree species, especially *Quercus velutina* Lam. (Black Oak), *Quercus alba* L. (White Oak), and *Quercus ilicifolia* Wangenh. (Scrub Oak), dominate extensive xeric outwash deposits where fires occurred historically. Mesic uplands with less frequent

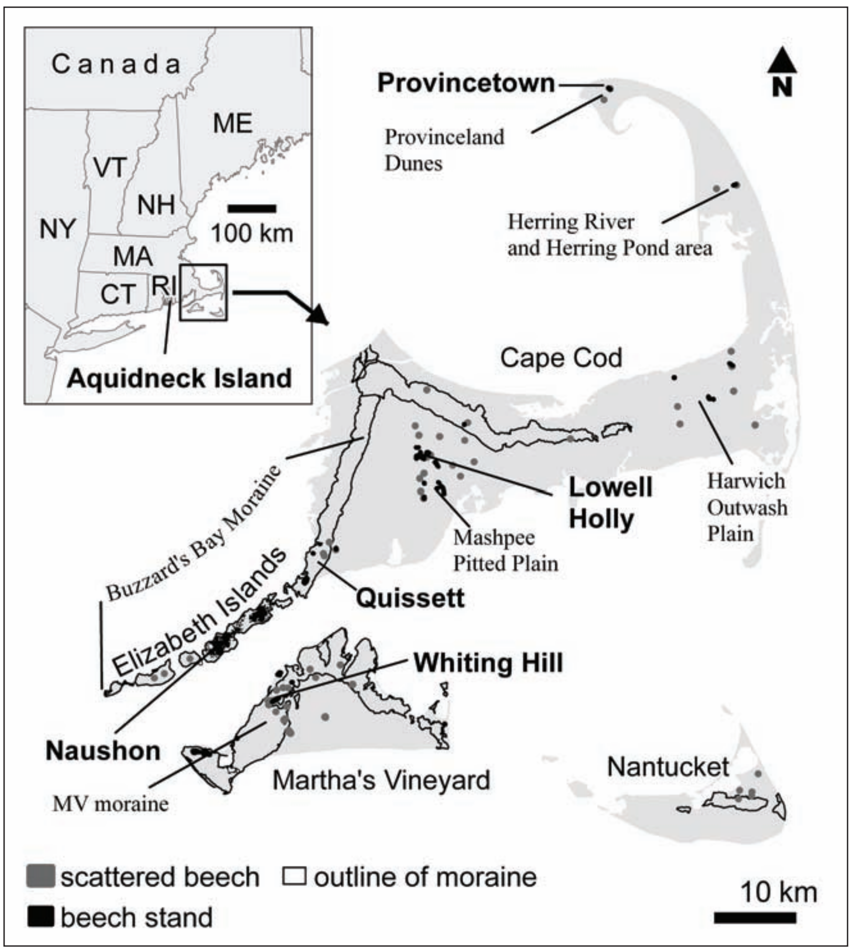

Figure 1. Map of study region with place names, showing locations of scattered beech and beech stands, and six intensive-study sites (in bold).

fire, where beech might be expected, are uncommon (Dunwiddie and Adams 1995, Eberhardt et al. 2003, Foster et al. 2002, Hinds 1966, Motzkin et al. 2002, Parshall et al. 2003, Patterson et al. 1983).

Beech occurs infrequently in the study area. In a previous study, beech stands or individual trees >2.5 cm dbh were found in only 7 out of 613 (≈1 %) randomly sampled plots on Cape Cod, Martha's Vineyard, and Nantucket; stems <2.5 cm dbh occurred in 29 (≈5%) of these plots (Eberhardt et al. 2003, Motzkin et al. 2002, Von Holle and Motzkin 2007).

Methods

Beech distribution

A digital map of the modern distribution of American Beech across the coastal region was developed based on: (1) prior studies (Hinds 1966, Schroeder 2002, VanLuven 1990), including 613 randomly located plots (Eberhardt et al. 2003, Motzkin et al. 2002, Von Holle and Motzkin 2007); (2) site location information provided by knowledgeable individuals; and (3) de novo field reconnaissance. In mapping beech distribution, we distinguished two broad categories of abundance: "beech stands" (i.e., beech-dominated forests as well as mixed stands where beech was common) and "scattered beech" (i.e., single or occasional beech trees located in forests dominated by other species). Estimates of the coverage of beech forests in the region are based exclusively on "beech stands," whereas spatial analyses were based on all documented beech occurrences; results of comparable analyses excluding "scattered beech" were very similar (data not shown).

We compiled a series of GIS data layers for the study region that were used in spatial analyses to identify environmental and historical factors that may influence the distribution of American Beech. Surficial geology was digitized from Oldale and Barlow (1986), and soil drainage was determined from NRCS (2007). NRCS soil drainage categories were given integer values for analyses as follows: very poorly drained = 1; poorly drained = 2; somewhat poorly drained = 3; moderately well drained = 4; well drained = 5; somewhat excessively drained = 6; excessively drained = 7. Distance from water bodies and the percentage of water within 1 km of a site were determined from the MassGIS (2002) land-cover data layer. Distance from water bodies was transformed by taking the logarithm base 10 to improve normality; percentage of water within a 1-km distance was transformed by taking the square root. Terrain shape index, aspect, and slope were calculated from National Elevation Data (USGS 2002). Slope was transformed by taking the square root to improve normality. Terrain shape index was calculated using the "Landform.aml" function from the esri.com website. The index is an elevation-derived measurement of the concavity and convexity of an area, varying between -1 and 1; negative numbers are more concave and positive numbers are more convex (McNab 1989). Historical land use was determined by digitized land-cover maps from the mid-19th century (Massachusetts Archives 1830, USCGS 1845–61). Several previous studies determined that patterns of historical land cover depicted on these detailed maps strongly influence modern vegetation composition across the study region (Eberhardt et al. 2003, Foster and Motzkin 1999, Motzkin et al. 2002, Von Holle and Motzkin 2007).

To characterize environmental and historical variables associated with beech occurrence, we used random-point placement extension (Beyer 2004) within ArcMap GIS (ESRI 2006) to randomly sample points at a density of 1 point per 10 ha for areas containing beech (stands and scattered) (n = 112) and for all forested areas without beech (n = 5661). We forced placement so that every beech stand or area of scattered beech had at least one sample point. Environmental and historical variables of beech vs. non-beech forests were then compared for the entire study region. In addition, we made similar comparisons for Cape Cod alone (excluding the coastal islands), to determine whether patterns of beech distribution on Cape Cod differed from region-wide patterns.

Pearson's Chi-Square tests were used to compare categorical variables (i.e., surficial geology and mid-19th century woodland cover), and t-tests were used for quantitative environmental variables after appropriate transformations for non-normally distributed data (Systat 10; SPSS 2000). Results were back-transformed prior to reporting. Bonferroni adjustments were not conducted, as per Moran (2003) and Gotelli and Ellison (2004).

Stand composition, age structure, and dynamics

Six study sites were selected for intensive vegetation sampling to characterize composition, structure, and long-term forest dynamics. These six sites are distributed across substrate types, and support some of the largest beech stands across the study region (Fig. 1, Table 1). In addition, for several smaller stands (n = 7), we determined overstory composition in variable radius plots (n = 5 per site), using a 10-factor cruise-all to estimate tree basal area along a transect oriented along the main axis of the stand. Sample points were separated from each other by a minimum of 100 m.

We used data on stand age and growth dynamics to assess the role of disturbance on beech forest development in the six intensive-study sites. In fixed-area plots (400 m^2), species and diameter at breast height (dbh, 1.4 m from the ground) were recorded for all trees >7 cm dbh, and increment cores were taken from 15–20 trees >7 cm dbh for age determination and radial growth analysis. Additional old trees located outside of study plots were also cored to facilitate reconstructing long-term forest dynamics. Cores were dried, mounted, and sanded with increasingly fine sandpaper to reveal the cellular structure. Tree rings were counted and measured to the nearest 0.01 mm using a Velmex measuring system (East Bloomfield, NY). Cores were used to determine tree ages, excluding cores that were rotten or substantially missed the pith. All cores were used to examine radial growth dynamics.

To characterize growth responses to disturbance in the intensive-study sites, we generated disturbance chronologies for beech. The densities of other species were too low to permit comparable analyses. By identifying the percentage of trees that experienced growth releases each decade, a disturbance chronology is used to estimate the average level of decadal small-scale disturbance, and to approximate the timing of stand-level disturbance events based on pulses in decadal release. The severity of a disturbance event is estimated by the percentage of trees released, with a stand-level disturbance defined as growth release in a minimum of 25% of stems (Nowacki and Abrams 1997). For beech, we defined a growth release as a percent growth change (GC) of 100% (Lorimer and Frelich 1989). Percent growth change was calculated for all years using prior (M_p) and subsequent (M_s) ten-year growth means: $GC = [(M_s – M_p) / M_p] \times 100$. Running comparisons of sequential ten-year means were made and release dates were assigned to years in which the maximum GC reached the pre-determined threshold (Nowacki and Abrams 1997). We examined growth changes based on ten-year averages to filter out short-term tree responses to climate while detecting sustained growth responses caused by disturbance (Lorimer and Frelich 1989, Nowacki and Abrams 1997).

Soil sampling

To characterize soil conditions in coastal beech stands, mineral soil grab samples (0–15 cm) from all intensive-study plots were analyzed for physical and chemical soil properties. Soil samples were oven-dried (105 °C for

Table 1. Site location, substrate, and tree species dominance for 13 beech-dominated stands in coastal New England. Species abbreviations are: Fagr = *Fagus grandifolia*, Acru = *Acer rubrum*, Nysy = *Nyssa sylvatica*, Piri = *Pinus rigida*, Pist = *Pinus strobus* L. (Eastern White Pine), Quve = *Quercus velutina*, Qual = *Quercus alba*, Cagl = *Carya glabra* (P. Mill) Sweet (Pignut Hickory), Cato = *Carya tomentosa* (Lam. ex Poir.) Nutt. (Mockernut Hickory), Osvi = *Ostrya virginiana* (Mill.) K. Koch (American Hophornbeam). BA = Fagr basal area (m^2/ha), RBA = Fagr Relative Basal Area (%), FD = Fagr density (stems/ha), and Stand size = approximate size of stand (ha).

Site	Plots (*n*)	Substrate	Dominant tree species[A]	BA	RBA	FD	Stand size
Massachussets							
Provincetown[B]	2	Dune	Fagr, Acru, Nysy, Piri	18.75	66.1	525.0	3
Herring River	5	Outwash	Fagr, Piri, Quve, Nysy	17.01	52.1	NA	1
Brewster	5	Outwash	Fagr, Piri, Quve, Qual	15.63	45.3	NA	2
Nickerson State Park	5	Outwash	Fagr, Piri, Quve, Pist	19.53	60.7	NA	2
Lowell Holly[B]	3	Outwash	Fagr, Quve, Piri, Qual	28.20	85.4	641.7	26
Ryder Conserv. Lands	5	Outwash	Fagr, Quve, Pist, Piri	9.20	32.0	NA	5
Goodwill Park	5	Moraine	Fagr, Quco, Cagl, Acru	29.41	82.1	NA	3
Beebe Woods	5	Moraine	Fagr, Qual, Cagl, Quve	46.70	89.4	NA	1
Quissett[B]	3	Moraine	Fagr, Quve, Qual, Acru	15.88	66.2	325.0	17
Cedar Tree Neck, MV	5	Moraine	Fagr, Quve, Qual	36.77	78.4	NA	8
Whiting Hill, MV[B]	2	Moraine	Fagr, Cato, Quve, Osvi	19.29	64.0	650.0	11
Naushon Island[B]	19	Moraine	Fagr, Qual, Quve, Acru	30.78	95.3	668.4	980
Rhode Island							
Aquidneck Island[B]	2	Till	Fagr, Qual, Acru	30.25	86.4	562.5	4

[A]Four tree species with greatest relative basal area, listed in order of decreasing importance.
[B]Intensive-study sites.

48 hours) and sieved (2 mm). Samples were analyzed by Brookside Laboratories (New Knoxville, OH) to determine soil texture, pH, total exchange capacity (TEC), percent organic matter (SOM%; Store 1984), and exchangeable cation and macronutrient concentrations (ppm) (P, Ca, Mg, K, Na; Mehlich 1984).

Results

Beech distribution

American Beech is uncommon across the study area, with substantial variation in local distribution and abundance (Fig. 1). While scattered beech are occasionally found distant from beech stands, most scattered individuals are near extant stands (Fig. 1). We documented 19 beech stands on Cape Cod, most of which are <2 ha in size; beech is unevenly distributed across the peninsula (see below). Small beech stands (n = 7) and scattered trees occur on portions of the western moraine of Martha's Vineyard, but are rare or absent elsewhere on the island. Beech occurs infrequently on Nantucket and on the western Elizabeth Islands (Pasque, Nashawena, Cuttyhunk), with no well-developed beech stands on these islands. Beech is ubiquitous on Naushon Island, where the most extensive beech forests in the region occur (approximately 1000 ha). The total acreage of beech stands in the study region is estimated at approximately 1115 ha, 90% of which occurs on Naushon Island (Table 1). Excluding Naushon Island, beech stands in the region range in size from <0.5 ha–26 ha, but few sites exceed 5 ha. Beech stands represent <2% of forests in the coastal study region.

Beech stands occur primarily in the following physiographic settings (Fig. 1; Oldale and Barlow 1986): (1) the "Buzzard's Bay" moraine at the southwestern tip of Cape Cod and adjacent Naushon Island, (2) the moraine on the western side of Martha's Vineyard, (3) "Mashpee" pitted plain deposits on the inner Cape, (4) "Harwich" outwash plain near the "elbow" of Cape Cod, (5) pitted plain deposits near Herring River and Herring Pond on outer Cape Cod, and (6) dunes in the Provincelands at the outer tip of Cape Cod. The Aquidneck Island site occurs on glacial till.

For the study region as a whole, beech occurrence is significantly related to surficial landform, with beech most common on moraines ($P < 0.001$; Table 2). Beech is also more likely to occur on sites with greater slopes ($P < 0.001$; Table 2), near water (ocean, freshwater, or wetlands, or all combined, $P < 0.01$; Table 2), and in areas with a higher percentage of water and wetlands within a 1-km radius than forested sites that do not support beech ($P < 0.001$; Table 2). Across the study region, the distribution of beech is not related to the location of mid-19th-century woodlands.

The distribution of American Beech on Cape Cod (excluding the islands) is also significantly associated with slope, distance to water, and the percent of water within a 1-km radius (Table 2). However, beech distribution on Cape Cod is not related to surficial landform. Overall, beech distribution on Cape Cod does not preferentially occur on mid-19th-century woodlands; conversely, an analysis of Cape Cod's beech stands

Table 2. Results of spatial analyses for American Beech (scattered and stands) abundance and distribution in coastal New England. For the Chi-square tests, the values shown are the frequency ocurring on sites wooded in the mid-19th century and the frequency occuring on moraine; for the t-tests, values shown are mean and (standard deviation).

		Chi-square		*t*-test					
	n	Mid-19th. c. open vs. woodland[A]	Outwash vs. moraine[B]	Soil drainage[C]	Terrain Shape Index[D]	Aspect (degrees)	Slope (%)	Distance to water (m)	% Water in 1 km buffer
Whole Region									
Beech	112	57	63	6.15 (1.60)	0.0003 (0.047)	184 (106)	3.0 (1.1)	196 (3.1)	14.9 (2.2)
Non-Beech	5661	3163	1738	6.08 (1.70)	0.0016 (0.046)	182 (104)	2.3 (1.1)	300 (2.8)	8.6 (2.8)
Chi-square or *t* value		1.105	32.971	0.459	0.301	0.243	3.164	3.166	5.002
P		0.293	<0.001	0.647	0.764	0.809	<0.001	0.002	<0.001
Cape Cod Only									
Beech	53	27	9	6.22 (1.49)	-0.0032 (0.054)	191 (102)	3.3 (0.1)	136 (3.9)	12.7 (2.2)
Non-Beech	4289	2561	964	6.17 (1.65)	0.0019 (0.050)	182 (104)	2.5 (1.1)	284 (2.6)	8.7 (2.5)
Chi-square or *t* value		1.671	0.885	0.278	0.680	0.614	2.320	3.359	2.382
P		0.196	0.347	0.782	0.499	0.542	0.024	0.002	0.021

[A]Number of observed occurences on sites that were wooded in the mid-19th century.
[B]Number of observed occurences on moraine.
[C]NRCS soil drainage categories were given integer values for analyses as follows: very poorly drained = 1; poorly drained = 2; somewhat poorly drained = 3; moderately well drained = 4; well drained = 5; somewhat excessively drained = 6; excessively drained = 7.
[D]The terrain shape index is from McNab (1989) and measures the concavity and convexity of an area. The index varies between -1 and 1; negative numbers are more concave and positive numbers are more convex (note: these values are of the opposite signs originally published by McNab [1989]).

alone (excluding "scattered beech" occurrences) indicated a significant association with areas that were cleared of woodlands in the mid-19th century (P = 0.045; data not shown).

Soils

Soil texture at the intensive-study sites varied considerably. The Provincetown site, which occurs on dune deposits, had extremely sandy soils (94% sand) with low organic matter content (<2%; Table 3). In contrast, Aquidneck Island supported the most fine-textured soils, with only 33–36% sand (65% silt plus clay), and the highest organic matter content (7%; Table 3). Soils at Naushon Island, Whiting Hill, Lowell Holly, and Quissett had intermediate sand and organic matter contents (Table 3). Whereas Provincetown had the lowest pH (4.0) and Ca levels (17 ppm), Whiting Hill had the highest values (pH: 5.0–5.1, Ca: 168–954 ppm; Table 3). Whiting Hill also had the highest vascular plant species richness of the study sites (P. Busby, unpubl. data).

Modern forest composition and dynamics

The relative basal area of American Beech in sampled stands ranged from 32% to >95%, with an average of 70% (Table 1). In the two largest beech forests (Naushon Island and Lowell Holly), beech represents 85% to >95% relative basal area. The most common tree species associated with beech were White Oak and Black Oak, Pitch Pine, *Acer rubrum* L. (Red Maple), *Nyssa sylvatica* Marsh. (Black Gum), and *Carya* spp. (hickory) also occasionally occurred with beech.

All of the intensive-study sites supported trees that exceeded 150 years of age, with the oldest White Oak (355 years) known from New England recorded outside of a plot on Naushon Island (Busby 2006). At all sites, establishment patterns since the mid-to-late 19th century were characterized by an increase in beech and a decline in associated species (Fig. 2). While beech, oaks, and other species all established in the early-mid 1800s, establishment in more recent decades was dominated by beech alone. In the 20th century, beech establishment and peaks in growth releases occurred in the 1940s at Lowell Holly, Naushon Island, and Whiting Hill, with additional

Table 3. Soil characteristics for intensive-study sites.

	Provincetown	Lowell Holly	Quissett	Whiting Hill	Naushon Island	Aquidneck Island
Sand (%)	94.00	57.14	69.75	57.24	70.99	34.57
Silt (%)	4.44	30.10	25.23	27.95	22.65	41.76
Clay (%)	1.56	12.76	5.02	14.82	6.36	23.68
Calcium (ppm)	17.00	122.33	136.33	561.00	144.00	132.00
Magnesium (ppm)	9.00	45.67	40.33	57.00	35.95	34.50
Potassium (ppm)	9.00	44.33	37.00	67.50	25.79	33.50
Sodium (ppm)	17.00	35.00	26.33	38.00	30.53	32.00
Sulfur (ppm)	8.00	37.67	35.33	34.50	32.79	37.50
Total exchange capacity	5.59	3.32	3.81	7.50	3.88	3.21
pH	4.00	4.57	4.30	5.05	4.31	4.50
Organic matter (%)	1.50	5.27	5.56	4.36	4.01	7.14

establishment in the 1920s (Lowell Holly), 1930s (Whiting Hill), and 1950s (Naushon). For Quissett, mixed species establishment occurred in the 1930s, followed by beech release in the 1940s. Aquidneck Island was characterized by beech release and establishment in the 1920s, with abundant establishment continuing in the 1930s. Provincetown was characterized by continuous beech establishment since the mid-19th century (Fig. 2). Growth releases peaked in Provincetown in the 1920s and 1940s. Thus, with the exception of Provincetown, abundant beech establishment and release occurred at all sites in the 1920s–1950s (Fig. 2).

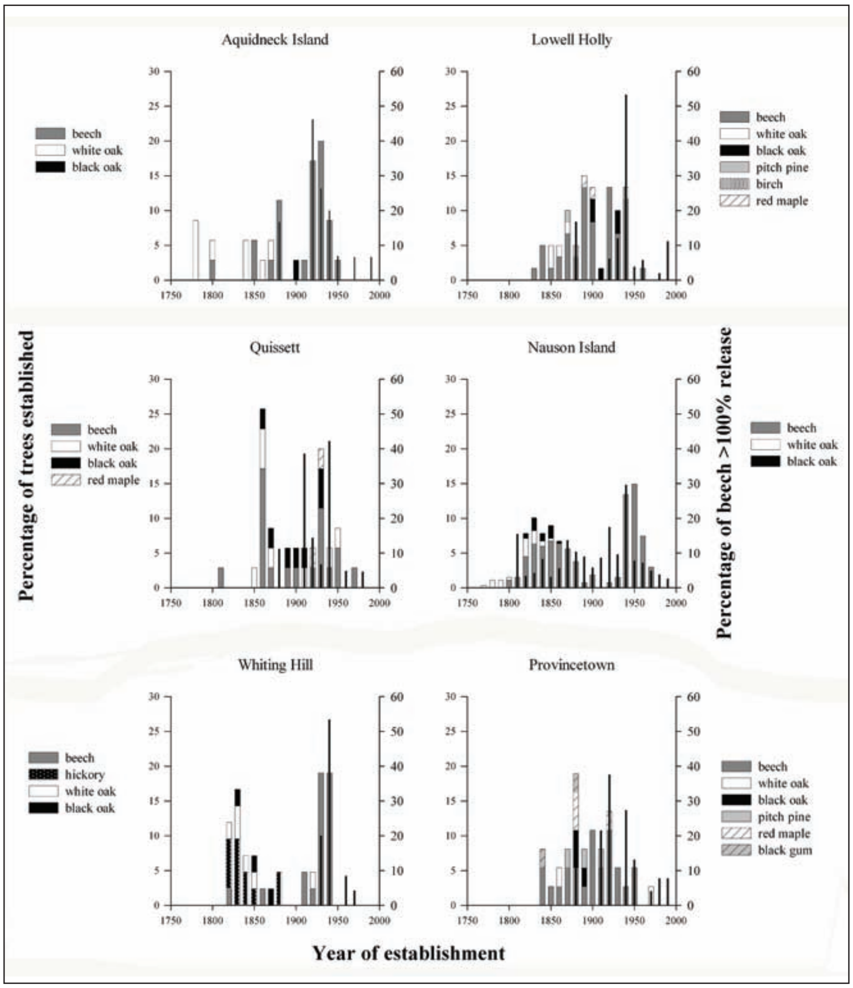

Figure 2. Tree establishment patterns and beech growth release for intensive-study sites showing an increase in beech and a decline in associated species since the mid-to-late 19th century. For establishment data, species are identified in site-specific legends. Thin black lines represent the percentage of beech stems showing release (>100%), reported only for $n > 5$.

Discussion

American Beech is uncommon and irregularly distributed along the coast of southern New England. However, where it occurs, beech frequently forms monodominant stands with abundances that are considerably higher than in many portions of its geographic range (Braun 1950). In contrast to northern New England and New York where beech is widespread in mixed northern hardwood forests characterized by small-scale gap dynamics (Braun 1950, Canham 1990, Cogbill 2005), our results indicate that in coastal sites, beech dynamics are frequently characterized by episodic establishment and growth release associated with major disturbance events. In particular, an increase in beech dominance observed in study sites over the past century has been facilitated by hurricane disturbance.

Distribution of American Beech in coastal New England

Beech is rare on outer Cape Cod as well as portions of the mid-Cape, and absent from large portions of Martha's Vineyard and Nantucket. In contrast, beech is occasional in portions of inner Cape Cod, on several of the Elizabeth Islands, and on the western moraine of Martha's Vineyard. On Naushon Island, beech is ubiquitous. Witness tree data from early historical land surveys and early travel accounts indicate that beech distribution in the 17^{th}–18^{th} centuries was broadly similar to modern patterns: beech occurred at low frequency (<1%) on inner Cape Cod, was largely absent from the mid-Cape region (Cogbill et al. 2002, Motzkin et al. 2002), and occurred on the Elizabeth Islands (Archer 1602). Interestingly, beech was recorded at low levels by early surveyors from towns on outer Cape Cod where it is now extremely uncommon. Additionally, beech was apparently somewhat more frequent (1–5%) in the early historical period in southeastern Rhode Island (including Aquidneck Island), and nearby portions of southeastern Massachusetts (Cogbill et al. 2002, Motzkin et al. 2002). However, witness tree data do not support suggestions that mesic forests with abundant beech may have been widespread in the study region at the time of European arrival (Altpeter 1937, McCaffrey 1973).

While beech was abundant in portions of the study region at various times in the Holocene (Dunwiddie 1990, Foster et al. 2006, Oswald et al. 2007), a regional beech decline began about a thousand years before European colonization (Russell et al. 1993). By the time of European arrival, beech was relatively uncommon in the region, and its distribution was apparently broadly comparable with its modern distribution.

Landscape setting, the importance of fire, and land-use history

For the study region as a whole, beech distribution is related to landform and distance to water, with beech occurring more frequently on moraines than on outwash plains, and on sites that are close to fresh or salt water and with a high percentage of water within 1 km (Table 2). In some instances, the disproportionate occurrence of beech on moraines and on sites near water bodies may result from increased moisture availability and reduced drought stress on these relatively "mesic" sites. The varied topography and soils of moraines, and close proximity to water bodies, may also substantially reduce the long-term probability of wildfires (Foster et al. 2002, Givnish 1981, Parshall et al. 2003). Beech is fire-sensitive (Tubbs and Houston 1990) and is largely absent from those portions of the coastal region that have for millennia experienced some of the highest fire frequencies in the northeastern US (Foster et al. 2002, Parshall et al. 2003, Patterson et al. 1983, Stevens 1996).

Although beech is associated with moraines across the study region, its distribution on moraines is not uniform. In particular, beech is most frequent and abundant on portions of the "Buzzards Bay" moraine in southwestern Cape Cod and Naushon Island, where rolling topography, numerous ponds and wetlands, and close proximity to the ocean limit the occurrence of wildfire (Parshall et al. 2003). Similarly, beech is occasional on portions of the western moraine of Martha's Vineyard where, as a result of predominant westerly winds, fires are rare (Foster and Motzkin 1999, Foster et al. 2002, Stevens 1996). In contrast, beech is absent or uncommon on both moraines and nearby outwash deposits on portions of inner Cape Cod (e.g., Massachusetts Military Reservation) where fire was frequent in the historical period (Patterson and Ruffner 2002; M. Ciaranca, Natural Resource Manager, Camp Edwards National Guard Training Facility, MA, pers. comm.). Additionally, beech is almost completely absent from mid- and outer Cape Cod and the central portion of Martha's Vineyard, which are characterized by coarse-textured outwash deposits that have experienced repeated fires through the historical period (Dunwiddie and Adams 1995, Eberhardt et al. 2003, Foster and Motzkin 1999, Foster et al. 2002, Patterson et al. 1983). The few occurrences of beech on outwash deposits on the mid- and outer Cape are found along streams or adjacent to ponds, and thus are relatively protected from both drought stress and wildfire. Similarly, the relatively high frequency of beech on outwash deposits on the inner Cape may be explained in part by the fact that: (1) the outwash deposits in this area are substantially more fine-textured (25–65% silt plus clay) than the coarse-textured deposits found on the outer Cape, central Martha's Vineyard, or elsewhere, and are thus less prone to drought stress (Fletcher 1993, Motzkin et al. 2002); and (2) numerous large ponds occur in this area, reducing long-term fire probability. In fact, the second largest beech forests in the study area (i.e., Lowell Holly and nearby beech stands) occur on a peninsula and along the shores of a large pond in this area.

In addition to the sensitivity of beech to moisture availability and exposure to fire, beech is slow to re-colonize former agricultural lands (Whitney 1994). As a result, we anticipated that beech would occur predominantly on continuously wooded sites. However, we found no correlation between modern beech distribution and patterns of 19th-century land use across the study region. In fact, for Cape Cod, when we excluded "scattered beech" occurrences, we found that beech stands were actually more likely to occur on former agricultural lands. This result conflicts with age-structure data from our intensive-study sites which confirmed that each of these stands was wooded in the mid-19th century. Thus, the relationship between modern beech distribution and patterns of historical land-use remains unresolved for Cape Cod, despite well-documented relationships of historical land-use activities to modern vegetation patterns in the region (Eberhardt et al. 2003, Motzkin et al. 2002, Von Holle et al. 2007; though see Neill et al. 2007).

Dynamics of coastal beech forests

Age structure and growth patterns illustrate broad consistency in coastal beech forest development. The six intensive-study sites were not cleared for agriculture; however, we suspect that forest harvesting was common on these sites into the 19th century, allowing a mix of species to persist. For example, almost half of the approximately 1000-ha forest on Naushon Island was clear-cut in the 1820s, resulting in substantial regeneration of White and Black Oak, as well as beech (Busby et al. 2008). However, in the past >150 years, harvesting on Naushon has been extremely limited, enabling shade-tolerant beech to establish widely. The absence of harvesting and fire since the mid-19th century, in combination with high herbivory from a large deer population, apparently prevented oak regeneration from occurring in what is now the largest beech-dominated forest in the region (Busby et al. 2008). Although comparable data on the history of anthropogenic disturbance are unavailable for much of the region, the increase in beech abundance and decline in pine, oaks, and other hardwoods that we documented from our study sites are consistent with a region-wide reduction in fire and harvesting over the past century (Abrams 2003, Foster and Motzkin 1999).

In addition to anthropogenic disturbance, natural disturbance has also apparently facilitated the transition to beech dominance in the intensive-study sites. The study region is characterized by frequent hurricanes (0.15/year; Boose et al. 2001), with the most severe events resulting in dramatic increases in growth and new establishment for beech (Busby et al. 2009). All of our study sites demonstrated pulses of beech establishment and release from the 1920s to the 1950s, corresponding to several significant hurricanes that affected the coastal region during this time period (1924, 1938, 1944, and 3 storms in 1954; Busby 2006). We interpret a pulse of beech growth release and establishment on Aquidneck Island in the 1920s and 1930s, as well as beech release on Naushon Island at that time, as a response to the 1924 hurricane. The most significant storm to affect the coastal region during the 20th century was the Great Atlantic Hurricane of 1944, which caused severe damage to forests throughout the region and prompted timber salvage operations in some areas (Busby et al. 2009, Dunwiddie 1991). We interpret widespread pulses of beech establishment and/or release in the 1940s across our study sites as largely resulting from this storm. The storm track of the 1938 hurricane was farther west than the 1944 storm; thus, despite considerable property damage to coastal communities from the storm surge associated with the 1938 hurricane, inland forests were more strongly affected than those in the coastal region (Boose et al. 2001). Nonetheless, some coastal forests were damaged by the 1938 hurricane (Trustees of the Naushon Trust 1939), suggesting that beech establishment and release in the 1940s may also, in part, reflect response to this storm.

Results of this study indicate that hurricanes facilitated the recent increase in beech in our intensive-study sites. While hurricanes also occurred before the 1920–1950 period associated with beech increase, stands at this particular time may have been predisposed to severe storm damage (i.e., as a result of size/age structure). The high frequency of beech growth increases following hurricanes confirms the importance of advanced regeneration in establishing beech dominance (Cooper-Ellis et al. 1999, Peterson and Pickett 1995). Abundant beech regeneration following the 1944 hurricane in most of our study sites, and after the 1924 hurricane on Aquidneck Island, suggests that large-scale wind disturbances also facilitate beech establishment in the coastal region. Beech's ability to develop root sprouts in response to uprooting or crown damage is likely important for this disturbance-response (Cooper-Ellis et al. 1999, Russell 1953, Peterson and Pickett 1995, Putz and Sharitz 1991).

Conclusion

In a region characterized by extensive xeric Pitch Pine-oak forests that have burned repeatedly, American Beech occasionally develops almost pure stands on moraines and near lakes, wetlands, and along the coastline, in areas that are protected from wildfire. Once established, minimal fire and forest harvesting and frequent and intense hurricanes enable their persistence. With the potential for more frequent and intense hurricanes (Emanuel 2005, Webster et al. 2005), we expect the importance of beech in the coastal region may increase in the coming decades.

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