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Subregional variability in the response of New England vegetation to postglacial climate change

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Abstract

Aim: We analysed a dataset composed of multiple palaeoclimate and lake-sediment pollen records from New England to explore how postglacial changes in the composition and spatial patterns of vegetation were controlled by regional-scale climate change, a subregional environmental gradient, and landscape-scale variations in soil characteristics.

Location: The 120,000-km^2 study area includes parts of Vermont and New Hampshire in the north, where sites are 150–200 km from the Atlantic Ocean, and spans the coastline from southeastern New York to Cape Cod and the adjacent islands, including Block Island, the Elizabeth Islands, Nantucket, and Martha's Vineyard.

Methods: We analysed pollen records from 29 study sites, using multivariate cluster analysis to visualize changes in the composition and spatial patterns of vegetation during the last 14,000 years. The pollen data were compared with temperature and precipitation reconstructions.

Results: Boreal forest featuring *Picea* and *Pinus banksiana* was present across the region when conditions were cool and dry 14,000–12,000 calibrated ^{14}C years before present (ybp). *Pinus strobus* became regionally dominant as temperatures increased between 12,000 and 10,000 ybp. The composition of forests in inland and coastal areas diverged in response to further warming after 10,000 ybp, when *Quercus* and *Pinus rigida* expanded across southern New England, whereas conditions remained cool enough in inland areas to maintain *Pinus strobus*. Increasing precipitation allowed *Tsuga canadensis*, *Fagus grandifolia*, and *Betula* to replace *Pinus strobus* in inland areas during 9,000–8,000 ybp, and also led to the expansion of *Carya* across the coastal part of the region beginning at 7,000–6,000 ybp. Abrupt cooling at 5,500–5,000 ybp caused sharp declines in *Tsuga* in inland areas and *Quercus* at some coastal sites, and the populations of those taxa remained low until they recovered around 3,000 ybp in response to rising precipitation. Throughout most of the Holocene, sites underlain by sandy glacial deposits were occupied by *Pinus rigida* and *Quercus*.

Main conclusions: Postglacial changes in the composition and spatial pattern of New England forests were controlled by long-term trends and abrupt shifts in temperature and precipitation, as well as by the environmental gradient between coastal

and inland parts of the region. Substrate and soil moisture shaped landscape-scale variations in forest composition.

1 | INTRODUCTION

Palaeoecological studies illustrate that the response of vegetation to climate change is influenced by both large-scale climatic conditions and finer scale physiographic and edaphic variability (Webb, 1993). Analyses of pollen data from areas with high densities of lake-sediment records can be used to explore how the composition and spatial pattern of vegetation are controlled by the interactions among regional climate change, the niches of different species, and subregional variations in soils, topography, and/or other environmental gradients (e.g., Bradshaw & Lindbladh, 2005; Brubaker, 1975; Graumlich & Davis, 1993; Jackson & Whitehead, 1991; Jacobson, 1979; Lindbladh, Bradshaw, & Holmqvist, 2000; Muller, Richard, Guiot, de Beaulieu, & Fortin, 2003; Oswald, Brubaker, Hu, & Kling, 2003; Richard, 1994). Several studies of this type have been carried out in New England, a region featuring a climate gradient from coastal to inland areas, as well as landscape-scale topographic and edaphic variability (Gaudreau, 1986; Gaudreau & Webb, 1985; Oswald et al., 2007; Shuman, Newby, Huang, & Webb, 2004; Spear, Davis, & Shane, 1994; Webb, Richard, & Mott, 1983).

The recent development of multiple palaeoenvironmental records from sites across New England has greatly improved our understanding of the region's postglacial climate history (Gao, Huang, Shuman, Oswald, & Foster, 2017; Hou, Huang, Oswald, Foster, & Shuman, 2007; Hou, Huang, Shuman, Oswald, & Foster, 2012; Hou et al., 2006; Huang, Shuman, Wang, & Webb, 2002; Marsicek, Shuman, Brewer, Foster, & Oswald, 2013; Newby, Donnelly, Shuman, & MacDonald, 2009; Newby, Shuman, Donnelly, Karnauskas, & Marsicek, 2014; Newby, Shuman, Donnelly, & MacDonald, 2011; Shuman & Burrell, 2017; Shuman, Huang, Newby, & Wang, 2006; Shuman & Marsicek, 2016; Shuman et al., 2001). Lake-level reconstructions from several sites in Massachusetts (Figure 1) show that effective moisture has risen steadily since the early Holocene, with a particularly rapid increase between 9,000 and 8,000 calibrated ^{14}C years before present (where present is 1950 CE, hereafter ybp; Figure S3.1a; Newby et al., 2009, 2014; Marsicek et al., 2013). However, the trend towards moister conditions has been interrupted periodically by a series of regionally coherent dry events, with multi-century droughts occurring during the middle and late Holocene (Newby et al., 2014; Shuman & Burrell, 2017). New insights into postglacial changes in temperature have been afforded by isotopic analyses of lake-sediment cores (Gao et al., 2017; Hou et al., 2006, 2007, 2012; Huang et al., 2002; Shuman et al., 2006) and sea-surface temperature (SST) reconstructions based on alkenone palaeothermometry (Sachs, 2007; Shuman & Marsicek, 2016).

Temperatures increased across the region following the late-glacial interval, with peak warmth occurring during 8,000–6,000 ybp (Figure S3.1b; Shuman & Marsicek, 2016). Temperatures then declined between 6,000 ybp and the present, with particularly dramatic cooling at 5,500–5,000 ybp and after 2,100 ybp (Shuman & Marsicek, 2016).

The multivariate regional climate history that emerges from the synthesis of numerous palaeoenvironmental records can, in turn, be used as a framework for re-examining the postglacial sequence of vegetation changes in New England. For example, Shuman et al. (in revision) demonstrated that the aforementioned shifts in moisture and temperature broadly controlled the regional vegetation history, including the middle Holocene decline of *Tsuga canadensis* (eastern hemlock). Our next step in understanding changes in vegetation through time and across space is to examine finer-scale patterns within the region using the dense network of lake-sediment pollen records that is available for New England. Knowledge of subregional responses of vegetation to climate change is of particular value to scientists, conservationists, and land managers, because it is at this scale that they often study, manage, and anticipate future changes in ecosystems and natural resources. Previous studies have analysed multiple pollen records from New England to explore past vegetation patterns (Gaudreau, 1986; Gaudreau & Webb, 1985; Oswald et al., 2007; Shuman et al., 2004), but a large number of additional, detailed records has been developed over the last decade.

In this paper we present a regional dataset composed of 29 lake-sediment pollen records. We analyse the histories of individual tree taxa, in some cases at the species level, as well as the vegetation assemblages that arise over time through different combinations of species. Comparison of these pollen data with palaeoclimate records allows us to explore how changes in the composition and spatial patterns of vegetation are controlled by both regional-scale climate and landscape-scale factors, including edaphic variability. Two questions are of particular interest: (a) How did the regional environmental gradient between coastal and inland areas of New England influence spatial patterns of vegetation as climate changed through time? (b) Did areas with well-drained, sandy substrates have different postglacial vegetation histories from those underlain by glacial till?

2 | MATERIALS AND METHODS

2.1 | Study area

Current and historical spatial patterns of vegetation in New England are strongly influenced by a regional-scale climatic gradient
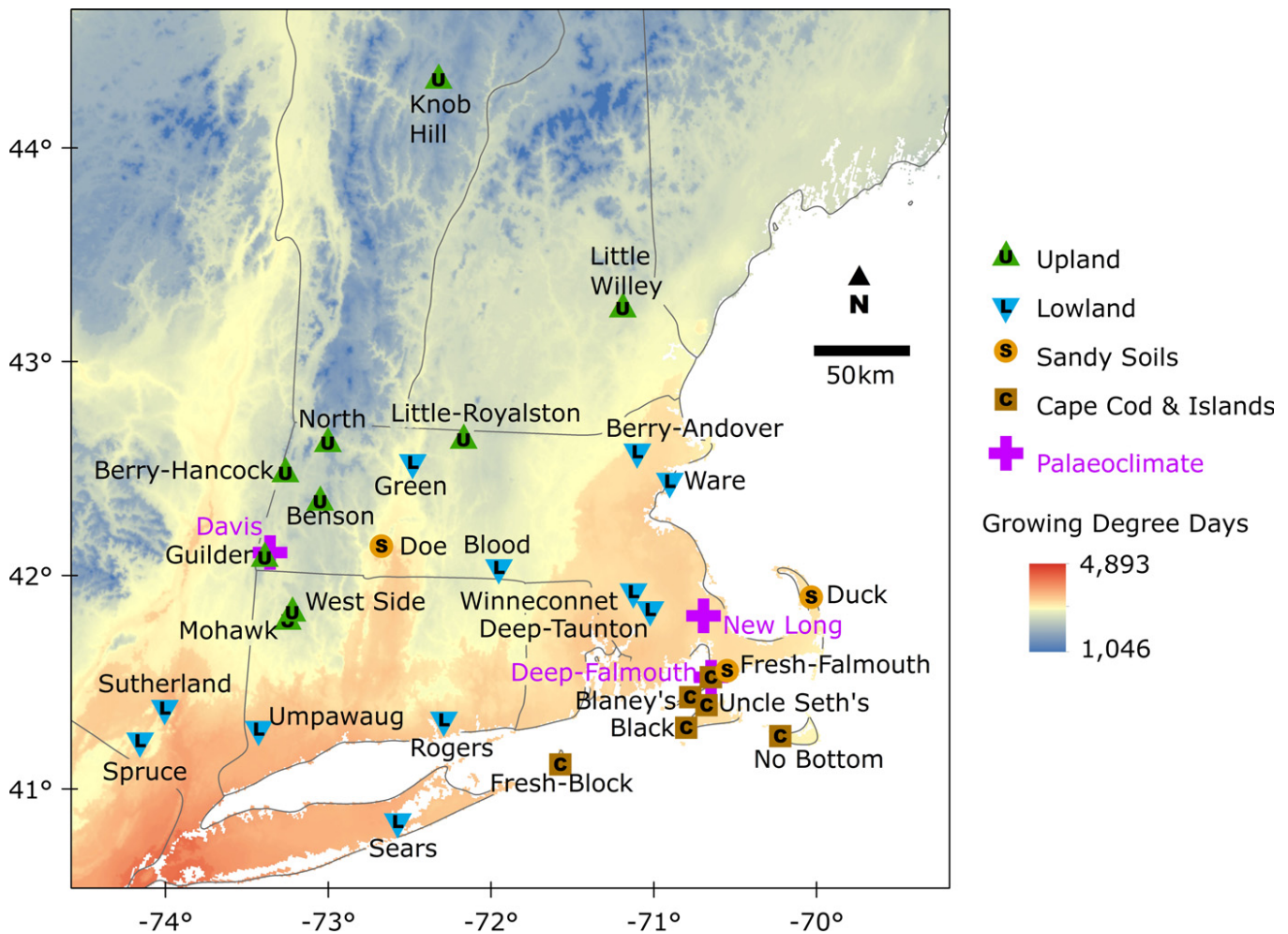
FIGURE 1   Map of New England showing the location of study sites and the regional environmental gradient (growing degree days, 5°C base); symbols reflect the geographical/edaphic groups to which the study sites are assigned. Palaeoclimate data from Davis, New Long, and Deep-Falmouth are from Shuman and Marsicek (2016). Palaeoclimate site GGC30 (Sachs, 2007; Shuman & Marsicek, 2016) is located northeast of the study area, offshore from Nova Scotia

associated with elevation, latitude, and distance from the Atlantic Ocean (Figure 1), as well as by finer-scale variations in topography, soils, and land use (Cogbill, Burk, & Motzkin, 2002; Thompson, Carpenter, Cogbill, & Foster, 2013). The study area, which includes parts of Vermont and New Hampshire in the north, covers all of Connecticut and Massachusetts, and spans the coastline from the Hudson Highlands in southeastern New York to Cape Cod and the adjacent islands (Block Island, the Elizabeth Islands, Nantucket, and Martha's Vineyard) in the south (Figure 1), features warm summers, cold winters, and an even distribution of precipitation across the year (totalling 1,000–1,500 mm/year). Most of the region is characterized by acidic soils that developed on glacial deposits and granitic or metamorphic bedrock, although some areas of calcareous bedrock occur in Vermont, western Massachusetts, and Connecticut (Zen, Goldsmith, Ratcliffe, Robinson, & Stanley, 1983). The northern, inland part of New England is characterized by relatively cold conditions, with growing degree days (GDD) in the 2,500–3,500 range, whereas the southern, coastal part of the study area is warmer, with GDD values of 3,500–4,000 (Figure 1). The southern, coastal areas are

particularly susceptible to hurricane damage (Boose, Chamberlin, & Foster, 2001) and, prior to European settlement, likely experienced greater fire activity than inland parts of the region (Cogbill et al., 2002; Parshall & Foster, 2002).

This environmental gradient has a strong influence on the distribution and abundance of the major tree species. *Tsuga canadensis*, *Fagus grandifolia* (American beech), *Acer saccharum* (sugar maple), *Pinus strobus* (white pine), and *Betula* species (birch) are common in the cooler northern, inland, and higher elevation parts of New England, whereas *Quercus* species (oak), *Carya* species (hickory), and, historically, *Castanea dentata* (American chestnut) dominate in the warmer southern part of the region. *Acer rubrum* (red maple) is common across New England (Cogbill et al., 2002; Thompson et al., 2013). At finer spatial scales, other tree species become locally important due to edaphic controls on moisture availability. In particular, *Pinus rigida* (pitch pine) is prevalent on sites with well-drained, sandy soils, including large glaciolacustrine deltas in the Connecticut River Valley and areas of glacial outwash on Long Island, Cape Cod, and the island of Martha's Vineyard (Cogbill et al., 2002; Motzkin, Patterson, & Foster, 1999).

2.2 | Study sites

This study involves analyses of lake-sediment pollen records from 29 study sites (Figure 1; Table 1). The sites are distributed across the study area, representing a wide range of elevation (from <10 to >600 m), temperature (GDD varies from 2,500 to 3,900), and precipitation (from 1,000 to 1,400 mm/year). The lakes and ponds are relatively small in size (all <16 ha, with the exception of Winneconnet and Rogers; Table 1), such that the pollen data should reflect landscape-scale variations in vegetation composition (Sugita, 1994). Most of the study sites are located in areas of glacial till or moraines, although a few sites are located on either glacial outwash (Duck and Fresh-Falmouth) or glaciolacustrine kame-delta deposits (Doe) and thus have sandier soils (Figure 1). We assigned the study sites to four groups based on geography and soils: upland, lowland, Cape Cod and adjacent islands, and sandy soils (Figure 1). Green Pond also sits on sandy delta deposits, but its pollen source area (Sugita, 1994) extends beyond the delta to upland areas underlain by glacial till, so it is included with the lowland sites. Sears Pond is located on a moraine near the eastern end of Long Island, and thus is a lowland site, but we note that it is surrounded by a large area of outwash. The pollen records have a minimum time span of 9,000 ybp, and most extend beyond 13,000 ybp.

2.3 | Field and laboratory work

Pollen and chronological data for 10 of the study sites (Berry-Hancock, Duck, Fresh-Block, Mohawk, No Bottom, North, Rogers, Spruce, Sutherland, and Winneconnet) were obtained from the Neotoma Paleoecology Database (www.neotomadb.org). We collected and analysed sediment cores from the 19 other study sites, using a similar approach in all cases. Upper sediments (100–150 cm), including an undisturbed sediment–water interface, were collected with a 10 cm diameter plastic tube fitted with a piston. These surface cores were transported to the laboratory and extruded vertically in 1 cm segments. Lower sediments

TABLE 1 Study sites and geographical information

Site	Latitude °N	Longitude °W	Elevation (m)	Area (ha)	GDD*	Precip. (mm)	Surficial geology	Previous publications
Benson	42.3776	−73.0954	497	2.3	2,918	1,290	Till	
Berry-Andover	42.6201	−71.0873	42	1.6	3,530	1,236	Till	Oswald et al. (2007)
Berry-Hancock	42.5054	−73.3189	630	3.7	2,917	1,310	Till	Whitehead (1979)
Black	41.3281	−70.7923	13	1.4	3,605	1,212	Moraine	
Blaney's	41.4717	−70.7652	5	1.0	3,617	1,263	Moraine	
Blood	42.0800	−71.9615	211	8.5	3,218	1,241	Till	Oswald et al. (2007)
Deep-Falmouth	41.5641	−70.6358	19	1.0	3,608	1,259	Outwash	Marsicek et al. (2013)
Deep-Taunton	41.8824	−71.0115	7	1.5	3,563	1,261	Till	
Doe	42.1754	−72.7024	79	1.4	3,429	1,182	Kame-delta	
Duck	41.9328	−70.0006	3	5.1	3,541	1,132	Outwash	Winkler (1985)
Fresh-Block	41.1583	−71.5750	38	1.0	3,610	1,064	Moraine	Dunwiddie (1990)
Fresh-Falmouth	41.5935	−70.5338	6	5.3	3,605	1237	Outwash	
Green	42.5668	−72.5111	82	5.0	3,276	1,210	Kame-delta	
Guilder	42.1094	−73.4372	622	6.3	2,825	1,273	Till	
Knob Hill	44.3605	−72.3737	370	7.1	2,568	1,015	Till	Oswald and Foster (2012)
Little Willey	43.2918	−71.1778	254	11.4	3,049	1,203	Till	
Little-Royalston	42.6750	−72.1917	302	4.0	3,066	1,200	Till	Oswald et al. (2007)
Mohawk	41.8167	−73.2833	351	6.6	3,083	1,292	Till	Gaudreau (1986)
No Bottom	41.2846	−70.1141	5	0.2	3,430	1,037	Moraine	Dunwiddie (1990)
North	42.6510	−73.0531	585	7.8	2,779	1,414	Till	Whitehead and Crisman (1978)
Rogers	41.3635	−72.2994	11	107.0	3,702	1,259	Till	Davis (1969)
Sears	40.8845	−72.5783	7	6.1	3,907	1,188	Moraine	
Spruce	41.2369	−74.1833	273	1.9	3,643	1,276	Till	Maenza-Gmelch (1997b)
Sutherland	41.3931	−74.0370	379	4.1	3,452	1,428	Till	Maenza-Gmelch (1997a)
Umpawaug	41.3061	−73.4497	138	5.3	3,807	1,289	Till	
Uncle Seth's	41.4331	−70.6647	13	4.6	3,592	1,252	Moraine	
Ware	42.4825	−70.8825	4	1.1	3,685	1,188	Till	
West Side	41.8556	−73.2566	390	15.7	3,002	1,294	Till	
Winneconnet	41.9667	−71.1167	22	60.0	3,572	1,265	Till	Suter (1985)

*Growing degree days; 5°C base.

were raised in 1 m drive lengths using a 5 cm diameter modified Livingstone piston sediment sampler (Wright, Mann, & Glaser, 1984). Those core segments were extruded horizontally in the field, wrapped in plastic and aluminium foil, and subsampled at 1–2 cm intervals in the laboratory. All samples were subsequently refrigerated and archived.

Sediment samples of 1–2 cm^3 were prepared for pollen analysis following standard procedures (Fægri & Iversen, 1989). Pollen residues were mounted in silicone oil and analysed at 400×–1,000× magnification.

Chronological control is provided by accelerator mass spectrometry ^{14}C analysis of plant macrofossils and bulk-sediment samples, pollen evidence for European forest clearance, and, in some cases, ^{210}Pb analysis of recent sediments (Binford, 1990; see Appendices S1–S2 in Supporting Information).

2.4 | Data analysis

^{14}C dates were calibrated with the IntCal13 calibration curve (Reimer et al., 2013) and age models were constructed using Bchron (Haslett & Parnell, 2008; Parnell, Haslett, Allen, Buck, & Huntley, 2008; see Appendices S1–S3 in Supporting Information).

Percentage values were calculated relative to the sum of pollen and spores from upland plant taxa. The mean pollen sum per site ranged from 321 to 1,013 (see Appendix S4 in Supporting Information). For six of the study sites (Blaney's, Deep-Falmouth, Deep-Taunton, Doe, Fresh-Falmouth, and Uncle Seth's) pollen grains of the *Pinus* subgenus *Pinus* type were identified as either *Pinus banksiana* (jack pine) type or *Pinus rigida* type (which includes both *Pinus rigida* and *Pinus resinosa*; red pine) following McAndrews, Berti, and Norris (1973). A calibration dataset was generated using those samples for which >15 *Pinus* subgenus *Pinus* pollen grains were identified. In samples >11,000 ybp, the large majority of identified *Pinus* subgenus *Pinus* grains were *Pinus banksiana* type (1,637 of 1,708). In samples dating to 11,000–8,000 ybp, *Pinus* subgenus *Pinus* grains were identified as *Pinus banksiana* and *Pinus rigida* types in approximately equal numbers (386 and 474 respectively). In samples <8,000 ybp, most identified *Pinus* subgenus *Pinus* grains were *Pinus rigida* type

(1,499 of 1,564). Based on these findings, the following *Pinus banksiana*:*Pinus rigida* ratios were set and applied to the allocation of unidentified *Pinus* subgenus *Pinus* grains in all other samples: >11,000 ybp = 1:0; 11,000–8,000 ybp = 0.5:0.5; <8,000 ybp = 0.1:0.9 (Figure 2). The calibration dataset features no samples from upland sites and relatively few from lowland sites, so the use of uniform ratios seems prudent. We are confident in our application of these ratios to samples >11,000 ybp and <8,000 ybp, but less so for the 11,000–8,000 ybp interval, where the *Pinus banksiana*:*Pinus rigida* ratio varies greatly among the calibration samples. However, *Pinus* subgenus *Pinus* pollen percentages are low during 11,000–8,000 ybp, averaging 13%, such that adjusting the *Pinus banksiana*:*Pinus rigida* ratio does not generate major changes in the estimated percentages for the *Pinus banksiana* and *Pinus rigida* types. For example, in the case of a sample with a *Pinus* subgenus *Pinus* percentage value of 13%, the application of a ratio of 0.75:0.25 instead of 0.5:0.5 yields a *Pinus banksiana* pollen percentage of 10% rather than 6%. *Pinus* pollen was not separated into the *Pinus* subgenus *Pinus* and *Pinus* subgenus *Strobus* types for Berry-Hancock, North, Rogers, and Spruce, and thus the *Pinus* subgenus *Pinus* calibration could not be used for those sites.

The temporal resolution for pollen samples varies both across sites and through time for individual records. To reduce the influence of uneven sampling on multivariate analysis of the pollen data, we interpolated the records at 200-year intervals, which is similar to the mean sampling interval of 219 years between samples (see Appendix S4 in Supporting Information).

We used multivariate cluster analysis to visualize changes in pollen assemblages through time and across space. Cluster analysis (Ward's method) was performed in R (R Core Development Team, 2009) including the interpolated pollen data from 25 of the sites (excluding the four sites for which *Pinus* pollen was not separated: Berry-Hancock, North, Rogers, and Spruce), and including the following 10 major tree taxa: *Picea* (spruce), *Pinus banksiana*, *Pinus strobus*, *Pinus rigida*, *Betula*, *Tsuga*, *Fagus*, *Quercus*, *Carya*, and *Castanea*. We generated plots of the cluster assignments for each site through time and in maps at 1,000-year intervals. We also used the interpolated

FIGURE 2 Calibration of *Pinus* subgenus *Pinus* pollen data. Points show the *Pinus banksiana*:*Pinus rigida* ratio for selected samples from Blaney's, Deep-Falmouth, Deep-Taunton, Doe, Fresh-Falmouth, and Uncle Seth's; symbols reflect the geographical/edaphic groups to which those study sites are assigned. Thick grey lines are the ratios applied to unidentified *Pinus* subgenus *Pinus* grains in all other samples: >11,000 ybp = 1:0; 11,000–8,000 ybp = 0.5:0.5; <8,000 ybp = 0.1:0.9
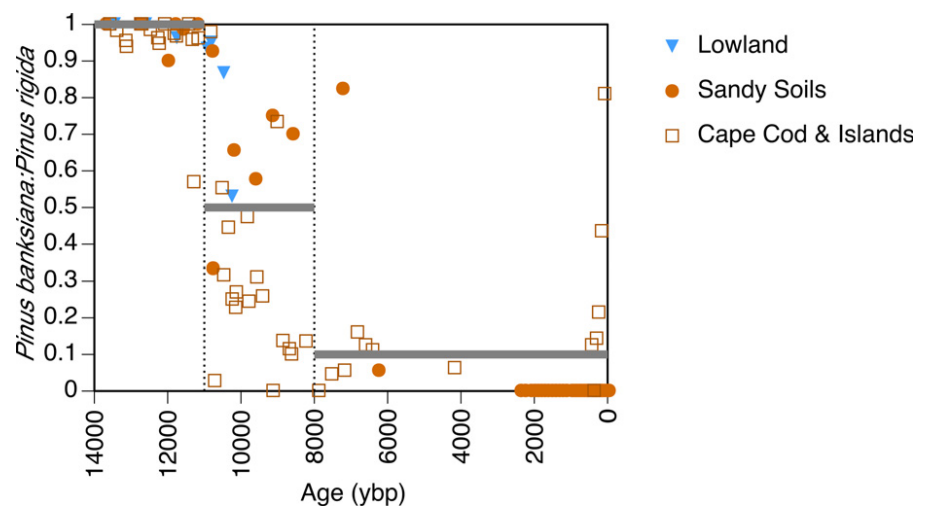
pollen data to make maps of pollen percentage values for the same 10 major tree taxa, as well as *Ambrosia* (ragweed).

3 | RESULTS

In this section we describe the major patterns that emerge from the dataset, including both the pollen percentage data for individual taxa and the cluster analysis. The pollen and chronological data for each site (Figures S3.2–30) and the mapped pollen data (Figures S3.31–41) are available as Supplementary Figures in Appendix S3.

3.1 | *Picea* (spruce)

Picea pollen percentages are high at nearly all sites between 14,000 and 12,000 ybp, in many cases reaching 50–70% (Figure S3.31). *Picea* abundance declines to <5% after 12,000 ybp, with the exception of three sites in western Massachusetts (Benson, Berry-Hancock, and Guilder) and three coastal sites (Blaney's, Uncle Seth's, and Fresh-Block), where *Picea* pollen percentages remain >5% until 11,000–10,000 ybp. After 10,000 ybp, *Picea* is very rare across the entire region. At upland sites, including Berry-Hancock, North, Little-Royalston, and Knob Hill, percentages increase slightly (to 3–10%) after 2,000 ybp.

3.2 | *Pinus banksiana* (jack pine)

Like *Picea*, *Pinus banksiana* has uniformly high pollen percentages during the late-glacial interval, with values reaching 20–50% at most sites during 14,000–12,000 ybp (Figure S3.32). *Pinus banksiana* abundance declines after 12,000 ybp, although its pollen percentages remain elevated at some sites until 10,000 ybp, with values remaining >10% in a few coastal records (No Bottom, Blaney's, Uncle Seth's, and Duck) until 9,000–8,000 ybp. *Pinus banksiana* abundances are low after 8,000 ybp.

3.3 | *Pinus strobus* (white pine)

Pinus strobus pollen percentages reach high values (generally 40–60%) at nearly all sites between 12,000 and 10,000 ybp (Figure S3.33). Its abundance declines across the region between 10,000 and 8,000 ybp, and during 8,000–5,000 ybp it exceeds 10% at only a few sites. *Pinus strobus* becomes more abundant after 5,000 ybp, with pollen percentages in the range of 10–30% at some coastal (Duck) and upland sites (Green and Little Willey).

3.4 | *Pinus rigida* (pitch pine)

Pinus rigida increases in abundance after 11,000–10,000 ybp, and during 10,000–7,000 ybp its pollen percentages reach 10–50% at sites in eastern Massachusetts and along the coast (Figure S3.34). After 7,000 ybp, *Pinus rigida* is prevalent at sites with sandy substrates in the Connecticut River Valley (Doe) and on Long Island

(Sears) and Cape Cod (Fresh-Falmouth and Duck). *Pinus rigida* increases during the late Holocene at several other sites, including Green, Deep-Taunton, and Uncle Seth's, as well as increasing after European forest clearance at West Side, Deep-Falmouth, and No Bottom.

3.5 | *Betula* (birch)

Betula pollen percentages are relatively high (generally 10–20%) during the late-glacial interval (Figure S3.35), with a peak occurring at 12,000–11,000 ybp for many sites (reaching 40% at Knob Hill). *Betula* abundance falls below 15% at all sites at 10,000 ybp, then increases at upland sites, reaching 10–25% (and returning to >40% at Knob Hill) between 8,000 ybp and today. Sites in the southwestern part of the region, including Spruce, Sutherland, and Umpawaug, feature a late Holocene increase in *Betula* abundance, with values rising from <5% to >10% after 4,000 ybp. *Betula* pollen percentages increase at many sites after European forest clearance, such that overall *Betula* is currently more common than at any other point during the postglacial interval.

3.6 | *Tsuga* (hemlock)

Tsuga pollen percentages increase at 11,000–10,000 ybp, reaching values of 20–50% at upland sites between 9,000 and 6,000 ybp (Figure S3.36). *Tsuga* percentages decline abruptly at most sites between 5,500 and 5,000 ybp, and *Tsuga* remained at low abundances during 5,000–3,000 ybp. However, in a few of the records, including Benson and Little Willey, *Tsuga* percentages never fall below 5%, suggesting that *Tsuga* populations persisted in some areas throughout the middle Holocene. Indeed, maps of *Tsuga* abundance for 5,000–3,000 ybp and today are similar (Figure S3.36). *Tsuga* percentages increase after 3,000 ybp, but then decline again between 1,000 ybp and the present.

3.7 | *Fagus* (beech)

Fagus first increased in abundance at sites in western Connecticut (West Side and Mohawk) and Massachusetts (Benson, Berry-Hancock, and Guilder) at 9,000 ybp, followed by increasing values across New England between 8,000 and 7,000 ybp, with its highest pollen percentages (20–30%) at upland sites (Figure S3.37). During the middle Holocene (5,000–3,000 ybp), *Fagus* percentages increase to 20–40% in records from Cape Cod (Deep-Falmouth), the Elizabeth Islands (Blaney's), and Martha's Vineyard (Black). Like *Tsuga*, *Fagus* abundance decreases during 1,000–0 ybp.

3.8 | *Quercus* (oak)

Quercus pollen percentages increase between 12,000 and 11,000 ybp, initially rising to >10% in the southwestern part of the study area, then increasing at other sites during 10,000–9,000 ybp (Figure S3.38). Throughout the Holocene, *Quercus* abundance is

higher (>50%) in southern New England than at upland sites, although a few pollen records from coastal areas feature declines of *Quercus* during the middle Holocene. For example, at Deep-Falmouth *Quercus* drops from >60 to 30% at 5,300 ybp, and in the records from Sutherland and Umpawaug *Quercus* declines from 50–60% to 30–40% at 3,900 ybp.

3.9 | *Carya* (hickory)

The postglacial expansion of *Carya* into the study region occurs after most of the other major tree taxa. *Carya* first reaches 5% at Umpawaug at 7,500 ybp, then becomes relatively abundant (5–10%) at other sites in southern New England between 6,000 and 4,000 ybp (Figure S3.39). *Carya* pollen percentages decline after European forest clearance.

3.10 | *Castanea* (chestnut)

The expansion of *Castanea* into southeastern New England appears to have taken place even later than that of *Carya*. *Castanea* pollen percentages first exceed 2% at Sutherland at 5,000 ybp, followed by increases at Umpawaug, West Side, and Mohawk at 3,500–3,000 ybp, and at some sites in western and central Massachusetts between 2,000 and 1,000 ybp (Figure S3.40). The highest *Castanea* pollen percentages were observed at Sutherland (>10% at 3,700 ybp) and at Mohawk (>15% during 2,200–900 ybp).

3.11 | *Ambrosia* (ragweed)

An early-Holocene interval of elevated *Ambrosia* pollen percentages in southern New England was described by Faison, Foster, and Oswald (2006). This pattern was interpreted as indicating open forest structure. In our dataset, multiple sites feature relatively high (>2%) percentages of *Ambrosia* during 10,000–8,000 ybp (Figure S3.41), after which its abundance declines to consistently low levels across the region. *Ambrosia* abundance is substantially higher in samples postdating European forest clearance than in any prior period.

3.12 | Cluster analysis

On the basis of the results of the cluster analysis (Figure S3.42), we identified seven distinct pollen assemblages (Figure S3.43). The **spruce-jack pine cluster** (dark blue in Figures 3–4 and S3.43) represents boreal forest vegetation and features high percentages of *Picea* and *Pinus banksiana* (averaging 27% and 28% respectively). *Pinus strobus*, *Betula*, and *Quercus* are also present in this cluster. This vegetation type occurred at nearly all sites between 14,000 and 13,000 ybp, then decreased in prevalence between 12,000 and 11,000 ybp (Figure 3). By 11,000 ybp samples in this cluster are found only in a few sites in western Massachusetts (Benson) and southeastern Massachusetts (Deep-Taunton and Blaney's). It is not present in any of the records after 10,000 ybp.

Samples in the **white pine cluster** (light blue) are dominated by *Pinus strobus* pollen (38%) with lower percentages of *Betula*, *Tsuga*, and *Quercus* (Figure S3.43). *Pinus strobus*-dominated forest replaced boreal forest at all sites between 12,500 and 11,500 ybp (Figure 3), and at 11,000 ybp all but three sites are assigned to the white pine cluster (Figure 4). The longevity of the *Pinus strobus* assemblage varies across the sites. In some records, including Benson, Fresh-Falmouth, Deep-Falmouth, Blaney's, and Sears, this forest type lasts for <300 years. At the majority of sites, however, its duration is longer. In most of those cases *Pinus strobus* dominance ends by 10,000–9,500 ybp, but it continues until 8,500–7,000 ybp at several of the upland sites, including Knob Hill, Little Willey, Little-Royalston, and Green (Figures 3–4). There is also a shift to the white pine cluster during the last few centuries at Green.

The **hemlock-birch-beech cluster** (purple) represents the northern hardwood-hemlock forest and features high pollen percentages of *Tsuga* (25%), *Betula* (24%), and *Fagus* (16%; Figure S3.43). *Pinus strobus* and *Quercus* are present at lower abundances. The hemlock-birch-oak cluster only occurs in records from the upland parts of the study area (Figures 3–4). Other than a brief interval at Knob Hill at 12,000 ybp, it becomes established between 10,500 ybp (Benson) and 8,500–7,400 ybp (Knob Hill, Guilder, West Side, Little Willey, and Little-Royalston; Figure 3). At Knob Hill, the northern forest vegetation persists until today. However, at West Side this vegetation type lasts only until 7,000 ybp, and at Guilder, Benson, Little Willey, and Little-Royalston it occurs until 5,500–5,000 ybp. This is the time of the middle Holocene *Tsuga* decline, and that event shifts these records from hemlock-birch-beech to other clusters. Northern hardwood-hemlock forest returns at Benson and Little Willey at 3,600 ybp and at Little-Royalston at 2,000 ybp, but it does not return in the Guilder record.

The **oak-beech cluster** (grey) is dominated by *Quercus* (32%) and *Fagus* (14%), but *Tsuga*, *Betula*, and *Pinus strobus* also occur regularly in those samples (Figure S3.43). This vegetation type first occurs at Guilder at 10,600 ybp, where it replaces the white pine cluster. At other sites, including West Side, Mohawk, Green, Doe, and Berry-Andover, it becomes established somewhat later (9,500–7,000 ybp). Oak-beech vegetation persists until near the present at Green, but at other sites it shifts to other clusters during 8,000–7,000 ybp. Then, it occurs at several of the upland sites (Guilder, Benson, Little Willey, and Little-Royalston) during and, in the case of Guilder, after the *Tsuga* decline (5,500–5,000 ybp to 3,500–2,000 ybp). The oak-beech cluster also appears in some coastal records during the middle Holocene. Between 5,500–4,000 ybp and 3,000–1,800 ybp, *Fagus*-dominated forests occur at Uncle Seth's, Black, Deep-Falmouth, and Blaney's.

Pollen samples assigned to the **oak cluster** (yellow) are dominated by *Quercus* (45%), with *Betula* and *Pinus strobus* regularly present at lower percentages (Figure S3.43). This forest type has occurred mainly in the southern, coastal records, beginning between 10,600 and 8,500 ybp when it replaces either *Pinus strobus* or oak-pitch pine forest (Figure 3). The oak cluster shifts to oak-pitch pine at 8,000 ybp at Duck, Fresh-Falmouth, and Sears. At other sites
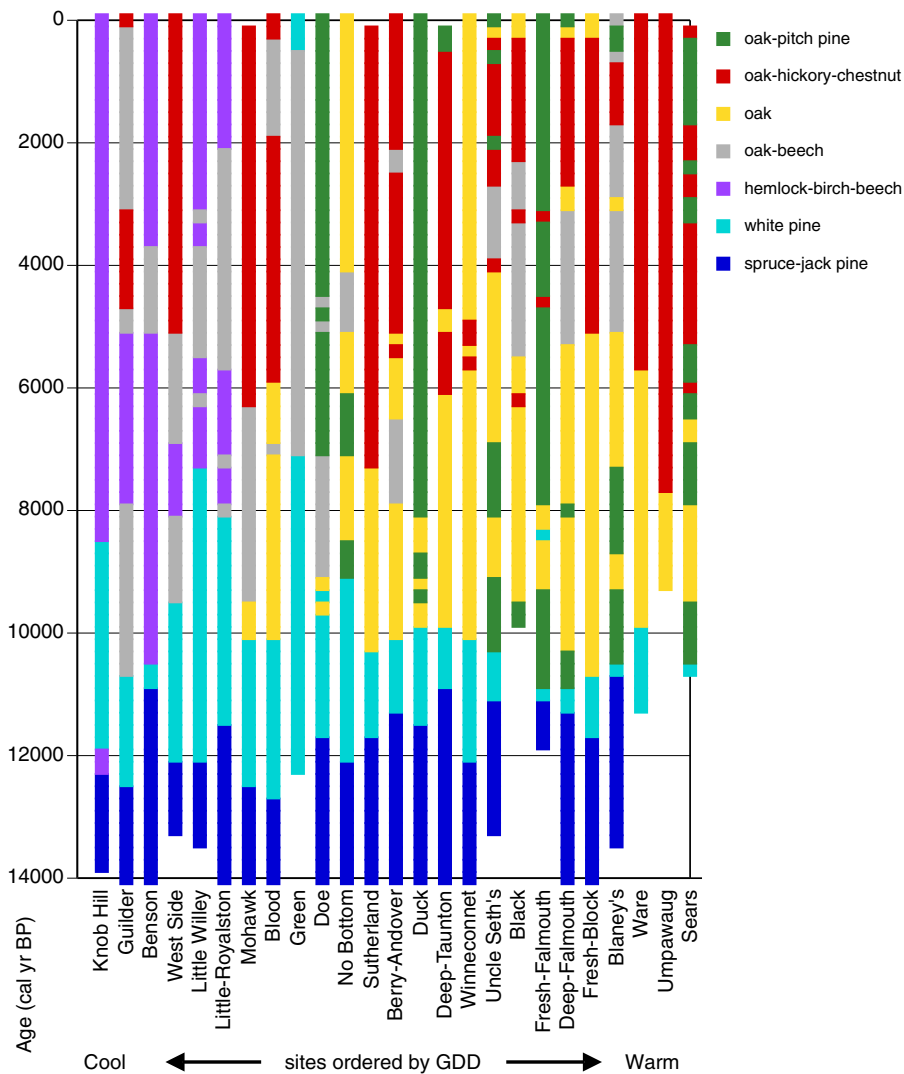
FIGURE 3 Results of cluster analysis of pollen percentage data from New England lake-sediment pollen records; cluster assignments for pollen data interpolated at 200-year intervals. Sites are ordered by modern growing degree days (GDD, 5°C base), with cool sites on the left and warm sites on the right

Quercus-dominated forest persists until 7,000–5,000 ybp, when it is replaced by either the oak-hickory-chestnut cluster (Sutherland, Deep-Taunton, Fresh-Block, Ware, and Umpawaug) or the oak-beech cluster (Uncle Seth's, Black, Deep-Falmouth, and Blaney's). The oak cluster continues to the present day at No Bottom and Winneconnet, and occurs during the last few centuries at several other coastal sites.

Samples in the **oak-hickory-chestnut cluster** (red) are dominated by *Quercus* pollen (46%), and are notable for relatively high percentages of *Carya* (5%) and *Castanea* (1.4%; Figure S3.43). This vegetation type becomes established first at Umpawaug (7,600 ybp) and Sutherland (7,200 ybp) in the southwestern part of the region (Figures 3–4). It then establishes at 6,200–5,000 ybp at several sites (West Side, Mohawk, Blood, Berry-Andover, Deep-Taunton, Fresh-Block, Ware, and Sears) and at 2,600–1,600 ybp at other sites (Uncle Seth's, Deep-Falmouth, and Blaney's), replacing either oak or oak-beech vegetation. Oak-hickory-chestnut also occurs at Guilder during the *Tsuga* decline. During the late Holocene it is replaced by oak-beech forest at Blood and by oak-pitch pine at Sears, but in both cases the oak-hickory-chestnut type returns in the uppermost samples. On the other hand, during the last few centuries

oak-hickory-chestnut forest shifts to oak, oak-beech, and/or oak-pitch pine at a number of sites, including Deep-Taunton, Uncle Seth's, Black, Deep-Falmouth, Fresh-Block, and Blaney's.

Samples in the **oak-pitch pine cluster** (green) have high percentages of *Quercus* (33%) and *Pinus rigida* type (20%; Figure S3.43). *Pinus strobus* is present at lower abundances. This vegetation type has occurred at various times at sites in the southern, coastal part of the study area. In several cases, such as No Bottom, Uncle Seth's, Fresh-Falmouth, Deep-Falmouth, Blaney's, and Sears, oak-pitch pine forest replaced *Pinus strobus* starting between 11,000 and 9,000 ybp (Figures 3–4). Then, between 9,500 and 8,000–6,000 ybp, vegetation composition alternates between the oak-pitch pine and oak clusters at a number of coastal sites, including No Bottom, Duck, Uncle Seth's, Fresh-Falmouth, and Blaney's. Oak-pitch pine has persisted from 8,000–7,000 ybp until the present day at Doe, Duck, and Fresh-Falmouth, all of which are located in areas with sandy soils. The oak-pitch pine vegetation type has also occurred intermittently at Sears, including during 8,000–5,400 ybp and between 3,000 ybp and today.

Nearly all of the vegetation assemblages identified in the cluster analysis are present in the modern samples (Figures 3–4) and recognizable in terms of present-day forest types (Braun, 1950; Westveld
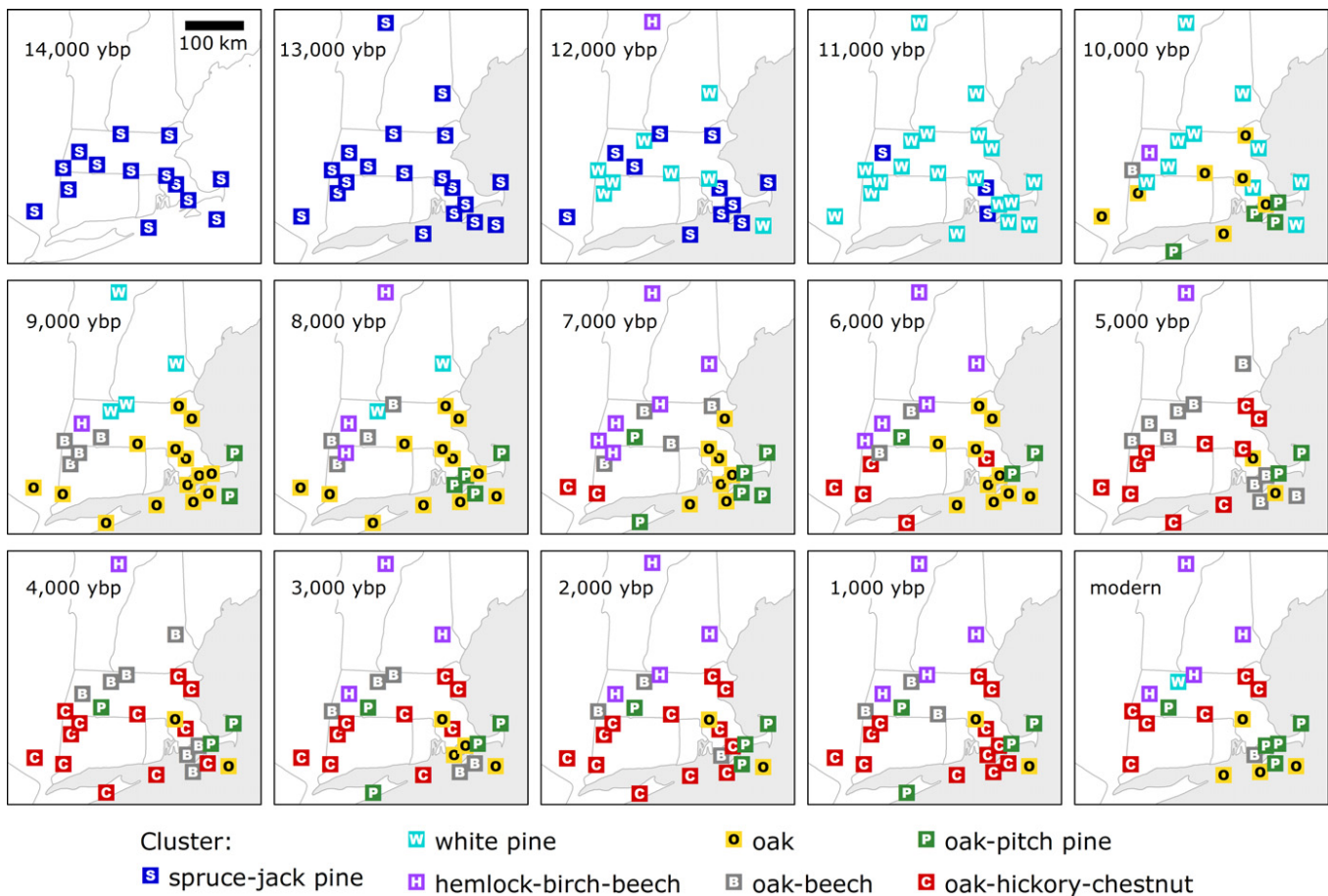
FIGURE 4 Results of cluster analysis of pollen percentage data from New England lake-sediment pollen records; cluster assignments mapped at 1,000-year intervals

et al., 1956). The spruce-jack pine cluster was identified only during the late-glacial interval, a time when climate conditions differed substantially from those found in New England at present (e.g., Shuman & Marsicek, 2016), and an interval of no-analogue pollen assemblages across much of eastern North America (e.g., Williams & Jackson, 2007). Oak-beech forest is much less common today than during the early Holocene and middle Holocene, but it does occur at present in limited areas on Cape Cod and the adjacent islands (Busby, Motzkin, & Hall, 2009; Foster, 2017).

4 | DISCUSSION

Comparison of the pollen records with regional palaeoclimate data and subregional variations in physiography and soils allows us to interpret the spatial and temporal shifts in New England vegetation in terms of (a) changes in temperature and precipitation, (b) the environmental gradient between coastal lowland and inland parts of the region, (c) edaphic differences between glacial till/moraines and sandy outwash deposits, and (d) the environmental niches of different species.

Across New England, boreal forest featuring *Picea* species and *Pinus banksiana* occurred during the cold, dry conditions that existed during 14,000–11,500 ybp (Figure 5). The composition of the

vegetation varied little across the present-day environmental gradient (Figures 4–5b). Ecological changes within this late-glacial interval, including a transition from *Picea glauca* to *Picea mariana*, have been discussed by Lindbladh et al. (2007). Boreal forest declined across the region around 12,000 ybp, although *Picea* and/or *Pinus banksiana* persisted at a few sites in western Massachusetts and along the coast until 11,000–9,000 ybp. The persistence of boreal taxa in western Massachusetts and on Martha's Vineyard and Block Island may be attributable to relatively cool temperatures at higher elevations and under maritime conditions along the coast. As climate warmed between 12,000 and 10,000 ybp, boreal vegetation was replaced by *Pinus strobus*-dominated forest (Figure 5). As was the case during the late-glacial interval, vegetation composition was similar across much of the region at 11,000 ybp (Figures 4–5b). The uniformity of the regional vegetation prior to 10,000 ybp was likely due to the ranges of the dominant taxa (*Picea* and *Pinus banksiana* at 14,000–12,000 ybp, *Pinus strobus* at 12,000–10,000 ybp) spanning the regional environmental gradient during that interval (Figure 6; Oswald et al., 2007).

The composition of forests in the coastal and inland parts of New England diverged during 10,000–8,000 ybp (Oswald et al., 2007). At most southern and coastal sites, *Pinus strobus* was replaced by *Pinus rigida* and/or *Quercus* at 10,000–9,000 ybp, when temperatures were increasing yet precipitation remained low. Elevated
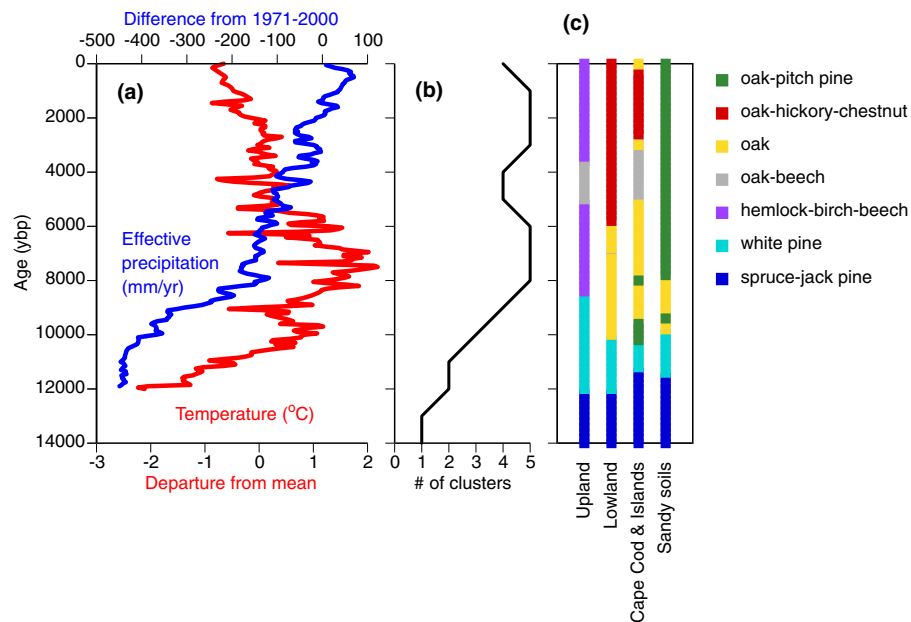
FIGURE 5 Summary of palaeoclimate and pollen data from New England. (a) blue line is effective precipitation (average of reconstructions from Davis, New Long, and Deep-Falmouth; Shuman & Marsicek, 2016); red line is sea-surface temperature reconstruction from site GGC30 (Sachs, 2007; Shuman & Marsicek, 2016). (b) number of clusters (occurring at >1 study site) assigned to the pollen data, shown at 1,000-year intervals. (c) most-common cluster assignments for pollen data interpolated at 200-year intervals for four groups of study sites: upland = Benson, Guilder, Knob Hill, Little-Royalston, Little Willey, Mohawk, and West Side; lowland = Berry-Andover, Blood, Deep-Taunton, Green, Sears, Sutherland, Umpawaug, Ware, and Winneconnet; sandy soil = Doe, Duck, and Fresh-Falmouth; Cape Cod & Islands = Black, Blaney's, Deep-Falmouth, Fresh-Block, No Bottom, and Uncle Seth's

percentages of *Ambrosia* at this time may reflect open forest structure resulting from moisture stress (Faison et al., 2006). In the inland part of the region, it appears that temperatures remained cool enough that *Pinus strobus* persisted at multiple sites until at least 9,000 ybp. Then, with further warming and an increase in precipitation between 9,000 and 8,000 ybp, vegetation composition shifted across the region. As *Fagus grandifolia* expanded across the inland part of the study area, the hemlock-birch-beech and oak-beech forest types replaced *Pinus strobus*. With *Quercus*-dominated forest occurring across southern New England at 9,000–8,000 ybp, a spatial pattern of vegetation not unlike that of the present day had arisen across the regional environmental gradient (Figures 4–6; Oswald et al., 2007).

The differences between inland and coastal areas of New England continued during 8,000–6,000 ybp, an interval featuring the warmest temperatures of the Holocene and precipitation that remained below that of today. Inland and northern parts of New England continued to be dominated by hardwood-hemlock forest featuring *Betula* species, *Tsuga canadensis*, and *Fagus grandifolia* (Figure 5). In coastal areas, where climate was particularly warm, *Tsuga* and *Fagus* were less abundant and *Quercus* species prevailed. *Carya* began to expand across southern New England between 7,000 and 6,000 ybp, likely in response to increasing moisture. This expansion of *Carya* created a combination of tree species, differentiated as the oak-hickory-chestnut type in the cluster analysis, that had not occurred in the region during the early Holocene (Figures 3–4).

Abrupt cooling at 5,500–5,000 ybp resulted in the dramatic decline of *Tsuga canadensis* across the region (Shuman et al., in revision). At

most upland sites, hardwood forest featuring *Quercus* and *Fagus grandifolia* became common during the interval of low *Tsuga* abundance (5,500–3,000 ybp). Sites on Cape Cod and the adjacent islands (including No Bottom, Black, Deep-Falmouth, and Blaney's) also experienced pronounced changes in forest composition at 5,500–5,000 ybp, as *Quercus* abundance declined sharply and *Fagus* increased in abundance (Foster, Oswald, Faison, Doughty, & Hansen, 2006). With these changes, the compositional differences between inland and coastal areas lessened compared with the period from 8,000 to 6,000 ybp (Figures 4–5b). During the middle Holocene, inland areas of New England became drier, whereas moisture increased along the coast (Shuman & Burrell, 2017). However, the temperature gradient between inland and coastal areas was reduced because of coastal cooling (Marsicek et al., 2013; Shuman & Marsicek, 2016).

At many of the upland sites, *Tsuga canadensis* populations recovered between 3,000 and 2,000 ybp. Shuman, Oswald, and Foster (in revision) suggest that, despite the continuation of the regional cooling trend, the biogeographical niche of *Tsuga* is arrayed such that rising moisture resulted in an increase in its abundance. With higher *Tsuga* abundance at upland sites and reduced abundance of *Fagus* on Cape Cod and the islands, the regional vegetation of the late Holocene became as varied as it was during 8,000–6,000 ybp (Figures 4–5b).

The differences in the vegetation history of coastal and inland parts of the study area are also evident when comparing the trajectories of proximate sites with different topographic positions. For example, Green is located in the Connecticut River Valley at an elevation 220 m below nearby Little-Royalston. These sites had similar
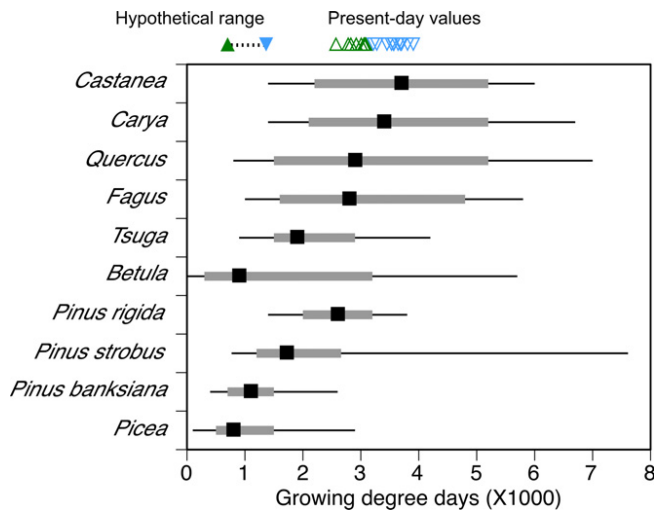
FIGURE 6 Growing degree day (GDD, 5°C base) ranges of selected taxa (Thompson, Anderson, & Bartlein, 1999). For *Picea*, *Tsuga*, and *Quercus* the range represents only those species from eastern North America. Thin line, entire range; thick line, 10–90% of distribution; black square, median value. Also shown are present-day GDD values for the upland (green symbols) and lowland study sites (blue symbols) and a hypothetical GDD range for the study area during the late-glacial interval (closed symbols; width of 666 GDD corresponds to the difference between the average modern GDD of upland and lowland sites)

vegetation composition for most of the late-glacial and early-Holocene intervals, but they diverged after 8,000 ybp, with oak-beech forest present near Green and hemlock-birch-beech at Little-Royalston for most of the middle and late Holocene. However, as we observed for forests across the regional environmental gradient, these sites became more similar during 5,500–3,000 ybp when the abundance of *Tsuga* declined substantially at upland sites (Figures 3–4 and S3.36). Similarly, West Side and Mohawk are located 230–270 m lower than nearby Guilder. All three sites experienced shifts from spruce-jack pine to white pine to oak-beech during the late-glacial and early Holocene, with oak-beech and/or hemlock-birch-beech occurring between 8,000 and 6,000–5,500 ybp (Figures 3–4). Both high- and low-elevation sites featured oak-hickory-chestnut vegetation during the 5,500–3,000 ybp interval of low *Tsuga* abundance, but their assemblages were generally different after the middle Holocene, with oak-hickory-chestnut forest at West Side and Mohawk and oak-beech at Guilder (Figures 3–4). Overall, variations in topography contributed to the heterogeneity of the vegetation at landscape scales (Gaudreau, 1986; Gaudreau & Webb, 1985).

Most of the study sites located on glacial outwash and other sandy deposits, including Doe, Duck, and Fresh-Falmouth, were occupied by *Pinus rigida* and/or *Quercus* for much of the Holocene (Figure 5). This forest type likely included *Quercus* trees and scrub oaks, such as *Quercus ilicifolia* and *Quercus prinoides*. Oak-pitch pine vegetation also occurred at Sears Pond at times during the late Holocene. While Sears is located on a moraine, it is surrounded by a larger area of sandy outwash, and it likely receives substantial amounts of pollen from that part of the landscape. On the other hand, Green, like Doe, sits on

sandy glaciolacustrine kame-delta deposits, and yet it does not feature *Pinus rigida* during the Holocene. In this case, the limited area of sandy soils falls within a region dominated by glacial till, such that the pond receives pollen from broad uplands that are unlikely to support *Pinus rigida*. Overall, it appears that despite the major changes in climate that have occurred during the last 11,000 years, including the progressive increase in precipitation, areas with well-drained sandy substrates experience chronic low soil moisture availability, and thus *Pinus rigida* dominates where other trees have been unable to survive.

The general patterns for the middle and late Holocene described above (Figure 5), including the prevalence of northern hardwood-hemlock forest in inland parts of the study area, oak-hickory-chestnut forest in southern New England, and oak-pitch pine vegetation in areas with sandy soils, were regularly interrupted by relatively short-lived shifts between vegetation types (Figure 3). This created a dynamic mosaic of forest assemblages that changed through time and across space. This aspect of the regional pollen dataset deserves further study, but may represent changes in vegetation associated with extended droughts (Newby et al., 2014) or other landscape-scale disturbances, such as fire and wind events.

Changes in forest composition during the last millennium, including declines in the abundance of *Tsuga* and *Fagus* (Figures S3.36–37), likely resulted from the late-Holocene trend towards cooler and wetter conditions (Figure 5). Furthermore, the signature of European forest clearance is clearly evident in New England pollen records. *Ambrosia* and other weedy taxa increased in abundance during the agricultural era, and various changes in forest composition took place. The changes vary with location, but they include reduced abundance of *Quercus* and *Carya* at some sites (Figures S3.38–39), further declines in *Tsuga* and *Fagus*, and increasing abundance of *Betula*, *Pinus strobus*, and *Pinus rigida* (Figures S3.33–35). These changes in the regional pollen record resemble those observed when comparing eighteenth-century town proprietor surveys with present-day vegetation composition (Cogbill et al., 2002; Thompson et al., 2013).

5 | CONCLUSIONS

Our analyses of pollen records from 29 sites across New England provide new insights into the postglacial vegetation history of this region. Subregional variations in vegetation through time and across space are consistent with palaeoclimate data and the regional environmental gradient, with changes in forest composition occurring in response to long-term trends and abrupt shifts in temperature and precipitation. Landscape-scale variations in topography and substrate have also influenced spatial patterns in vegetation, with *Pinus rigida*-dominated forests occurring in areas with sandy soils for much of the Holocene. With the development of these regional pollen and palaeoclimate datasets for New England, it will be possible to explore a wide range of additional questions about the timing, pace, spatial pattern, and drivers of past vegetation change in this region.

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DATA ACCESSIBILITY

All data will be made available on the Harvard Forest Data Archive website: http://harvardforest.fas.harvard.edu/harvard-forest-data-archive

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.