ORIGINAL ARTICLE

Post-glacial changes in spatial patterns of vegetation across southern New England

W. Wyatt Oswald[1]*, Edward K. Faison[1], David R. Foster[1], Elaine D. Doughty[1], Brian R. Hall[1] and Barbara C. S. Hansen[2]

[1]*Harvard University, Harvard Forest, Petersham, MA 01366, USA and* [2]*University of Minnesota, Limnological Research Center, Minneapolis, MN 55455, USA*

ABSTRACT

Aim We analysed lake-sediment pollen records from eight sites in southern New England to address: (1) regional variation in ecological responses to post-glacial climatic changes, (2) landscape-scale vegetational heterogeneity at different times in the past, and (3) environmental and ecological controls on spatial patterns of vegetation.

Location The eight study sites are located in southern New England in the states of Massachusetts and Connecticut. The sites span a climatic and vegetational gradient from the lowland areas of eastern Massachusetts and Connecticut to the uplands of north-central and western Massachusetts. *Tsuga canadensis* and *Fagus grandifolia* are abundant in the upland area, while *Quercus*, *Carya* and *Pinus* species have higher abundances in the lowlands.

Methods We collected sediment cores from three lakes in eastern and north-central Massachusetts (Berry East, Blood and Little Royalston Ponds). Pollen records from those sites were compared with previously published pollen data from five other sites. Multivariate data analysis (non-metric multi-dimensional scaling) was used to compare the pollen spectra of these sites through time.

Results Our analyses revealed a sequence of vegetational responses to climate changes occurring across southern New England during the past 14,000 calibrated radiocarbon years before present (cal yr BP). Pollen assemblages at all sites were dominated by *Picea* and *Pinus banksiana* between 14,000 and 11,500 cal yr BP; by *Pinus strobus* from 11,500 to 10,500 cal yr BP; and by *P. strobus* and *Tsuga* between 10,500 and 9500 cal yr BP. At 9500–8000 cal yr BP, however, vegetation composition began to differentiate between lowland and upland sites. Lowland sites had higher percentages of *Quercus* pollen, whereas *Tsuga* abundance was higher at the upland sites. This spatial heterogeneity strengthened between 8000 and 5500 cal yr BP, when *Fagus* became abundant in the uplands and *Quercus* pollen percentages increased further in the lowland records. The differentiation of upland and lowland vegetation zones remained strong during the mid-Holocene *Tsuga* decline (5500–3500 cal yr BP), but the pattern weakened during the late-Holocene (3500–300 cal yr BP) and European-settlement intervals. Within-group similarity declined in response to the uneven late-Holocene expansion of *Castanea*, while between-group similarity increased due to homogenization of the regional vegetation by forest clearance and ongoing disturbances.

Main conclusions The regional gradient of vegetation composition across southern New England was first established between 9500 and 8000 cal yr BP. The spatial heterogeneity of the vegetation may have arisen at that time in response to the development or strengthening of the regional climatic gradient. Alternatively, the differentiation of upland and lowland vegetation types may have occurred as the climate ameliorated and an increasing number of species arrived in the region,

*Correspondence: W. Wyatt Oswald, Harvard University, Harvard Forest, 324 North Main Street, Petersham, MA 01366, USA.
E-mail: woswald@fas.harvard.edu

arranging themselves in progressively more complex vegetation patterns across relatively stationary environmental gradients. The emergence of a regional vegetational gradient in southern New England may be a manifestation of the increasing number of species and more finely divided resource gradient.

INTRODUCTION

Continental-scale syntheses of late-Quaternary palaeoecological records from eastern North America have provided key insights into the regional response of vegetation to orbital- and millennial-scale climatic forcing (Bernabo & Webb, 1977; Gaudreau & Webb, 1985; Williams *et al.*, 2001; Shuman *et al.*, 2002a,b, 2004, 2005). Such studies have informed ecological theory by illustrating that (1) environmental change can alter both the range and local abundance of a given plant species, (2) species respond individualistically to climate change, (3) different combinations of climatic parameters yield different and often novel plant assemblages, and (4) vegetation assemblages may be ephemeral in space and time (Davis, 1981; Webb, 1986; Overpeck *et al.*, 1992; Williams *et al.*, 2001; Jackson & Williams, 2004).

Few studies have systematically addressed past spatial patterns of vegetation at regional or landscape scales, where the abundance and distribution of plant species are determined not only by large-scale climatic conditions, but also by finer-scale variations in topography, substrate or disturbance (but cf. Brubaker, 1975; Jacobson, 1979; Webb *et al.*, 1983; Jackson & Whitehead, 1991; Graumlich & Davis, 1993; Spear *et al.*, 1994). In regions where the density of palaeoecological sites is sufficiently high, a hierarchical 'zoom-lens' approach can be employed to examine patterns of past vegetation across continental, regional and local spatial scales (Webb *et al.*, 1983; Webb, 1993). Smaller spatial scales are often those where natural-resource managers, conservationists and vegetation scientists assess, monitor and manage ecosystems and environmental resources, thus a long-term perspective on changing spatial patterns of vegetation can improve our understanding and inform decision making.

Current and historical vegetation patterns in southern New England are strongly influenced by environmental variations associated with elevation, latitude, substrate and distance from the Atlantic Ocean (Fig. 1). The strongest climatic and ecological gradient is controlled by physiography, extending from the relatively warm and dry 'lowland' area along the coast (eastern Massachusetts, Rhode Island and Connecticut) to the cooler, moister 'upland' area of north-central and western Massachusetts. The variations in environment associated with this gradient have important consequences for the distribution and abundance of the major tree species. For example, *Tsuga canadensis* (eastern hemlock), *Fagus grandifolia* (American beech) and *Betula* (birch) species are prevalent in the uplands,

whereas *Quercus* (oak), *Carya* (hickory) and *Pinus* (pine) species have higher abundances in the lowlands along the coast (Cogbill *et al.*, 2002; Fig. 1). This vegetational transition has been recognized for decades in southern New England and elsewhere (Raup, 1940; Braun, 1950; Westveld *et al.*, 1956; Curtis, 1959; Schauffler & Jacobson, 2002). In addition, disturbance regimes vary along the regional environmental gradient. The lowland area is particularly susceptible to hurricane damage (Boose *et al.*, 2001), and prior to European settlement it experienced greater fire activity than the upland region, perhaps related to higher human population levels near the coast (Cogbill *et al.*, 2002; Parshall & Foster, 2002). Analyses of pollen in lake sediments across southern New England show that pollen data have the ability to represent the regional gradients in climate and vegetation (Fuller *et al.*, 1998; Fig. 2), which allows the exploration of questions relating to spatial patterning of vegetation in the past.

In this paper we explore the role of this physiographic and environmental gradient in structuring the vegetation of southern New England through time. We contribute three new post-glacial pollen records to the existing network of records in this region, resulting in a density of palaeoecological sites that is equalled in only a few other areas of North America (Webb *et al.*, 1983; Jackson & Whitehead, 1991; Graumlich & Davis, 1993; Spear *et al.*, 1994). Detailed analysis of eight post-glacial records allows us to address questions concerning: (1) regional variation in ecological responses to post-glacial environmental conditions, (2) fine-scale heterogeneity of vegetation during different intervals of the past, and (3) changes through time in the relative importance of certain abiotic controls on spatial patterns of vegetation.

MATERIALS AND METHODS

Study area

Sites analysed in this study are located in the states of Massachusetts and Connecticut in southern New England (Fig. 1). Most of this area is characterized by acidic soils that developed on glacial deposits and granitic or metamorphic bedrock, although some areas of calcareous bedrock are present in the western region (Zen *et al.*, 1983; MassGIS, 1999). The uplands portion of the study area reaches elevations > 500 m, while much of the lowlands area is at sea level. This elevational gradient, combined with covarying changes in latitude and distance from the Atlantic Ocean, creates a strong
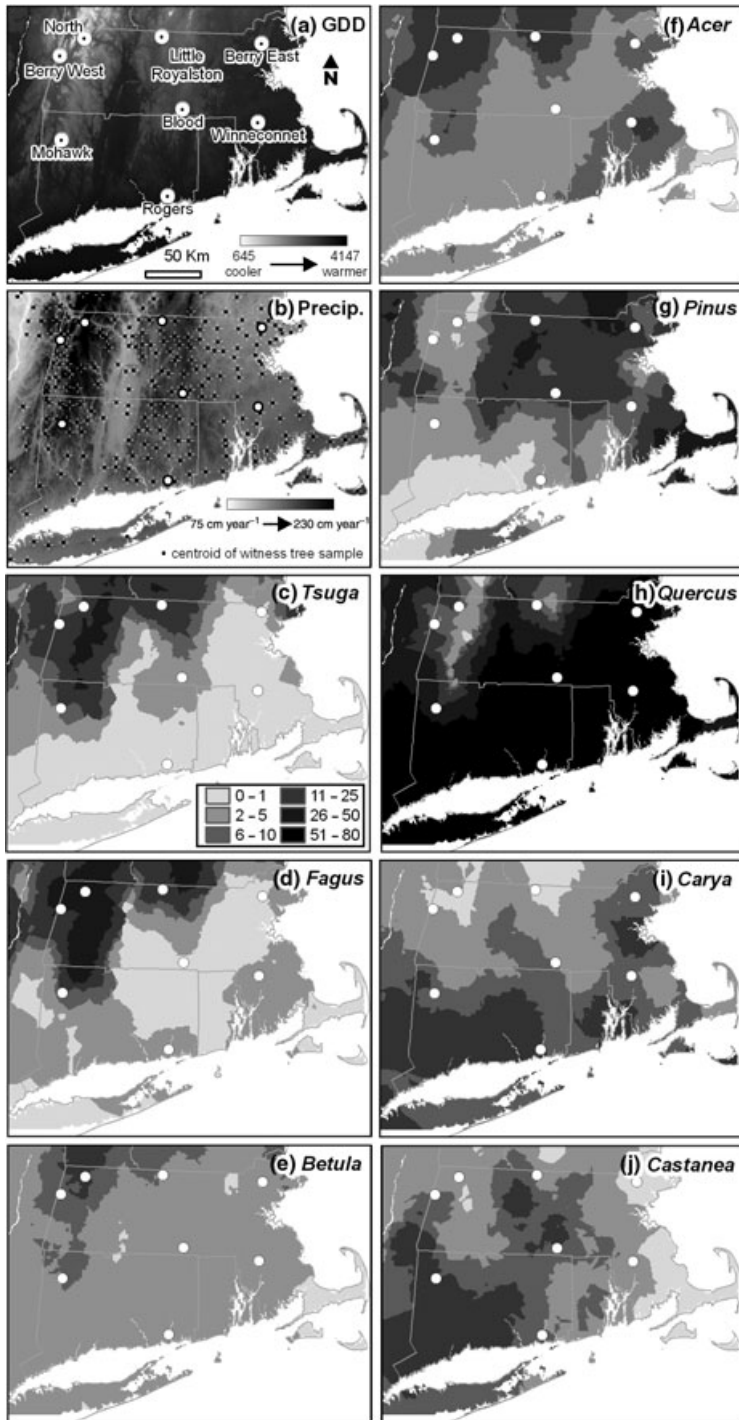
Figure 1 (a) Map of southern New England showing study sites and growing degree days (GDD; 5°C base). (b) Map of mean annual precipitation; dots are locations of witness-tree data points (data shown in subsequent panels). (c–j) Patterns of pre-settlement abundance (relative frequencies) for selected taxa as revealed by town-level witness-tree survey data (Cogbill *et al.*, 2002). Continuous grids of witness-tree distributions were made by extrapolating from the centroid of each town through ordinary kriging with a spherical model using Geostatistical Analyst in ArcMap ver. 9.0 (ESRI).

environmental gradient across the region. Western and north-central Massachusetts are relatively cool and wet, whereas eastern Massachusetts, Connecticut and Rhode Island are warmer and drier (Hall *et al.*, 2002). The upland area is classified as part of the Northeastern Highlands ecoregion, whereas the lowland area is part of the Northeastern Coastal Zone ecoregion (Griffith *et al.*, 1994). This study does not include the Atlantic Coast Pine Barrens ecoregion that occurs on Cape Cod and the adjacent islands; we focus on that region in other studies (Foster *et al.*, 2002; Parshall *et al.*, 2003).

Lake-sediment records

We collected sediment cores from three sites to achieve better spatial coverage in southern New England (Fig. 1; Table 1). Berry East and Blood Ponds are located at relatively low elevations in eastern Massachusetts; Little Royalston Pond is in the higher elevation region of north-central Massachusetts. Blood Pond was cored through ice (February 2001), while Little Royalston and Berry East were cored from a raft (July and September 2003). We used a 7-cm-diameter plastic tube fitted
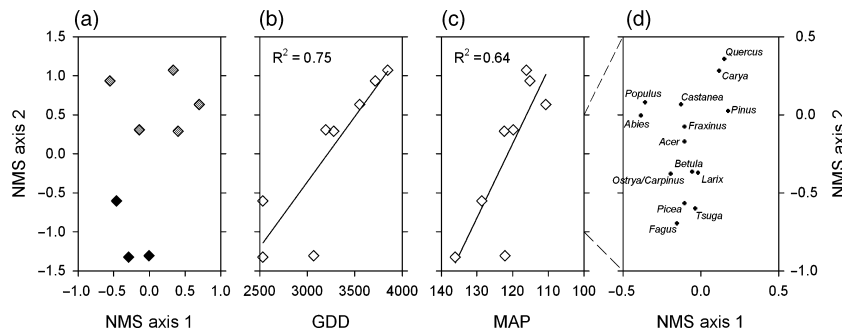
Figure 2 (a) Non-metric multi-dimensional scaling (NMS) analysis (see Materials and methods) of pre-settlement pollen data from the eight sites analysed in this study. Data points are centroids of NMS axis 1 and 2 scores of an analysis of the three samples immediately before settlement for each record. Black symbols, upland sites; grey symbols, lowland sites. (b, c) Comparison of NMS axis 2 centroids with present-day growing degree day (GDD; 5°C base) and mean annual precipitation (MAP) values for the study sites. These strong relationships illustrate the ability of the pollen data to reflect the regional gradients in climate and vegetation. (d) Taxon scores for NMS ordination.

Table 1 Study sites

Site	Latitude	Longitude	Elevation (m)	Growing degree days (5°C base)	Mean annual precipitation (cm)	Lake area (ha)	Reference
Lowland							
Berry East	42.620	−71.087	43	3552	110.63	1.6	This paper
Blood	42.080	−71.962	214	3282	122.32	8.5	This paper
Mohawk	41.817	−73.283	360	3197	119.81	6.6	Gaudreau (1986)
Rogers	41.367	−72.117	91	3848	116.08	107.0	Davis (1969)
Winneconnet	41.971	−71.133	22	3717	115.09	60.0	Suter (1985)
Upland							
Berry West	42.505	−73.319	631	2536	128.58	3.7	Whitehead (1979)
Little Royalston	42.675	−72.192	302	3069	122.07	4.0	This paper
North	42.651	−73.054	586	2537	136.04	7.8	Whitehead & Crisman (1978)

with a piston to collect upper sediments (*c.* 100–150 cm) and a 4.5-cm-diameter square-rod piston sampler (Wright *et al.*, 1984) to collect lower sediments in 1-m-long drive lengths. The lower drives were extruded horizontally in the field, and the cores were wrapped in plastic wrap and aluminum foil. The upper cores were extruded vertically in the laboratory at 1–2-cm intervals. The upper cores were matched to the lower cores by comparison of variations in organic content.

Sediment organic content was determined by percentage weight loss on ignition; 1-cm^3 samples were dried at 90°C then combusted at 550°C. Samples of 1 or 2 cm^3 were prepared for pollen analysis following standard procedures (Faegri & Iversen, 1989). Tablets containing *Lycopodium clavatum* marker spores were added to the samples to allow estimation of pollen concentrations and influx rates (Stockmarr, 1971). Pollen residues were mounted in silicone oil and examined microscopically at ×400 or ×1000 magnification. A minimum of 300 pollen grains and spores of upland plant taxa were identified for each sample (the sum normally exceeded 500 grains and spores), and all pollen and spore abundances are expressed as a percentage of that sum.

For each sediment core, chronological control is provided by accelerator mass spectrometry ^{14}C analysis of bulk sediment samples or plant macrofossils, as well as by age assignments based on stratigraphic changes in the pollen record (Table 2).

The ^{14}C dates were converted to calibrated years before present (cal yr BP) using OxCal ver. 3.9 (Bronk Ramsey, 1995, 2001). The age–depth models used to calculate influx rates and to assign sample ages were based on linear interpolation between selected dates.

We compared the pollen data from Berry East, Blood and Little Royalston with previously published data from five other sites in southern New England (Table 1). Rogers Lake (Davis, 1969), Winneconnet Pond (Suter, 1985) and Mohawk Pond (Gaudreau, 1986) are located in the relatively warm lowland part of the region; Berry West Pond (Whitehead, 1979) and North Pond (Whitehead & Crisman, 1978) are located in the Berkshire region of north-western Massachusetts. Pollen and chronological data for Rogers, Winneconnet, Mohawk, Berry West and North were obtained from the North American Pollen Database (http://www.ncdc.noaa.gov/paleo/pollen.htm). Age–depth models for those records were converted to calibrated ages using the method described above.

We identified stratigraphic transitions in the eight records by clustering the pollen spectra using the constrained incremental sum of squares (CONISS) method on square-root-transformed pollen percentages (Grimm, 1987), and defined pollen zones that were generally consistent among all sites. Taxa included in the analysis were *Picea*, *Pinus*, *Tsuga*, *Betula*, *Fagus* and *Quercus*. To compare changes in the eight pollen

Table 2 Results of ^{14}C analysis and other chronological data

Site	Depth (cm)	Material dated	Laboratory number	^{14}C age	^{14}C error	Cal ^{14}C age	$\pm 2\sigma$
Berry East	0*					−51.0	
	68†					306.0	
	101	Lake sediment	Beta 174842	750	40	692.4	40.4
	159	Lake sediment	Beta 174843	1310	40	1233.8	62.2
	283	Lake sediment	Beta 174844	2560	50	2627.0	139.0
	381	Lake sediment	Beta 174845	3460	50	3713.6	126.8
	510	Lake sediment	Beta 189306	4620	40	5379.0	85.0
	608	Wood	AA 58102	5490	60	6291.0	114.2
	690	Lake sediment	Beta 189307	6670	50	7523.6	90.8
	936	Lake sediment	Beta 189308	8640	40	9618.4	85.6
	1192	Lake sediment	Beta 189309	12230	70	14637.6	793.2
Blood	0*					−51.0	
	72†					236.0	
	93	Lake sediment	AA 47066	800	40	725.8	61.4
	135	Lake sediment	AA 47067	1380	40	1303.2	43.6
	181	Lake sediment	AA 47068	1990	60	1967.0	147.0
	225	Lake sediment	AA 47069	2980	60	3149.2	195.2
	260	Lake sediment	AA 47070	3280	40	3514.8	117.2
	298	Lake sediment	AA 47071	3710	50	4062.8	166.0
	318‡	Lake sediment	AA 47072	3620	70	3932.8	213.6
	356	Lake sediment	AA 47073	4470	50	5088.8	216.4
	420	Lake sediment	AA 47074	5580	50	6368.4	81.6
	480	Lake sediment	AA 47075	6900	50	7720.4	104.0
	537‡	Lake sediment	AA 56943	6750	40	7594.4	82.4
	645	Lake sediment	OS 51403	8220	50	9209.5	190.0
	737‡	Lake sediment	AA 56944	7030	50	7845.4	110.2
	800	Lake sediment	Beta 192021	8990	50	10077.0	157.8
	953	Lake sediment	OS 51404	9670	55	10999.5	220.0
	957‡	Lake sediment	AA 56945	9300	50	10472.2	197.4
	1137‡	Lake sediment	AA 56946	8070	50	9007.0	227.0
	1236‡	Lake sediment	Beta 192022	10260	50	12234.8	487.6
	1265	Lake sediment	OS 51560	11500	70	13349.5	150.0
	1349	Lake sediment	OS 51561	12600	75	14724.5	425.0
	1429	Lake sediment	AA 56947	13910	70	16706.4	490.4
Little Royalston	0*					−53.0	
	80†					187.0	
	100	Lake sediment	AA 58093	800	30	714.4	46.4
	200	Lake sediment	AA 58094	2590	40	2660.6	113.8
	260	Lake sediment	AA 58095	3480	40	3739.4	102.2
	340	Lake sediment	AA 58096	4670	40	5442.6	133.4
	510	Lake sediment	AA 58097	7110	50	7905.2	112.8
	590	Lake sediment	AA 58098	8210	60	9207.2	194.4
	712§					11600.0	
	772	Moss	AA 58099	12910	80	15242.0	765.6

*Age assignment based on year core was collected.
†Age assignment based on pollen stratigraphy (European settlement).
‡Excluded from age–depth model.
§Age assignment based on pollen stratigraphy (*Picea* pollen percentages < 10%).

records through time, we analysed the data set using non-metric multi-dimensional scaling (NMS) of Bray–Curtis distances (Minchin, 1987). We performed the NMS using the autopilot mode in PC-ORD (McCune & Grace, 2002). The analysis included all samples < 14,000 cal yr BP and all those taxa that reached 5% in any sample.

Modern climate data

We use modelled growing degree days (GDD) and mean annual precipitation (MAP) values as indices of the relative locations of our study sites along the regional physiographic and environmental gradient. GDD and MAP were

determined using the model of Ollinger *et al.* (1995), which estimates climatic parameters based on elevation, latitude and longitude. The climate modelling was performed using the Spatial Analyst extension in ArcGIS ver. 9.0 (2004; ESRI, Redlands, CA, USA), with the 30-m-grid cell National Elevation Data set (available from US Geological Survey/EROS, Sioux Falls, SD, USA) as the base layer. For each study site, we present the average MAP and GDD values within a 5-km radius. MAP was modelled using regression coefficients from Ollinger *et al.* (1995). Similarly, we used equations from Ollinger *et al.* (1995) to calculate mean daily maximum and minimum temperatures for each month, then estimated the mean daily temperature for each month as the average of the maximum and minimum values. GDD values were determined on a 5°C base (Newman, 1980; Thompson *et al.*, 1999): if a month had a mean daily temperature ≥ 5°C, the temperature was multiplied by the number of days in the month to obtain its GDD. The monthly GDD values were then summed to determine annual GDD values. Ollinger *et al.* (1995) report estimated standard errors of 0.51–1.59°C for their monthly temperature equations, and 0.66–1.25 cm for their monthly precipitation equations.

RESULTS

Pollen records from Berry East, Blood and Little Royalston Ponds

The results of the CONISS analysis are consistent with the zonation framework applied previously to New England pollen records (Deevey, 1939; Davis, 1969; Shuman *et al.*, 2004), although we consider the late-glacial interval (Zone A) as a single zone, and we subdivide Zone B into three separate subzones (Fig. 3). In general, the zone boundaries and their timing are similar among all eight sites, although some exceptions are mentioned below.

Zone A (c. 14,000–11,500 cal yr BP)

Berry East and Blood are characterized by high percentages of *Picea* and *Pinus* subgenus *Pinus* (presumably *P. banksiana*) pollen during the interval from 14,000 to 11,500 cal yr BP. For most of this interval, Berry East has higher percentages of *Picea* (50–75%) than *Pinus* (10–30%), whereas Blood has intermediate percentages of both taxa (15–50%). Both sites have intermediate abundances (c. 10–30%) of *Alnus* and *Betula* in Zone A, with the highest values occurring at the end of the zone (c. 12,000 cal yr BP). Several taxa are present at low (< 10%) percentages during this interval, including *Abies*, *Larix*, *Populus*, *Ostrya–Carpinus*, *Fraxinus* and *Quercus*. Little Royalston also has relatively high percentages of *Picea* and *Pinus* in Zone A. Both taxa occur at c. 10–30% in samples older than c. 11,500 cal yr BP. The suite of minor taxa at Little Royalston resembles that of the lowland sites.

Zone B1 (c. 11,500–10,500 cal yr BP)

In the lowland pollen records, the transition from Zone A to B1 is marked by *Picea* abundance declining precipitously and *Pinus* percentages increasing sharply. *Pinus* subgenus *Strobus* pollen (presumably *P. strobus*) dominates the assemblages, reaching c. 50% at both Berry East and Blood. *Quercus* pollen percentages rise sharply to 20%, *Acer* percentages increase to > 3% at Blood, and many of the minor taxa prevalent in Zone A decline in abundance. Like the lowland sites, Little Royalston exhibits major changes at c. 11,500 cal yr BP. *Picea* and the associated minor taxa decline at that time, percentages of *Pinus* rise to 60%, and *Quercus* percentages increase to c. 20%.

Zone B2 (c. 10,500–9500 cal yr BP)

The dominance by *P. strobus* at the lowland sites is brief, and in Zone B2 *Pinus* percentages at Berry East and Blood decline from c. 50 to 20–30%. *Tsuga* pollen percentages increase at this time, reaching 20% at Blood Pond. *Quercus* percentages drop at Blood Pond, but continue to increase at Berry East. Zone B2 changes are similar at Little Royalston, although *Pinus* pollen declines to only c. 40%.

Zone B3 (c. 9500–8000 cal yr BP)

For Berry East and Blood Ponds, Zone B3 features relatively low percentages of both *P. strobus* and *Tsuga* pollen. *Quercus* percentages reach 50% at Berry East, but remain at c. 30–40% at Blood. *Pinus* subgenus *Pinus* (probably *P. banksiana*) increases in abundance at Berry East, while *Fagus* percentages increase gradually at Blood. Both sites have relatively high percentages (> 2%) of *Ambrosia* pollen in Zone B3. We discuss this feature in more detail elsewhere (Faison *et al.*, 2006). The transition to Zone B3 occurs slightly later at Little Royalston (c. 9000 cal yr BP). *Pinus* pollen percentages decline from c. 40% to 30%, while *Quercus* pollen reaches c. 20–30%. *Tsuga* pollen percentages increase slightly at Little Royalston, and *Fagus* percentages rise to > 5%. The interval of elevated *Ambrosia* pollen percentages observed in the lowland records is not present at Little Royalston.

Zone C1 (c. 8000–5500 cal yr BP)

In the Berry East and Blood pollen records, Zone C1 is marked by an increase in *Fagus* pollen percentages. *Fagus* reaches c. 5% at Berry East and exceeds 20% in a brief peak at c. 7000 cal yr BP in the Blood record. The rise in *Fagus* percentages is accompanied by a minor increase in *Tsuga* percentages at both sites. *Carya* pollen percentages increase at both sites at the end of Zone C1 (c. 6000 cal yr BP). *Fagus* pollen percentages also increase c. 8000 cal yr BP at Little Royalston, rising from c. 5–10% to 20–25%. *Pinus* and *Quercus* percentages decline slightly during Zone C1, whereas *Betula* abundance increases at the beginning of this zone, and *Tsuga* percentages continue to increase. Like the lowland sites, Little Royalston also features a
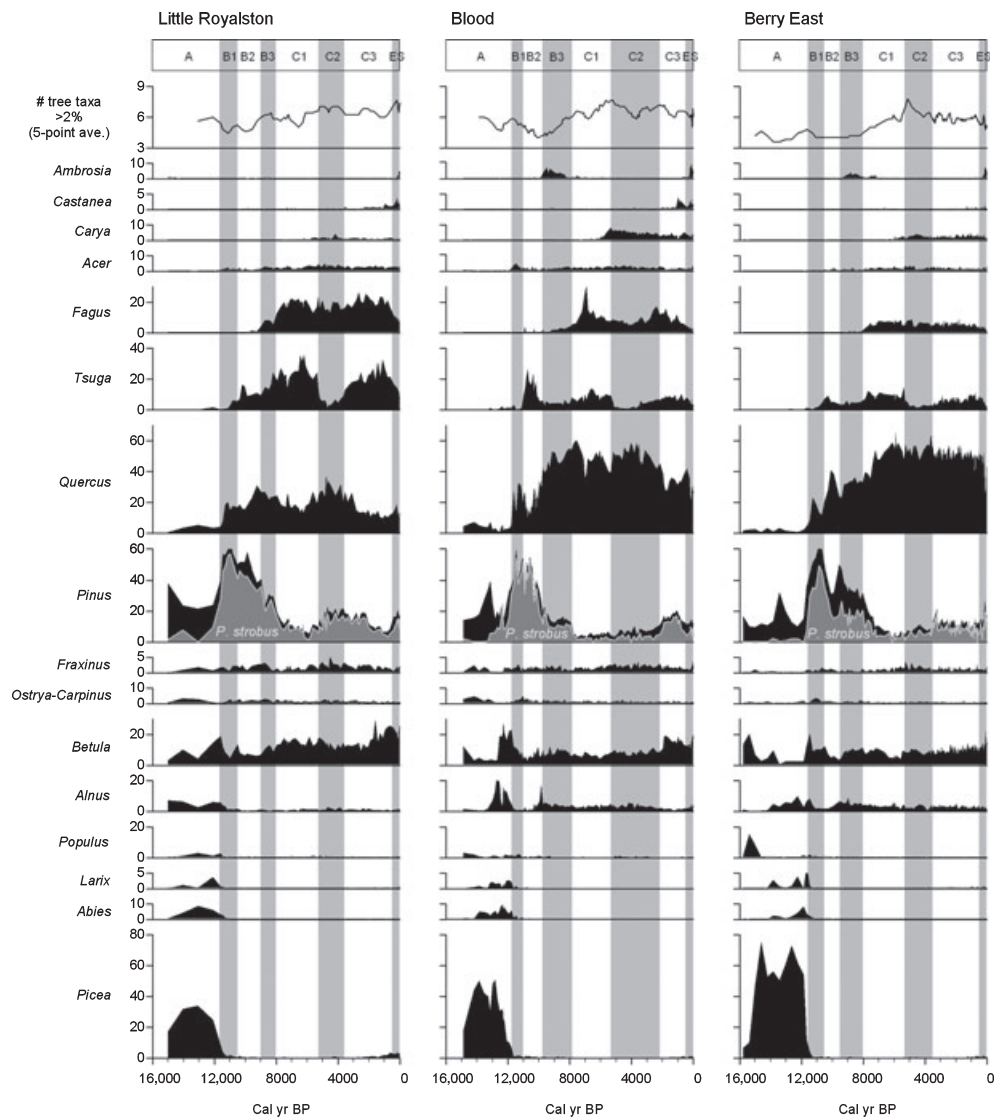
Figure 3 Pollen percentage diagrams for Little Royalston, Blood and Berry East. All taxa are expressed as a percentage of the sum of pollen and spores of upland plant taxa. The uppermost plots show changes in palynological diversity (number of tree taxa > 2%) through time, with a five-point moving average used to emphasize long-term trends.

rise in *Carya* pollen percentages at the end of Zone C1, although it is not as pronounced as at Blood Pond.

Zone C2 (c. 5500–3500 cal yr BP)

Tsuga pollen percentages decline abruptly at the beginning of Zone C2, dropping from *c*. 10% to 2% at Berry East and Blood. The *Tsuga* decline is even more striking at Little Royalston, where *Tsuga* percentages drop from *c*. 20–30% to < 5%. For Little Royalston, coincident with the *Tsuga* decline are increases in *Quercus* pollen from *c*. 20% to 30%, and in *Pinus* pollen from *c*. 10% to 20%.

Zone C3 (c. 3500–300 cal yr BP)

Zone C2 lasts until *c*. 3500 cal yr BP at Berry East, at which time *Tsuga* and *Pinus* pollen percentages increase. *Tsuga*

abundance also increases at that time in the Blood Pond pollen record, although Zone C3 does not begin until *c*. 2000 cal yr BP, at which point there are increases in *Pinus* and *Betula* percentages and a decrease in *Quercus* abundance. At Blood, *Fagus* pollen percentages increase between *c*. 3000 and 2000 cal yr BP, then decline during Zone C3. Within Zone C3 there is a rise in *Castanea* pollen percentages at both lowland sites. In the Blood Pond record, *Castanea* increases from < 1% to 4% at *c*. 1000 cal yr BP. The change in *Castanea* is barely perceptible in the Berry East record, but its pollen percentages do increase slightly, beginning at *c*. 1000 cal yr BP. A similar series of changes is observed at Little Royalston during Zone C3. The increase in *Tsuga* pollen percentages continues until the middle of this interval, at which point *Tsuga* abundance declines. *Fagus* percentages also decline at *c*. 1000 cal yr BP. *Quercus* percentages decrease at the start of Zone C3, *Pinus* abundance is reduced between *c*. 2000 and 1000 cal yr BP, and *Betula*

percentages increase at *c.* 2000 cal yr ʙᴘ. *Castanea* percentages increase slightly, beginning at *c.* 2000 cal yr ʙᴘ, then increase sharply to *c.* 3% during the latter 500 years.

Zone ES (European settlement; 300 cal yr ʙᴘ to present)

The uppermost part of all three records features the dramatic rise in the pollen of *Ambrosia* that marks European settlement of the region. The *Ambrosia* rise is also associated with increased abundance of other herbaceous taxa, including Poaceae, *Plantago* and *Rumex*, and decreased abundance of the major tree taxa.

Multivariate analyses of the pollen data

The NMS ordination of the pollen data from all eight sites (Table 1) illustrates shifts in regional vegetation in response to post-glacial environmental changes. Late-glacial pollen assemblages are plotted in the lower-right corner of ordination space, early-Holocene samples are higher on NMS axis 2, and middle- and late-Holocene samples occur in the upper-left corner (Fig. 4). This pattern suggests that the sites experienced broadly parallel changes as the climate changed during the late-glacial and early-Holocene intervals. However, the ordination also shows that the degree of similarity among the sites decreased later in the Holocene. In particular, samples from lowland and upland sites diverge after *c.* 9500–8000 cal yr ʙᴘ, with the lowland samples having higher scores on NMS axis 2 (Fig. 5). Comparison of the NMS axis 1 and 2 scores with modern-day GDD and MAP values of the sites (Fig. 6) tested whether past spatial patterns of vegetation were associated with the climatic gradient that exists at present, and is reflected in the modern and pre-settlement vegetation (Fig. 2). In Zone A, NMS axis 1 exhibits a moderately strong relationship with modern-day GDD and MAP values (Fig. 6), but in general the lowland and upland sites have similar pollen spectra (Fig. 5), dominated by *Picea* and *Pinus*. It does not appear that forest composition was driven by the regional physiographic
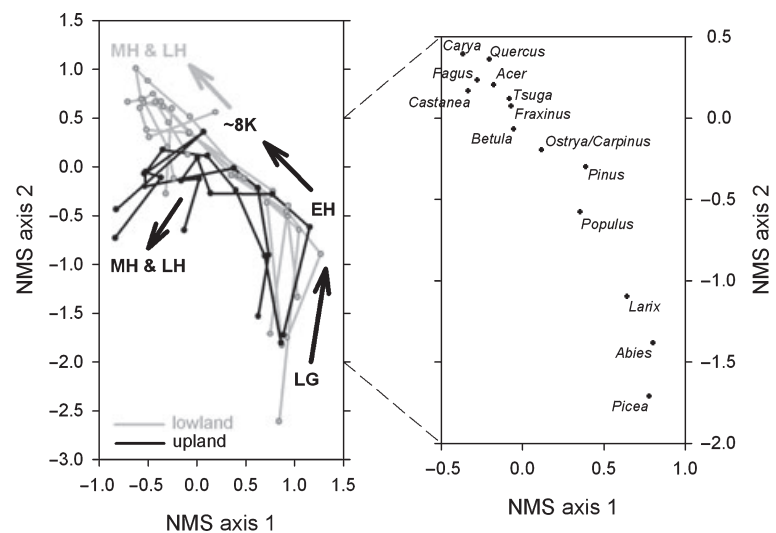
gradient. High similarity among the records continues in Zones B1 and B2 (Fig. 5), where all sites are characterized by high *Pinus* subgenus *Strobus* pollen percentages, and moderate abundances of *Betula*, *Quercus* and *Tsuga* pollen. The strength of the relationship between NMS axis 1 and 2 scores and modern-day GDD and MAP is particularly low during Zone B2 (Fig. 6).

The lowland and upland sites begin to differentiate in Zone B3 (*c.* 9500–8000 cal yr ʙᴘ; Fig. 5), as *Pinus* is replaced by *Quercus* as the dominant taxon at lowland sites, whereas *Tsuga* and *Fagus* pollen percentages rise as *Pinus* declines at upland sites. This differentiation, and the relationship between NMS axis 2 scores and modern-day GDD and MAP, becomes much stronger in Zone C1 (Figs 5 & 6). The increases in *Tsuga*, *Fagus* and *Betula* pollen percentages at Little Royalston and other upland sites further increase the dissimilarity between samples from those sites and *Quercus*-dominated samples from Berry East, Blood and other lowland sites, such that in multivariate space there is no longer any overlap between the upland and lowland sites (Fig. 5).
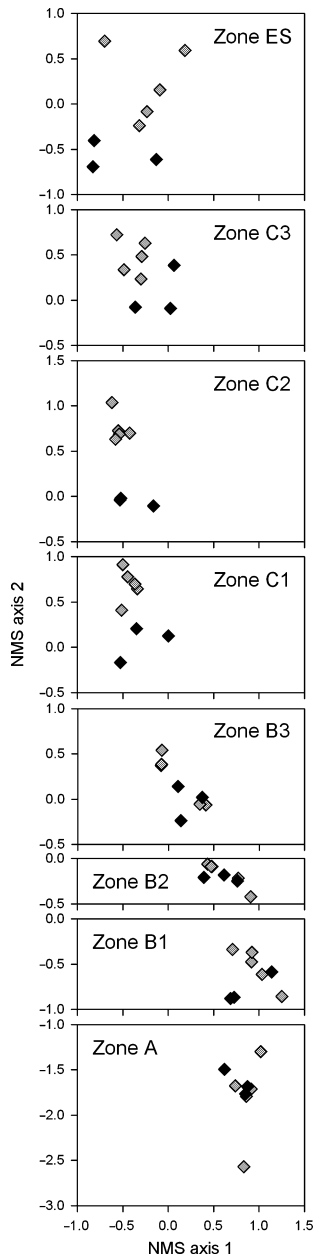
The ubiquitous decline of *Tsuga* in Zone C2 had a stronger impact on upland than lowland sites, as *Tsuga* pollen percentages were already relatively low at Berry East, Blood and the other lowland sites. However, the differentiation between upland and lowland sites remains robust despite the differential decline of *Tsuga*, because the palynological differences between upland and lowland involve other taxa as well as *Tsuga*. For example, percentages of *Fagus* remain higher at upland sites, while lowland sites had higher percentages of *Quercus* and *Carya* pollen. The association between NMS axis 2 and modern-day GDD and MAP for Zone C2 is only slightly weaker than in Zone C1 (Fig. 6), and the tight clustering of the upland and lowland sites in ordination space (Fig. 5) suggests that within-group homogeneity was particularly high during the *Tsuga* decline.

The differentiation of upland and lowland sites became weaker in Zones C3 and ES (Fig. 5). The relationship between NMS axis 1 and modern-day GDD and MAP strengthened

Figure 4 (a) Non-metric multi-dimensional scaling (NMS) analysis of pollen data from lowland (Berry East, Blood, Mohawk, Rogers, Winneconnet) and upland sites (Berry West, Little Royalston, North). Data points are centroids of NMS axes 1 and 2 scores for each site for each pollen zone. Bold arrows show the trajectory of records through time: LG, Late Glacial; EH, Early Holocene; MH, Mid Holocene; LH, Late Holocene. Note the differentiation of upland and lowland sites after *c.* 8000 cal yr ʙᴘ (*c.* 8 K). (b) Taxon scores for NMS ordination.
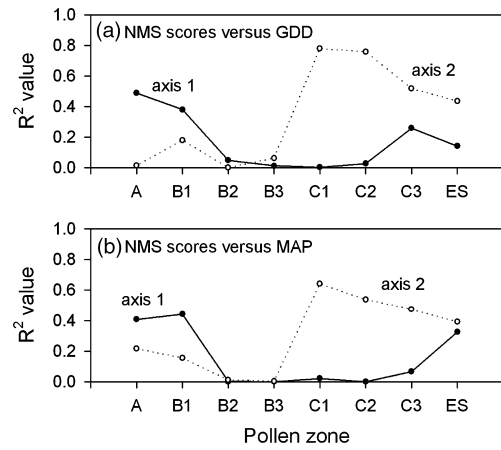
Figure 5 Plots of NMS centroids for axes 1 and 2 (same data as in Fig. 4), shown for each pollen zone. Black symbols, upland sites; grey symbols, lowland sites.

Figure 6 Regression coefficients (R^2) for the comparison of NMS axis 1 and 2 centroids for each pollen zone with (a) present-day growing degree days (GDD; 5°C base); (b) mean annual precipitation (MAP) for the eight study sites. Note the dramatic increase in strength of these relationships for axis 2 beginning in Zone C1.

because the late-Holocene rise in *Castanea* pollen percentages is greater at Rogers and Mohawk than the other lowland sites, and greater at Berry West than the other upland sites.

DISCUSSION

Early-Holocene environmental and vegetational dynamics

Relatively high-resolution analyses of the cores from Berry East, Blood and Little Royalston Ponds provide a more detailed record of early-Holocene vegetational changes than was afforded by many of the existing pollen records from the region (Davis, 1958; Whitehead, 1979; Gaudreau, 1986; but cf. Davis, 1969). As *Picea* pollen percentages declined at the beginning of the Holocene, *P. strobus* abundance increased rapidly, reaching > 50% for a period of *c.* 1000 years (Zone B1). Various palaeoclimatic proxies show rapid warming in southern New England at that time (Peteet *et al.*, 1993; Shemesh & Peteet, 1998; Huang *et al.*, 2002), while lake-level reconstructions indicate a decline in moisture balance at the end of the Younger Dryas Chronozone (Shuman *et al.*, 2001). These environmental conditions were clearly favourable to *P. strobus* (Shuman *et al.*, 2004). The rise in *Tsuga* abundance *c.* 10,500 cal yr BP, however, suggests that climate continued to change, perhaps becoming somewhat wetter given the contrasting moisture requirements of *P. strobus* and *T. canadensis* (Thompson *et al.*, 1999; Shuman *et al.*, 2004). The increase in *Tsuga* appears to have been synchronous regionally across lowland and upland sites in southern New England. A third early-Holocene vegetational phase began *c.* 9500 cal yr BP, characterized by further declines in *P. strobus*, relatively high percentages of *Quercus* pollen, minor increases in *Fagus* abundance in some records, and elevated percentages of *Ambrosia* at lowland sites, including Blood, Berry East and

slightly in the late-Holocene zones, but the previously strong relationship between NMS axis 2 and the climatic variables became weaker (Fig. 6). This change is a consequence of decreased heterogeneity in regional vegetation during the late-Holocene and European-settlement intervals due to decreasing abundance of *Fagus* and *Tsuga* at upland sites, declining percentages of *Quercus* pollen at lowland sites, and increasing percentages of *Pinus* and *Betula* at sites in both upland and lowland areas. However, at the same time that between-group similarity was increasing, within-group similarity decreased, as indicated by the widening spread of upland and lowland NMS centroids (Fig. 5). This within-group differentiation occurs

Rogers Lake. These changes coincide with particularly low lake levels in south-eastern Massachusetts (Newby *et al.*, 2000; Shuman *et al.*, 2001), suggesting that the compositional changes occurred in response to a shift to drier climatic conditions. Indeed, the relatively high pollen percentages of *Ambrosia* and other weedy taxa indicate decreased vegetation density (Davis, 1969; Faison *et al.*, 2006), which would be consistent with reduced moisture availability.

## Physiographic controls on vegetation patterns starting *c.* 9500–8000 cal yr BP

When viewed at the scale of eastern North America, late-glacial vegetation composition varied in response to broad environmental gradients. For example, higher elevations and latitudes across the Northeast generally had higher abundances of *Picea* at *c.* 12,000 cal yr BP (Gaudreau, 1988; Gaudreau *et al.*, 1989). The records examined in our study suggest that some vegetational heterogeneity existed in southern New England during the late-glacial and early-Holocene intervals, but the observed spatial patterns did not follow the continental-scale gradients. For example, late-glacial *Picea* and *Pinus* pollen percentages differ among our study sites, but *Picea* was not necessarily more abundant in the uplands. In the new records, Berry East has higher *Picea* and lower *Pinus* abundances than Blood and Little Royalston (Fig. 3). The strong relationship between the regional physiographic and vegetational gradients that we have seen in southern New England over the past *c.* 400 years (Cogbill *et al.*, 2002) did not develop until *c.* 9500–8000 cal yr BP. The compositional differences between lowland and upland sites arose at that time when increasing abundances of *Tsuga* and *Fagus* at upland sites differentiated them from the *Pinus*- and *Quercus*-dominated pollen assemblages of the lowland sites. Jackson & Whitehead (1991) described similar changes in heterogeneity of the vegetation of the Adirondack Mountains, *c.* 150 km north-west of our upland study sites. Their analyses of five pollen records from a *c.* 600-km^2 study area show that *Picea*-dominated forests extended across a *c.* 1300-m elevational gradient during the late-glacial interval. Forest zonation along that gradient, similar to that observed today, arose only after *c.* 10,000 cal yr BP. Pollen records from the White Mountains, located *c.* 200 km north of our study area, also suggest relatively homogeneous vegetation across an elevational gradient at *c.* 12,000 cal yr BP. Spear *et al.* (1994) found that *Picea* woodland occurred during the late-glacial interval at eight sites along a *c.* 1100-m elevational gradient.

Why did the vegetational gradient across southern New England, and elsewhere in the Northeast, become more fine-grained and zonal with respect to physiography at *c.* 9500–8000 cal yr BP? There are at least two explanations. First, the emergence of regional vegetational gradients may be a direct response to the development of an equivalent variation in regional climate. Shuman *et al.* (2006) present lake-sediment isotope geochemistry data indicating that climate was broadly similar across north-western and south-eastern Massachusetts

through the late-glacial and early-Holocene intervals, and diverged after *c.* 8000–7000 cal yr BP. Despite uncertainty regarding the specific mechanisms involved, it is possible that the environmental variation associated with the physiographic gradient from lowlands to uplands was muted during the interval of the Holocene when the Laurentide Ice Sheet exerted a strong influence on large-scale circulation patterns (Shuman *et al.*, 2002a).

An alternative, phytogeographical explanation is that a relatively consistent environmental gradient controlled by the regional physiography may have existed throughout the post-glacial interval, but the partitioning of this gradient by different species to form distinctive vegetation assemblages required the changes in taxa and species diversity that accompanied the late-glacial and early-Holocene shifts in environmental conditions. Under modern conditions, there is a well recognized latitudinal gradient in plant species diversity and an increasing division of environmental gradients by a larger number of vegetation assemblages from north to south (Currie & Paquin, 1987). For example, there are relatively few plant communities in north-eastern Canada compared with the increasing number of temperate forest types in New England and the Appalachians (Braun, 1950; Rowe, 1972; Foster, 1984). During the post-glacial period, New England experienced a transition from arctic to temperate conditions accompanied by associated changes in floristic composition and taxonomic diversity that parallel this latitudinal trend. Through the late-glacial and early-Holocene transitions, as the climate ameliorated from arctic to boreal and then to temperate conditions, the increasing number of species would have arranged themselves in progressively more complex vegetation patterns across relatively stationary environmental gradients. The emergence of a regional vegetational gradient in southern New England may be a manifestation of the increasing number of species and more finely divided resource gradient.

For example, *Picea* was the dominant taxon across upland and lowland sites during the late-glacial interval, in the same manner that today it dominates a broad environmental complex (temperature, moisture and edaphic conditions) in a limited number of species-poor vegetation types in subarctic and boreal regions (Foster, 1984). At *c.* 8000 cal yr BP, moisture increased under relatively warm conditions in southern New England (Shuman *et al.*, 2001, 2006) and a more complex vegetational pattern developed. The upland and lowland areas became distinct bioclimatic zones, with *Tsuga* and *Fagus* occurring in the cool, moist uplands and *Pinus*, *Quercus* and *Carya* dominating the warmer, drier, and perhaps more fire-prone lowlands (Cogbill *et al.*, 2002; Parshall & Foster, 2002). The present-day environment of southern New England supports a relatively high diversity of tree species, and our eight study sites currently span an interval of the regional environmental gradient where there is a transition between vegetation types (Fig. 7). For example, the upland sites occur in that interval of the GDD gradient where *Tsuga* and *Fagus* are abundant, whereas the lowland sites are located across the
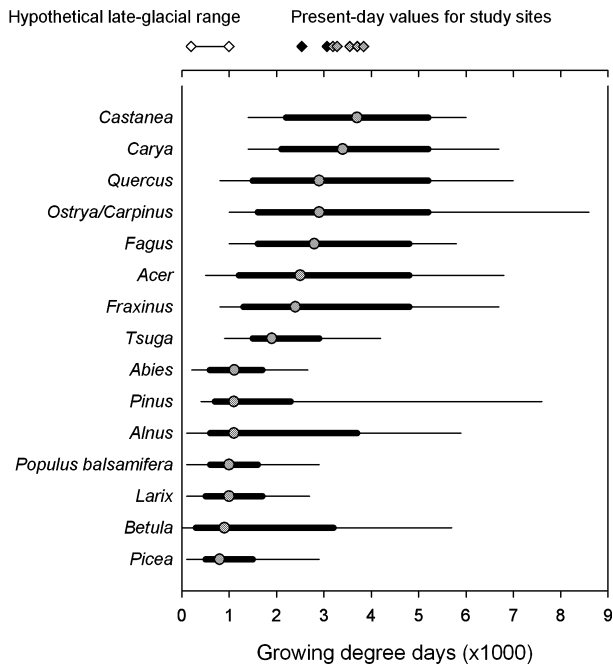
Figure 7 Growing degree day (GDD; 5°C base) ranges of selected taxa (Thompson *et al.*, 1999). For *Abies*, *Acer*, *Alnus*, *Fraxinus*, *Quercus*, *Pinus*, *Picea* and *Tsuga*, the range represents only those species from eastern North America. Climate data are not available at genus level for *Populus*, so *Populus balsamifera* is shown as an example but other *Populus* species may have been present. Thin line, entire range; thick line, 10–90% of distribution; circle, median value. Also shown are present-day GDD values for the eight study sites (black symbols, upland sites; grey symbols, lowland sites) and the hypothetical GDD range of the study area during the *Picea*-dominated late-glacial interval (width of 800 GDD corresponds to the difference between the average GDD of upland and lowland sites).

GDD values where other taxa (e.g. *Carya*) are abundant. However, under colder climatic conditions, like the late-glacial interval, *Picea* might dominate a similar range of GDD, but in a section of the gradient where the diversity of trees is lower (Fig. 7).

We have not conducted a systematic analysis of the relationship between palynological richness and species richness for the flora of eastern North America (Odgaard, 1999). However, the number of pollen types (tree taxa occurring at > 2%) does increase between Zones B and C (Fig. 3) coincident with the emergence of the physiographic differentiation of vegetation patterns. Similar trends in taxonomic diversity are observed across the boreal-to-temperate transition in other post-glacial records (Davis, 1969), paralleling modern biogeographical patterns (Currie & Paquin, 1987). Under this interpretation, fine-resolution regional palaeoecological studies provide a means of observing phytogeographical processes unfold within a spatially constrained observation window in which physiographic gradients, edaphic variations and most other physical environmental factors are held nearly constant. As the regional climate and the pool of available species change within this observational window, we can observe how they interact to form varying patterns of vegetation over time. This perspective provides an opportunity to test phytogeographical assertions and to document temporal changes in important ecological processes.

Spatial patterns of vegetation since 8000 cal yr BP

The compositional differences between the upland and lowland sites have remained in place since the onset of moister conditions *c.* 8000 cal yr BP (Shuman *et al.*, 2002a), including during the mid-Holocene *Tsuga* decline (Allison *et al.*, 1986; Foster *et al.*, 2006). In general, mid- to late-Holocene assemblages for upland sites had relatively high percentages of *Tsuga* and *Fagus* pollen, while lowland sites remained dominated by *Quercus*. However, the heterogeneity of vegetation both within and between the upland and lowland vegetation types appears to have varied since *c.* 8000 cal yr BP, as evidenced by the changing positions of the study sites relative to one another in NMS ordination space (Fig. 5). Compositional differences within these groups appear to have increased since *c.* 3000 cal yr BP, in part caused by the uneven expansion of *Castanea* across the region. Its pollen percentage values since *c.* 3000 cal yr BP are higher at the sites in the southern and western portions of the study area (Rogers, Mohawk and Berry West) than at the sites in eastern and north-central Massachusetts. This pattern is consistent with the findings of surveys of pre-settlement forest composition (Cogbill *et al.*, 2002; Hall *et al.*, 2002), which indicate that *Castanea* abundance did not vary along the main regional climatic gradient. The increasing similarity between upland and lowland vegetation types before and during the interval of European settlement is also consistent with other lines of evidence. Pollen records and witness-tree data from New England, as well as pollen data from the Upper Midwest, show a general homogenization of regional vegetation patterns resulting from late-Holocene declines in *Tsuga* and *Fagus* abundance, forest clearance during the era of European settlement, and ongoing disturbances (Webb, 1973; Russell *et al.*, 1993; Foster *et al.*, 1998; Fuller *et al.*, 1998; Russell & Davis, 2001). This suggests that broad-scale similarities in land use and post-settlement forest dynamics mask the environmental gradient that has controlled regional vegetation patterns during much of the Holocene.

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BIOSKETCHES

W. Wyatt Oswald is a palaeoecologist at the Harvard Forest. His research interests include palynology, plant community ecology, and the application of historical ecology to conservation and ecosystem management.

Edward K. Faison is a research assistant at the Harvard Forest. His interests range from palaeoecology to wildlife impacts on New England vegetation.

David R. Foster, Director of the Harvard Forest, is an ecologist and palaeoecologist interested in long-term vegetation dynamics and the conservation of dynamic landscapes.

Elaine D. Doughty is a research assistant at the Harvard Forest working on lake-sediment records from New England.

Brian R. Hall is a research assistant at the Harvard Forest specializing in GIS-based analysis and data presentation.

Barbara C.S. Hansen, Research Associate at the Limnological Research Center at the University of Minnesota, is a palynologist with experience working on records from the Americas and Asia.

Editor: Mark Bush