

Short Paper

A late-glacial transition from *Picea glauca* to *Picea mariana* in southern New England

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Abstract

Picea is an important taxon in late-glacial pollen records from eastern North America, but little is known about which species of *Picea* were present. We apply a recently developed palynological method for discriminating the three *Picea* species in eastern North America to three records from New England. *Picea glauca* was dominant at ~14,500–14,000 cal yr BP, followed by a transition to *Picea mariana* between ~14,000 and 13,500 cal yr BP. Comparison of the pollen data with hydrogen isotope data shows clearly that this transition began before the beginning of the Younger Dryas Chronozone. The ecological changes of the late-glacial interval were not a simple oscillation in the position of a single species' range, but rather major changes in vegetation structure and composition occurring during an interval of variations in several environmental factors, including climate, edaphic conditions, and atmospheric CO₂ levels.

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Introduction

Picea (spruce) was a dominant taxon in eastern North America during the transition from the Pleistocene to the Holocene (e.g., Watts, 1979; Davis, 1983; Davis and Jacobson, 1985; Jackson et al., 1997). In late-glacial lake sediments from New England, for example, *Picea* pollen percentages reached ~20–80% between ~16,000 and 11,000 calibrated ¹⁴C yr before present (cal yr BP) (e.g., Davis, 1969; Davis et al., 1975; Whitehead, 1979; Spear et al., 1994; Shuman et al., 2004). Paleoclimatic evidence suggests that abrupt climate fluctuations occurred during the late-glacial interval in the region (e.g., Levesque et al., 1993; Peteet et al., 1993; Shemesh and Peteet, 1998; Shuman et al., 2001; Hou et al., 2006), and pollen data indicate that the location and abundance of *Picea* varied in response to those changes (e.g., Shuman et al., 2002).

Despite the prevalence of *Picea* in New England during the late-glacial interval and its importance in interpreting the environmental changes of that period (Peteet et al., 1993; Newby et al., 2000; Shuman et al., 2002; 2004) we do not know which species of *Picea* were involved. Davis (1958) speculated that southern New England may have experienced a shift from either *Picea glauca* (white spruce) or *Picea rubens* (red spruce) to *Picea mariana* (black spruce), but that hypothesis has not been tested using quantitative palynological techniques and cannot be addressed by the limited available macrofossil evidence (Terasmae and Matthews, 1980; Anderson et al., 1990; Jackson et al., 1997).

Studies of the palynological differences among *Picea* species have been conducted for various regions of North America (Cain, 1948; Richard, 1970; Bagnell, 1975; Birks and Peglar, 1980; Hansen and Engstrom, 1985; Brubaker et al., 1987). Lindbladh et al. (2002) developed a method for differentiating pollen grains of the three *Picea* species in eastern North America (*P. glauca*, *P. mariana* and *P. rubens*), using a large

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reference collection of modern pollen from the region. A pilot study in Maine and Massachusetts applied the technique to fossil pollen at eleven levels of varying age from nine sites (Lindbladh et al., 2003). Here we apply the method for the first time to sequences of late-glacial sediment cores. We investigate three sites in southern New England, with the goal of interpreting the ecological and environmental changes of the late-glacial interval.

Methods

We applied the technique of Lindbladh et al. (2002) to lake-sediment pollen samples from three sites in Massachusetts: Blood Pond (BP), Berry East Pond (BEP), and Black Gum Swamp (BGS) (Fig. 1) (Table 1). Field methods, laboratory techniques, and dating results for Blood Pond and Berry East Pond are available elsewhere (Oswald et al., in press). We collected a core from Black Gum Swamp in April 2004 using a modified Livingstone piston sampler (Wright et al., 1984). The core was extruded in the field, wrapped in plastic and aluminum foil, and subsequently refrigerated.

Chronological control for the Black Gum Swamp core is provided by accelerator mass spectrometry (AMS) ^{14}C analysis of plant macrofossils sieved from the sediment (Table 2). ^{14}C dates were converted to calibrated ages using OxCal 3.9 (Bronk Ramsey, 1995, 2001). The age–depth model is based on linear interpolation between the midpoints of the 2σ calibrated age ranges of selected dates. Samples of 1 cm^3 were prepared for pollen analysis following standard procedures (Faegri and Iversen, 1989), with *Lycopodium clavatum* spores ($42,716$ per cm^3) added to allow estimation of pollen concentrations and influx rates (Stockmar, 1971). For all three sites, influx and concentration values (the latter not shown) had very similar patterns. Pollen residues were mounted in silicone oil, and pollen grains and spores were counted at $\times 400$ magnification. A minimum of 300 pollen grains and spores from upland taxa were identified for each level, and all percentages are expressed relative to that sum.

At each level where *Picea* pollen percentages exceeded 5%, thirty *Picea* grains were examined for species identification, with the exception of three levels with very low pollen concentrations (BGS 422 cm; BE 1030 and 1230 cm). All measurements were made by one individual (M. Lindbladh).

Table 1

Locations and characteristics of the study sites

	Berry East Pond	Blood Pond	Black Gum Swamp
Latitude	42°37' 13" N	42°04' 48" N	42°32' 30" N
Longitude	71°05' 14" W	71°57' 41" W	72°11' 30" W
Elevation (m)	43	214	358
Surface area (ha)	1.6	8.5	10.0
Maximum depth (m)	5.9	3.6	0.0 ^a
Core interval analyzed (cm)	1250–950	1360–885	420–275

^a Lacustrine sediments at Black Gum Swamp are overlain by a forested peatland (Foster and Zebryk, 1993; Anderson et al., 2003).

Only grains that were unbroken, symmetrical, and fully expanded in equatorial view were analyzed. Sand grains (50–100 μm) were added to the slides to avoid the flattening of the pollen grains by the cover slip (Cushing, 1961). Three quantitative (total grain size, corpus breadth, and saccus width at the base) and two qualitative (cap undulation, exine verrucation) variables were measured on each grain. The measurements were applied to a classification tree analysis (CART) procedure based on measurements of modern *Picea* pollen grains from the three *Picea* species of eastern North America: *P. glauca*, *P. mariana*, and *P. rubens* (Lindbladh et al., 2002). We examined a total of 1196 fossil *Picea* grains, and of those 840 were identified to species (70.2% identification rate). The 356 unidentified grains had intermediate characteristics; we assume that they were proportionally distributed among the identified species. Of the unidentified grains, only eight were equivocally identified (i.e. classified to more than one species). This low number of equivocally identified grains implies that the classification system is robust and conservative. A more detailed discussion of the modern pollen dataset and CART methodology is presented in Lindbladh et al. (2002).

We identified pollen zone boundaries for each site by clustering the pollen spectra using the constrained incremental sum of squares (CONISS) method on square-root transformed pollen percentages (Grimm, 1987). Taxa included in the analysis included *Abies*, *Acer*, *Alnus*, *Artemisia*, Asteraceae, *Betula*, Cupressaceae, Cyperaceae, Ericaceae, *Larix*, *Myrica/Comptonia*, *Ostrya/Carpinus*, *P. glauca*, *P. mariana*, *P. rubens*, Poaceae, *Populus*, *Quercus*, *Salix*, and *Tsuga*. We also compared vegetation changes at the three sites using detrended

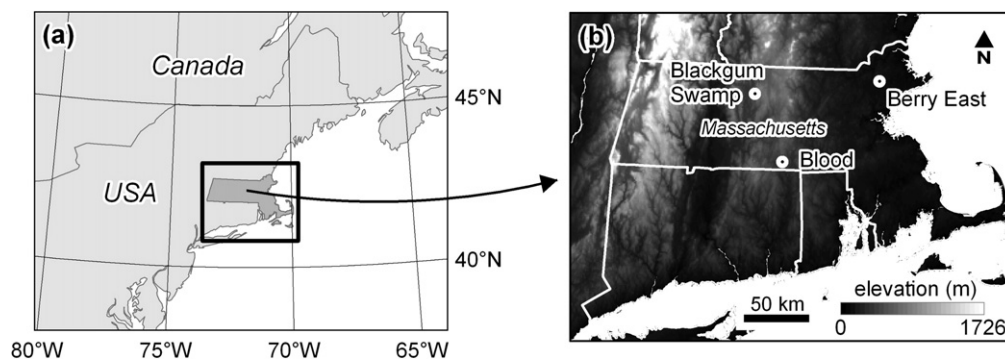


Figure 1. (a) Map of eastern North America showing study area (Massachusetts is highlighted). (b) Topographic map of southern New England showing study sites.

Table 2
Radiocarbon results for Black Gum Swamp

Depth (cm)	Material	Lab number	$\delta^{13}\text{C}$	^{14}C yr (BP)	2σ cal age range
294–296	Seeds	Beta-192018	-23.9	9580±50	11,139–10,729
352–354 ^a	Plant fragments	Beta-192019	-27.0	2130±40	2302–1989
403–404	Plant fragments	Beta-192020	-24.4	12,190±60	14,199–13,869

^a Excluded from age-depth model.

correspondence analysis (DCA) of all pollen spectra combined, using the same taxa as in the zonation.

Results

Quantitative zonation of the pollen records using CONISS resulted in three zones for each site (Figs. 2 and 3). The pollen spectra for each zone are similar for the three sites, but the timing of the zone boundaries differs somewhat between sites. The lack of strong chronological control makes it difficult to say whether the asynchrony is real, but given the proximity of the sites it also seems possible that the changes actually took place

synchronously. The general timing of the changes in *Picea* pollen percentages is consistent with several other studies in the region (e.g., Newby et al., 2000). Furthermore, the position of the Younger Dryas Chronozone (YDC) in the Blood Pond record, as revealed by isotope geochemical analyses (Hou et al., 2006), provides temporal context for that record and shows that its age-depth model is reasonable (Fig. 4).

Picea pollen reaches ~40% in Zone 1 at all three sites, and most of the *Picea* grains are *P. glauca*. Other common taxa include *Betula*, *Pinus* (mainly *P. banksiana*-type), *Salix*, and *Populus*. Low total pollen influx values and relatively high pollen percentages of Cyperaceae, Poaceae, and other herbaceous taxa

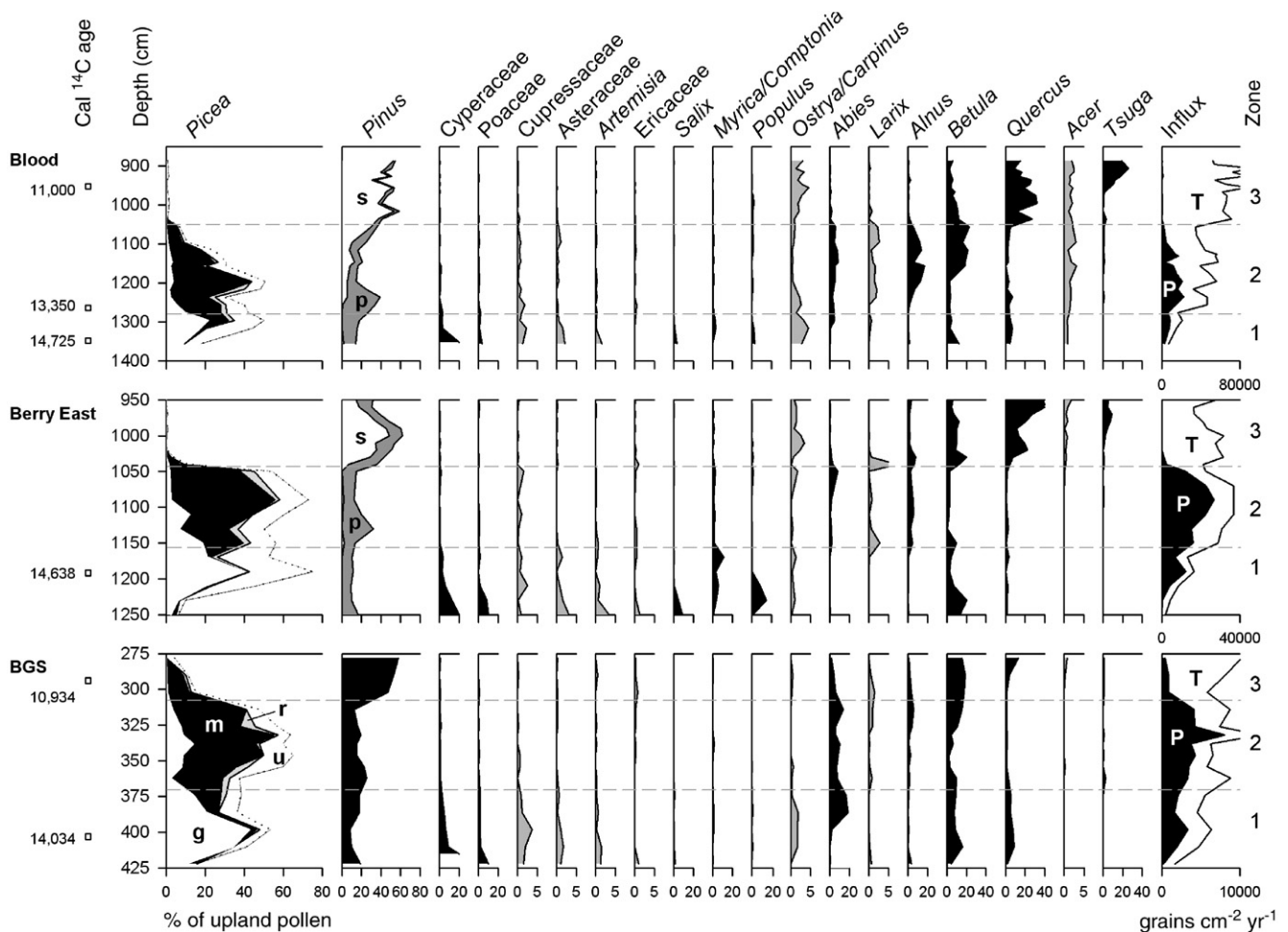


Figure 2. Pollen diagrams for Blood Pond, Berry East Pond, and Black Gum Swamp (BGS). *Picea* graphs show percentages of individual species. See BGS graph for key: g=*Picea glauca* (white fill); m=*Picea mariana* (black fill); r=*Picea rubra* (gray fill); u=undifferentiated *Picea* (dotted line). *Pinus* pollen grains were differentiated for Blood and Berry East: p=*Pinus* subgenus *Pinus*; s=*Pinus* subgenus *Strobus*. Influx graphs show values for *Picea* (P; black fill) and total upland pollen (T; white fill). Note change in x-axis range for major (black fill) and minor taxa (gray fill). The ^{14}C dates shown are the midpoints of the 2σ calibrated age ranges in yr BP.

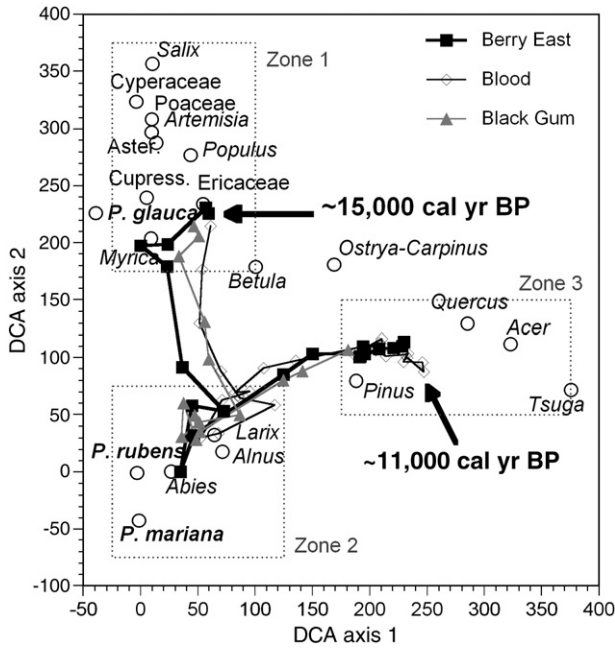


Figure 3. Results of detrended correspondence analysis (DCA) of pollen data from Blood Pond, Berry East Pond, and Black Gum Swamp. The variance explained by the ordination axes was determined by calculating the coefficient of determination between Relative Euclidian Distances in the ordination space and the original *n*-dimensional space: r^2 values for axis 1 and 2 were 0.42 and 0.40, respectively.

suggest a relatively open *P. glauca* forest. Very few *Picea* grains were identified as *P. rubens* in this and subsequent zones.

Zone 2 assemblages are also dominated by *Picea* pollen (~50–70%), and the dominant species after ~14,000–13,000 cal yr BP is *P. mariana*. Total and *Picea* influx values increase in this zone, particularly at Blood and Berry East. Pollen percentages for *Alnus*, *Betula*, *Abies*, and *Larix* are generally higher in Zone 2, and herbaceous taxa are less abundant than in the previous zone. *Pinus* (still *Pinus banksiana*-type) percentages remain relatively high, particularly at the beginning of the zone. These results suggest a change to a denser forest featuring *P. mariana* and other boreal trees and shrubs.

Picea pollen percentages decline at the beginning of Zone 3 (~11,500 cal yr BP), and *Quercus*, *Pinus* (mainly *P. strobus*-type), *Betula*, *Tsuga*, and *Ostrya/Carpinus* increase sharply. We interpret these changes as a shift from *P. mariana*-dominated forest to a Holocene community with a mix of deciduous and coniferous trees.

Discussion

Late-glacial environmental and ecological dynamics

At all three sites we documented two late-glacial peaks in *Picea* pollen abundance, as has been observed in other records in the region (e.g., Suter, 1985; Shuman et al., 2001). Moreover, by applying the Lindbladh et al. (2002) *Picea* pollen discrimination method to these records, we revealed that the first peak was dominated by *P. glauca*, while the second

featured *P. mariana*. This is the first compelling evidence for a late-glacial shift in dominance from *P. glauca* to *P. mariana* in New England, supporting and refining the hypothesis proposed by Davis (1958). Furthermore, the transition from *P. glauca* to *P. mariana* is accompanied by other changes in vegetation composition and structure (Figs. 2 and 3). The interval of *P. glauca* dominance featured relatively high pollen percentages of several herbaceous taxa (e.g., Cyperaceae and Poaceae) and relatively low pollen influx values, whereas the *P. mariana* zone had higher influx values and taxa characteristic of present-

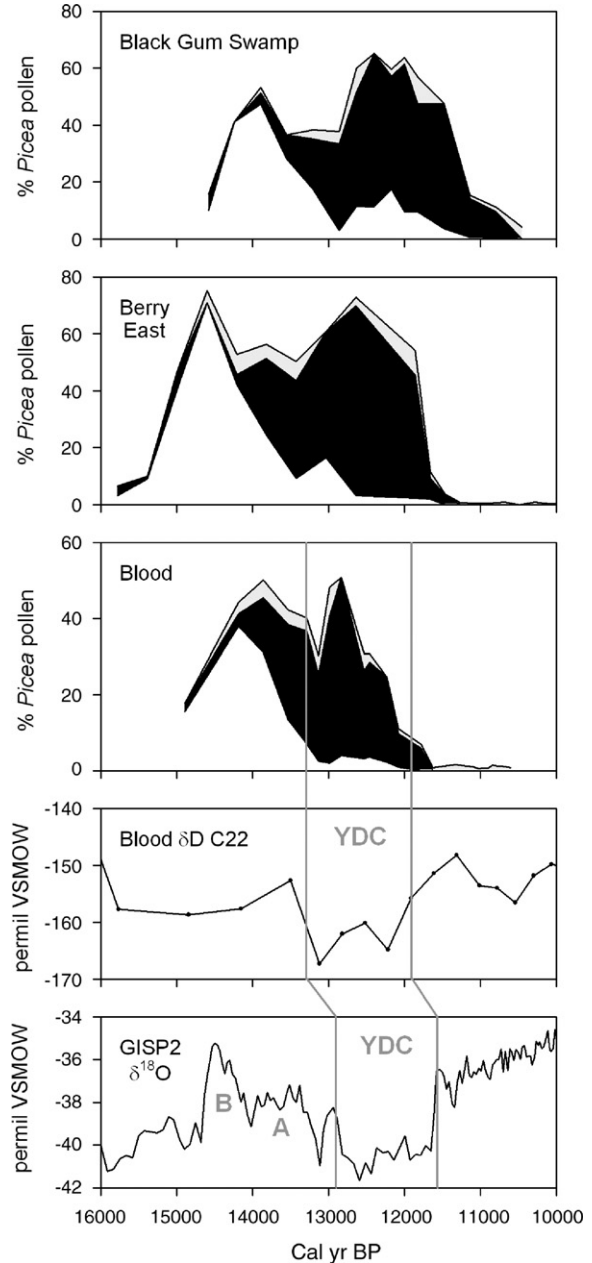


Figure 4. Summary of late-glacial changes in climate and vegetation. *Picea* pollen percentages for Black Gum Swamp, Berry East Pond, and Blood Pond (*Picea glauca*=white fill, *Picea mariana*=black fill; *Picea rubens*=gray fill); Hydrogen isotope ratios for Blood Pond (Hou et al., 2006); Oxygen isotope data from the GISP2 Greenland ice core (Stuiver et al., 1995): B=Bølling; A=Allerød; YDC=Younger Dryas chronozone.

day boreal forests (e.g., *Larix*, *Abies*, and *Alnus*). The decline in herbaceous taxa after the first *Picea* peak also appears in other records from the region (e.g., Peteet et al., 1993; Newby et al., 2000; Shuman et al., 2001). These changes suggest a transition at ~14,000–13,000 cal yr BP from open *P. glauca* forest-tundra to closed forest dominated by *P. mariana*.

The observed late-glacial vegetation dynamics, including the shift from *P. glauca* to *P. mariana*, may be attributable to the sequence of environmental changes that occurred across this interval. *P. glauca* increased sharply after ~15,000 cal yr BP, reaching its highest abundances at all three sites ~14,500–14,000 cal yr BP (Fig. 4). The maximal *P. glauca* pollen percentages appear to coincide with the Bølling event documented in the Greenland ice-core record, which was the warmest period of the late-glacial interval (e.g., Björk et al., 1998; Stuiver and Grootes, 2000; Southon, 2000). The Bølling peak in warmth does not appear in the Blood Pond isotopic record (Fig. 4; Hou et al., 2006), but its absence may be due to the relatively coarse sampling resolution. Moreover, the prevalence of *P. glauca* at ~14,500–14,000 cal yr BP may also be related to the edaphic conditions occurring at that time. *P. glauca* is abundant today on coarse-textured, nutrient-rich soils (e.g., Viereck et al., 1983; 1986; Yarie, 1983; Foster, 1984, 1985), substrates that likely were common on recently deglaciated landscapes in southern New England (e.g., Miller, 1980, 1987). This combination of relatively warm climate and well-drained soils may have allowed *P. glauca* to dominate during the early portion of the *Picea* interval.

At all three sites the transition from *P. glauca* to *P. mariana* begins ~14,000–13,500 cal yr BP, and comparison of the pollen and geochemical data from Blood Pond shows clearly that the shift began before the beginning of the YDC (Fig. 4). This result indicates that for the dominant tree genus in the region during the late glacial, *Picea*, the dynamics were not necessarily linked to the climate fluctuations of the YDC, as suggested by Shuman et al. (2002). On the other hand, the timing of this shift is consistent with the findings of a study by Viau et al. (2002), which identified a significant change in vegetation composition across North America at 13,800 cal yr BP. The decline in *P. glauca* and increase in *P. mariana* may have taken place in response to cooling that occurred across the North Atlantic during the Allerød period (e.g., Björk et al., 1998; Stuiver and Grootes, 2000; Southon, 2000). Cooler conditions would have promoted permafrost aggradation, leading to soil paludification and nutrient leaching (e.g., Klinger, 1996; Young et al., 1997). This type of progressive change in edaphic conditions would lead to a change from *P. glauca* to *P. mariana*, as *P. mariana* currently dominates in areas of wet, acidic, nutrient-poor soils (e.g., Viereck et al., 1983; 1986; Yarie, 1983; Foster, 1984; 1985). Subsequent changes in the environment during the YDC may have furthered the shift from *P. glauca* to *P. mariana*. Various lines of evidence indicate cold, moist conditions in eastern North America during the YDC (Levesque et al., 1993; Peteet et al., 1993; Cwynar and Levesque, 1995; Shemesh and Peteet, 1998; Shuman et al., 2001; Huang et al., 2002), and cooling may have accentuated the development of permafrost. This would have led to a further reduction in the availability of

the well-drained, nutrient-rich soils preferred by *P. glauca* and an increase in the extent of wet, acidic soils dominated by *P. mariana* (e.g., Viereck et al., 1986).

However, the hypothesis that these late-glacial ecological dynamics were initiated by cooling during the Allerød period is inconsistent with the paleoclimatic data that currently exist for the region. For example, no such cooling is evident in the Blood Pond geochemical data (Fig. 4) or in another isotopic record from southeastern Massachusetts (Huang et al., 2002). Likewise, chironomid data from the region indicate increasing temperatures throughout the late-glacial interval and warm conditions immediately before the YDC, rather than a sequence of declining temperatures from the Bølling to the Allerød to the YDC (e.g., Cwynar and Levesque, 1995).

An alternative explanation for the transition from *P. mariana* to *P. glauca* is that the shift was related to changes in atmospheric CO₂ levels. The ecological dynamics described in this study occurred during the most dramatic rise in CO₂ levels of the late Quaternary. Atmospheric CO₂ levels rose from ~200 ppm at ~16,000 cal yr BP to ~265 ppm at ~11,000 cal yr BP (Monnin et al., 2001). Such a rise is potentially important because of the known effects of CO₂ levels on plant water-use efficiency (Polley et al., 1993). *P. glauca* would likely have been more tolerant than *P. mariana* of moisture stress induced by low water-use efficiency when CO₂ levels were low, and thus *P. mariana* would have experienced a reduction in moisture stress as CO₂ levels rose through the late-glacial interval. Indeed, the shift from *P. glauca* to *P. mariana* precedes the abrupt climate change at the beginning of the YDC, but coincides closely with a rapid rise in CO₂ levels occurring between ~14,000 and 13,700 cal yr BP. Average CO₂ concentrations were ~225 ppm from 15,000 to 14,000 cal yr BP, and rose to ~240 ppm during the period from 14,000 to 11,600 cal yr BP (Monnin et al., 2001).

With the available data we are unable to assess the relative importance of changes in climate, substrate, and the composition of the atmosphere as drivers of the observed changes in vegetation composition and structure. However, it is possible that the shift from *P. glauca* to *P. mariana* resulted from the combined effects of late-glacial environmental change, its impacts on soil moisture, and the relatively gradual increase in CO₂ during the transition from the Pleistocene to the Holocene. This uncertainty about the mechanism notwithstanding, our results confirm that the environmental dynamics of the late-glacial interval were not a simple oscillation in temperature (Shuman et al., 2002) and show clearly that the ecological response was not a simple oscillation in the position of a single species' range. These findings highlight the critical importance of taxonomic resolution in reconstructions of vegetation and climate, and also illustrate the complex nature of environmental and ecological changes in southern New England during the late-glacial period.

The history of Picea rubens

This study supports the conclusions of Lindbladh et al. (2003) that *P. rubens* was uncommon or absent in New England

during the late-glacial and early-Holocene intervals. Very few *Picea* grains were classified as *P. rubens*, with the highest value (7.7%) occurring at ~12,000 cal yr BP in the Berry East record. Our studies of modern pollen indicate that grains of *P. mariana* are more likely than *P. glauca* to be misclassified as *P. rubens* (Lindbladh et al., 2002). The few grains classified as *P. rubens* in this study occurred almost exclusively when *P. mariana* was common, which suggests that the *P. rubens* grains may actually have been *P. mariana*. Consequently, the question of where *P. rubens* existed during the late-glacial interval remains to be answered. The only relevant evidence comes from two sites in southern Pennsylvania and western Virginia where Watts (1979) used the morphological approach of Birks and Peglar (1980) to identify some *Picea* pollen as *P. rubens* during the late-glacial and early-Holocene intervals. Additional palynological research in that region is needed to clarify the history of *P. rubens*.

Picea in New England during the Holocene

Picea was absent or very rare in southern New England for most of the Holocene. At the end of the YDC, the precession-driven maximum in summer solar radiation produced a climate characterized by greater seasonality and warmer growing seasons than today (e.g., Davis et al., 1980; Webb et al., 1993; Almquist et al., 2001). Vegetation changes at that time were rapid and synchronous across eastern North America (e.g., Jacobson et al., 1987; Viau et al., 2002; Shuman et al., 2002, 2004). Paleoclimatic data from New England and elsewhere (e.g., Stuiver et al., 1995; Huang et al., 2002; Hou et al., 2006) show a dramatic increase in temperature coincident with the decline in *Picea* and the corresponding increase in relatively thermophilous tree genera such as *Quercus* and *Tsuga* (Figs. 2 and 4). The decline in *P. mariana* may also have been associated with dry conditions, as lake-level reconstructions suggest that the beginning of the Holocene was the driest period of the last 13,000 yr (Shuman et al., 2001, 2004).

Picea pollen percentages remained low for much of the Holocene, but increased during the past ~2000 yr, apparently in response to the onset of cooler and moister conditions (e.g., Davis et al., 1980; Foster and Zebryk, 1993; Schaffler and Jacobson, 2002; Shuman et al., 2004). Today *P. glauca* is absent from southern New England, while *P. rubens* and *P. mariana* are present at low abundances. Both occur in areas of moist, acidic soils, with *P. mariana* associated with extremely nutrient-poor and ombrotrophic conditions and *P. rubens* preferring sites with somewhat higher nutrient availability (e.g., Anderson et al., 2003). Late-Holocene environmental and ecological changes in New England, including the recent histories of *P. rubens* and *P. mariana*, await further study.

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