Persistence of coastal spruce refugia during the Holocene in northern New England, USA, detected by stand-scale pollen stratigraphies

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Summary

1 Pollen data from wet, forested hollows in five spruce (Picea) stands on the eastern coast of Maine, USA, reveal that spruce has been well-established (spruce pollen > 6%) for at least 5000 years at four of the sites (Isle au Haut, Schoodic Peninsula, and Roque Island). Spruce became dominant in the fifth stand (Blackwoods, Mount Desert Island) only in the last 2000 years. This is in contrast to pollen stratigraphies from two inland forest hollows and from inland lakes that indicate a significant region-wide increase in the abundance of spruce only 1000 years ago.

2 All five coastal pollen stratigraphies suggest that conditions along the east coast of Maine became cooler and moister sometime between 6000 and 5000 years ago. Mid-Holocene changes in vegetation and sediment accumulation correspond with the timing of rapid increases in tidal amplitude and diurnal mixing of cold water in the Gulf of Maine, suggestive that these resulted in increased marine effects on the local climate at a time that was generally warmer than present.

3 Two inland forest-hollow stratigraphies do not show evidence of mid-Holocene cooling. Coastal effects therefore persisted for several thousand years despite regional climate changes.

4 The pollen data suggest that refugia along the coast (and probably in isolated sites inland), may have played a critical role in allowing the rapid regional expansion of spruce around 1000 years ago. The steep increases in the abundance of spruce pollen in all forest-hollow and lake pollen stratigraphies in northern New England at that time corroborate other evidence of a region-wide shift to cooler and moister conditions.

5 Pollen stratigraphies from small forested hollows provide a means to examine local vegetation dynamics and interpret those dynamics in the context of regional signals.

Key-words: climate change, forest hollows, Gulf of Maine, palaeoecology, spruce–fir forests

Introduction

Palaeoecological evidence from north-eastern North America has shown that the last millennium was a time of rapid vegetation change throughout the region (Jacobson et al. 1987; Gajewski 1988; Webb et al. 1993; Davis et al. 1980). One of the most notable of these changes is a large increase – as much as four-fold – in the amount of spruce (Picea spp.) between 1000 and 500 years ago. Pollen stratigraphies from lakes across northern New England and the Midwest indicate that for most of the Holocene, the north-eastern forests were dominated by changing assemblages of pine (Pinus spp.), hemlock (Tsuga canadensis (L.) Carrière) and hardwoods, with only small amounts of spruce. Spruce pollen percentages at these sites often begin to rise steeply around 1000 years ago (Fig. 1) but do not reach modern proportions until a few centuries before European settlement.

This recent expansion of the southernmost populations of spruce in North America accompanied a...
climate cooling on the order of 1 °C or less during the last millennium, and a longer-term cooling of approximately 2 °C and moistening since the mid-Holocene (Davis et al., 1980; Gajewski 1988; Almquist et al., 2001, and others). This cooling trend during the last half of the Holocene is also evident in European pollen data and was at least hemispheric in extent (Huntley & Prentice 1988). Spruce (Picea rubens, P. glauca, P. mariana) is favoured by cool and moist growing seasons, and, in association with fir (Abies balsamea), expanded rapidly to its present-day range. This extends across the northern part of Maine and along its eastern and middle
Persistence of coastal spruce refugia

coast, reaching farthest south in high-altitude sites along the western and central mountains (Davis 1966; Seymour 1992) (Fig. 2), where growing seasons are cooler and moister than in interior lowlands away from the cold tidal waters of the Gulf of Maine. In fact, the range for spruce–fir forests in northern New England follows the boundaries of a hook-shaped regional transition zone between temperate and northern vegetation types formed by a cluster of northern or southern range limits for more than 60 woody taxa of these cooler regions (McMahon 1990) (Fig. 2).

During the warmer middle Holocene, this regional-scale transition zone, and in particular the distribution of spruce-dominated forests, may have assumed a different position (and possibly a different shape). An isopoll map constructed from data stored in the North American Pollen Database (available electronically from NGDC, NOAA; Boulder, CO) shows the broad-scale spatial expansion of the southern populations of spruce in the Great Lakes–Maritimes region within the last millennium (Fig. 3). The map is based on a collation of fossil spruce-pollen records in lake and peat sediments from 289 sites in north-eastern North America, and provides a regional overview of spatial changes in the abundance of spruce during the last 3000 years in 250-year time-steps (Schaufler 1998). The rapid expansion of spruce around 1000 years ago is remarkable because it apparently occurred across a wide region within just a few centuries, i.e. within one or two generations.

Regional pollen records from lakes do not have sufficient spatial resolution to describe the long-term vegetation changes that occur locally within the transition zone and help define its position and shape. Here we examine local pollen records from forested hollows in coastal and inland sites in Maine and contrast and compare them with regional pollen records to refine further the interpretation of vegetation dynamics across a region during times of changing climate. Several studies have used forest-hollow pollen stratigraphies to reconstruct local ecological processes and land-use changes over time (Björkman 1996; Lagerås 1996; Davis et al. 1998; others) but few of these local reconstructions have been assessed in a regional palaeoecological context.

The two types of pollen data represent vegetation dynamics at different scales and comparisons between them can reveal much about the regional significance.
of local processes such as fire and other disturbances (Lindbladh, Bradshaw & Holmqvist 2000).

How did a relatively uncommon species in northern New England (e.g. spruce) increase so rapidly and widely with climate change? Were there many small but ecologically significant populations of spruce scattered over the landscape that allowed such a rapid expansion? If such refugia populations of spruce existed, how may they have been distributed on the landscape and to what extent have they escaped detection in the regional pollen records based on lake sediments? We selected five forest-hollow sites in red spruce stands along the eastern coast of Maine and two inland forest-hollow sites in spruce–fir stands in north-central Maine to reconstruct the local vegetation history at each site through analysis of fossil pollen and charcoal in sediments.

We investigated how long-term changes in the intensity of the marine influences might have an impact on terrestrial ecosystems during a time of regional climate change;

1. investigate how long-term changes in the intensity of the marine influences might have an impact on terrestrial ecosystems during a time of regional climate change;

2. compare and contrast evidence of local vegetation dynamics with regionally observed signals, and;

3. discuss insights gained from local pollen records about possible mechanisms for the rapid expansion of spruce in the region between 1000 and 750 years ago.

Materials and methods

Stand-scale vegetation dynamics can be identified by analyses of fossil pollen deposited in wet depressions within the forest (Bradshaw 1988). These forested depressions are from one to several tens of metres in radius, are under a closed canopy and are often positioned between shallow granite bedrock outcroppings or low rises with thin upland soils. Although the surface may appear dry in summer and autumn, trapped drainage and the absorbent organic material keep the underlying sediments dry in summer and autumn, trapped drainage and the absorbent organic material keep the underlying sediments are preserved stratigraphically for thousands of years.

Roughly half of the pollen deposited in wet depressions under a closed canopy comes from local sources (from within 50 m to a few hundred metres at most, depending on forest type and canopy structure), a proportion considered sufficient to describe changes in dominant taxa in the stand over time (Jackson & Wong 1994, Calcote 1995, 1998; Sugita 1995).

Table 1 Site characteristics for the seven forest-hollow sites in northern New England. Size refers to the rough dimensions of the contiguous wet depression from which the core was taken. The depth is the depth of the depression where the core was sampled.

<table>
<thead>
<tr>
<th>Site</th>
<th>Size (m)</th>
<th>Depth (cm)</th>
<th>Altitude (m a.s.l.)</th>
<th>Ground cover</th>
<th>Modern forest type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coastal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isle au Haut, north</td>
<td>5 × 15</td>
<td>68</td>
<td>80</td>
<td>Sphagnum, Carex</td>
<td>Red spruce</td>
</tr>
<tr>
<td>Isle au Haut, south</td>
<td>5 × 10</td>
<td>46</td>
<td>70</td>
<td>Sphagnum</td>
<td>Red spruce, red maple, pitch pine</td>
</tr>
<tr>
<td>Blackwoods</td>
<td>60 × 40</td>
<td>179</td>
<td>20</td>
<td>Sphagnum, Carex</td>
<td>Red spruce</td>
</tr>
<tr>
<td>Schoodic</td>
<td>10 × 30</td>
<td>66</td>
<td>10</td>
<td>Sphagnum</td>
<td>Red spruce, red cedar, fir</td>
</tr>
<tr>
<td>Roque Island</td>
<td>60 × 15</td>
<td>113</td>
<td>20</td>
<td>Sphagnum, Carex</td>
<td>Red spruce</td>
</tr>
<tr>
<td>Inland</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Big Reed Pond Hollow</td>
<td>15 × 40</td>
<td>56</td>
<td>370</td>
<td>Sphagnum, Carex</td>
<td>Spruce–fir, red cedar, mixed hardwood</td>
</tr>
<tr>
<td>Buckley Pond Hollow</td>
<td>1 × 2</td>
<td>82</td>
<td>360</td>
<td>Sphagnum</td>
<td>Spruce–fir, red cedar, mixed hardwood</td>
</tr>
</tbody>
</table>

SELECTION AND DESCRIPTIONS OF SITES

The hollows selected all have organic sediment 0.5 and 2.0 m deep, are free of large roots and stones, and have basal deposits between 4500 and 11 000 years old. They are at least 100 m from shorelines or forest edges, are on flat terrain, and are not near any apparent watercourses or seasonal flowages that would disturb the sediments. Soils are acidic and are covered by a Sphagnum carpet occasionally interspersed with sedges, grasses, and small forest herbs (Table 1). Altitudes are between 10 and 80 m above mean sea level (coastal sites) or < 360 m a.s.l. (inland).

Coastal sites

The five coastal sites are all located within 1.0 km of the saltwater shoreline (Fig. 2) and range from positions with island outer-shore exposure to the Gulf of Maine (the south end of Isle au Haut) to the leeward (east) side of Mount Desert Island (Blackwoods). The coastal stands are nearly pure red spruce (Picea rubens) with minor amounts of black and white spruce (P. mariana and P. glauca), fir (Abies balsamea), yellow birch (Betula allegheniensis), paper birch (B. papyrifera) and red maple (Acer rubrum). Although spruce and fir are typically associated with one another in Acadian forests, amounts of fir are relatively small here.

Inland sites

The five inland stands are located in Big Reed Pond Preserve (BRPP), a 1950-ha old-growth forest tract in north central Maine (Fig. 2) in the upper limits of the Aroostook River drainage. The Nature Conservancy Preserve is approximately 80 km north of Upper South Branch Pond, the nearest lake with a published regional pollen stratigraphy (Anderson et al. 1986), and approximately 250 km north-west of the coast. The two stands in
Although morphological distinctions have been described by Cronquist (1991), authorities for vascular plants follow Gleason & Cronquist (1950) (sect. Pinus). Pastoral pollen types from pollen collected only within the Acanadian region, the sole place where the three coexist (indicated by highly uniform loss on ignition curves in each case) except the bottom few centimetres in some of the cores, which contained a higher proportion of clay.

**POLLEN ANALYSIS**

For pollen analysis, 0.5 cm$^3$ of sediment was subsampled from each core at 0.5 cm intervals, except in sections of cores where pollen concentrations were predicted to be low, when 1.0 cm$^3$ was used. Subsamples were soaked in 10% KOH and sieved through 143-µm mesh; Lycopodium spore tablets were added for calculation of pollen concentration. Pollen was extracted using HF and acetylation, and then suspended in silicon oil, according to standard procedures used in the Laboratory for Palaeoecology and Paleohydrology at the University of Maine, modified from Faegri & Iversen (1989).

At least 300 terrestrial pollen grains (arboreal, shrub, and herbaceous taxa) were counted at each stratigraphic interval at 400× magnification (1000× was used for verification when necessary). The reported pollen percentages are based on the sum of terrestrial pollen and spore tablets added for calculation of pollen concentration. Pollen was extracted using HF and acetylation, and then suspended in silicon oil, according to standard procedures used in the Laboratory for Palaeoecology and Paleohydrology at the University of Maine, modified from Faegri & Iversen (1989).

Non-arboreal pollen (NAP) includes the total number of all herbaceous terrestrial pollen types and does not include shrubs or trees. Taxonomy and authorities for vascular plants follow Gleason & Cronquist (1991).

Spruce pollen was differentiated only to genus. Although morphological distinctions have been described for P. abies, P. glauca, and P. mariana pollen (Birks & Peglar 1980; Hansen & Engstrom 1985), until very recently no study has attempted to compare morphological types from pollen collected only within the Acanadian region, the sole place where the three coexist (Lindbladh, Jacobson & Schauffler, unpublished). *Pinus* pollen grains were differentiated into *Pinus* (sect. *Strobus*) (Pinus strobus, white pine) and *Pinus* (sect. *Pinea* (P. rigida (pitch pine), P. banksiana (jack pine), or P. resinosa (red pine)) whenever preservation was sufficient to distinguish the two. These are referred to as *Pinus strobus* and *Pinus* (sect. *Pinea*).

**INTERPRETATION OF POLLEN PERCENTAGES**

Local pollen contributes on the order of 45–50% of the pollen input to small forested hollows in mixed hardwood and softwood settings, which is enough to characterize the contributions of major taxa within about 50–100 m of the sample point (Jackson & Wong 1994; Calcote 1995, 1998; Sugita 1995). Taxa differ widely in pollen productivity and dispersivity, which complicates interpretation of pollen data. Pollen percentages of 6% (spruce), 20% (pine), 20% (birch) are taken to indicate presence of these taxa in the local stand, based on surface samples collected in a suite of 20 forest-stands in northern and coastal Maine (Schauffler 1998). Such values are typical where several to many trees are found; but lower percentages are usually associated with the taxa being absent. Pollen percentages as high as 7% for hemlock (*Tsuga canadensis*), 8% for oaks (*Quercus*), and 2% for beech (*Fagus*) were found in sediments, although these taxa were absent from local canopies (Schauffler 1998), but fir, generally under-represented in pollen assemblages, is assumed to be locally present whenever its pollen is found. Although larch and cedar (*Thuja*), are likely to have grown here, the very local representation of the former and inconsistent preservation of the latter leads (as here) to low levels in pollen assemblages, and thus to difficulty in determining the history of their abundance.

**MACROFOSSILS AND RADIOCARBON CHRONOLOGY**

Estimated time-scales in calibrated radiocarbon years (cal year BP) are based on linear interpolations between calibrated accelerator mass spectrometry (AMS) dates on plant macrofossils picked from the sediment. All cores were sieved with a 425-µm sieve and any identifiable material was picked and archived for possible dating. With the exception of the bottom section of the core from Blackwoods, the cores contained relatively few macrofossils intact enough to identify and thus be reliable for dating.

Samples were dried, weighed, and analysed by reduction to graphite according to standard AMS procedures used by Beta Analytic of Miami, Florida.

Ages reported in cal year BP are described in the text as ‘years ago’. Uncalibrated radiocarbon ages (before 1950) (14C BP) with 1 σ errors are presented in Table 2a and 2b to facilitate comparison with other published pollen stratigraphies from Maine. Calibrated age ranges and error bars on age-depth curves include the 2σ
### Table 2a Radiocarbon ages for coastal forest-hollow sites in northern New England expressed as conventional and calibrated ages and the type of material analysed. Calibrations were made by Beta Analytic, Inc., using the Pretoria calibration curve (Vogel et al. 1993)

<table>
<thead>
<tr>
<th>Site and laboratory number</th>
<th>Depth (cm)</th>
<th>Conventional $^{14}C$ age (±1σ)</th>
<th>Calibrated $^{14}C$ age (cal BP ±2σ)</th>
<th>Basis</th>
<th>$^{13}C/^{12}C$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Isle au Haut – north site</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta-92525</td>
<td>40–40.5</td>
<td>1020 ± 40</td>
<td>975–835</td>
<td>Charred material</td>
<td>-28.5</td>
</tr>
<tr>
<td>Beta-94801</td>
<td>47–47.5</td>
<td>1400 ± 60</td>
<td>1390–1190</td>
<td>Charred material</td>
<td>-29.7</td>
</tr>
<tr>
<td>Beta-92825</td>
<td>57–64</td>
<td>3880 ± 40</td>
<td>4415–4155</td>
<td>Mixed plant material</td>
<td>-27.3</td>
</tr>
<tr>
<td>Outliers</td>
<td>49–51</td>
<td>1046 ± 110</td>
<td></td>
<td>Bulk date</td>
<td>-27.7</td>
</tr>
<tr>
<td>Isle au Haut – south site</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta-89919</td>
<td>33.5–34</td>
<td>2520 ± 60</td>
<td>1145–1540</td>
<td>Charred material, twig</td>
<td>-30.2</td>
</tr>
<tr>
<td>Beta-94800</td>
<td>43–45</td>
<td>4410 ± 60</td>
<td>5275–4850</td>
<td>Charred material</td>
<td>-27.9</td>
</tr>
<tr>
<td>Beta-115565</td>
<td>24–24.5</td>
<td>120 ± 40</td>
<td></td>
<td>Bark</td>
<td>-28.2</td>
</tr>
<tr>
<td>Beta-94799</td>
<td>27–27.5</td>
<td>140 ± 60</td>
<td></td>
<td>Twigs</td>
<td>-30.0</td>
</tr>
<tr>
<td>Mt. Desert Island – Blackwoods</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta-113234</td>
<td>33–33.5</td>
<td>2980 ± 50</td>
<td>3330–2970</td>
<td>Charred material, bark</td>
<td>-30.4</td>
</tr>
<tr>
<td>Beta-113235</td>
<td>60–60.5</td>
<td>5490 ± 50</td>
<td>6395–6195</td>
<td>Charred material</td>
<td>-29.3</td>
</tr>
<tr>
<td>Beta-103240</td>
<td>89.5–90</td>
<td>7210 ± 70</td>
<td>8120–7895</td>
<td>$Aster$ seeds, wood</td>
<td>-32.4</td>
</tr>
<tr>
<td>Beta-115772</td>
<td>103–103.5</td>
<td>7280 ± 60</td>
<td>8145–7930</td>
<td>Seeds and bark</td>
<td>-30.4</td>
</tr>
<tr>
<td>Beta-113237</td>
<td>136–136.5</td>
<td>9510 ± 60</td>
<td>10895–10370</td>
<td>Mixed plant material</td>
<td>-27.4</td>
</tr>
<tr>
<td>Beta-113238</td>
<td>179–179.5</td>
<td>9970 ± 60</td>
<td>11480–11000</td>
<td>Mixed plant material</td>
<td>-34.9</td>
</tr>
<tr>
<td>Outliers</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta-113236</td>
<td>100–100.5</td>
<td>3620 ± 50</td>
<td></td>
<td>Wood &amp; charred material</td>
<td>-26.6</td>
</tr>
<tr>
<td>Schoodic Peninsula</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta-114802</td>
<td>42–42.5</td>
<td>3340 ± 50</td>
<td>3685–3455</td>
<td>Bark</td>
<td>-32.8</td>
</tr>
<tr>
<td>Beta-114803</td>
<td>50–51.5</td>
<td>3720 ± 40</td>
<td>4150–3925</td>
<td>Bark, seeds, insect parts</td>
<td>-28.4</td>
</tr>
<tr>
<td>Beta-103242</td>
<td>63–64</td>
<td>7140 ± 60</td>
<td>7995–7805</td>
<td>Bark and plant fragments</td>
<td>-36.6</td>
</tr>
<tr>
<td>Beta-113233</td>
<td>30–30.5</td>
<td>250 ± 40</td>
<td></td>
<td>Mixed plant material</td>
<td>-27.5</td>
</tr>
<tr>
<td>Roque Island</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta-104757</td>
<td>24–24.5</td>
<td>640 ± 50</td>
<td>670–535</td>
<td>Wood with bark</td>
<td>-32.5</td>
</tr>
<tr>
<td>Beta-104758</td>
<td>38–38.5</td>
<td>1250 ± 50</td>
<td>1280–1060</td>
<td>Wood with bark</td>
<td>-27.2</td>
</tr>
<tr>
<td>Beta-104759</td>
<td>55–55.5</td>
<td>2700 ± 40</td>
<td>2860–2750</td>
<td>Conifer cone bract, bark</td>
<td>-27.5</td>
</tr>
<tr>
<td>Beta-104760</td>
<td>75–75.5</td>
<td>5250 ± 40</td>
<td>6165–5925</td>
<td>Mixed plant material</td>
<td>-26.4</td>
</tr>
<tr>
<td>Beta-104761</td>
<td>87–87.5</td>
<td>6130 ± 50</td>
<td>7170–6875</td>
<td>Wood fragment, seeds</td>
<td>-24.1</td>
</tr>
<tr>
<td>Beta-89920</td>
<td>111–111.5</td>
<td>8510 ± 80</td>
<td>9565–9300</td>
<td>Bulk date</td>
<td>-28.7</td>
</tr>
<tr>
<td>Outliers</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta-113233</td>
<td>30–30.5</td>
<td>250 ± 40</td>
<td></td>
<td>Mixed plant material</td>
<td>-27.5</td>
</tr>
<tr>
<td>Beta-109079</td>
<td>23–23.5</td>
<td>840 ± 40</td>
<td>885–675</td>
<td>Wood</td>
<td>-24.9</td>
</tr>
<tr>
<td>Beta-94797</td>
<td>32–32.5</td>
<td>1170 ± 60</td>
<td>1245–950</td>
<td>Bark, needles</td>
<td>-31.5</td>
</tr>
<tr>
<td>Beta-115564</td>
<td>55–55.5</td>
<td>5550 ± 50</td>
<td>6425–6280</td>
<td>Wood</td>
<td>-28.8</td>
</tr>
<tr>
<td>Beta-81548</td>
<td>57–59</td>
<td>5490 ± 70</td>
<td>6415–6175</td>
<td>Mixed plant material</td>
<td>-27.3</td>
</tr>
<tr>
<td>Outliers</td>
<td>Beta-94798</td>
<td>44–44.5</td>
<td>2100 ± 50</td>
<td>Plant fragments, twig</td>
<td>-25.5</td>
</tr>
<tr>
<td>Big Reed Hollow</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Beta-112287</td>
<td>17–17.5</td>
<td>460 ± 50</td>
<td>540–330</td>
<td>Seeds, wood, insect elytra</td>
<td>-27.4</td>
</tr>
<tr>
<td>Beta-109080</td>
<td>24–24.5</td>
<td>1220 ± 60</td>
<td>1265–990</td>
<td>Insects, wood fragments</td>
<td>-29.6</td>
</tr>
<tr>
<td>Beta-112288</td>
<td>29–29.5</td>
<td>2350 ± 50</td>
<td>2465–2315</td>
<td>Wood, flower brace</td>
<td>-26.2</td>
</tr>
<tr>
<td>Beta-110901</td>
<td>40–40.5</td>
<td>3380 ± 50</td>
<td>3710–3475</td>
<td>Insects, wood fragments</td>
<td>-29.6</td>
</tr>
<tr>
<td>Beta-112291</td>
<td>69–69.5</td>
<td>6540 ± 50</td>
<td>7480–7295</td>
<td>Wood, plant fragments</td>
<td>-26.8</td>
</tr>
<tr>
<td>Beta-103239</td>
<td>77.5–78</td>
<td>9550 ± 110</td>
<td>10975–10330</td>
<td>Mixed plant material</td>
<td>-38.2</td>
</tr>
<tr>
<td>Outliers</td>
<td>Beta-112289</td>
<td>48.5–49</td>
<td>3680 ± 60</td>
<td>Wood fragment</td>
<td>-26.1</td>
</tr>
<tr>
<td>Beta-100902</td>
<td>52–52.5</td>
<td>2700 ± 50</td>
<td></td>
<td>Wood fragment</td>
<td>-25.9</td>
</tr>
<tr>
<td>Beta-112290</td>
<td>57.5–58</td>
<td>3850 ± 40</td>
<td></td>
<td>Wood with bark</td>
<td>-25.1</td>
</tr>
</tbody>
</table>
calibration error associated with the Pretoria Calibration Curve reported by Beta Analytic (Vogel et al. 1993). Age-depth relationships are also based on two key events evident in pollen stratigraphies throughout north-eastern North America: (1) a marked rise in ragweed (Ambrosia) pollen and other non-arboreal pollen types indicates the timing of forest clearance for timber and agriculture around the late 1700s (McLane 1982; McLane & McLane 1989), and (2) a broad-scale, rapid, and apparently synchronous decimation of hemlock (Tsuga) populations probably by a pathogen which occurred throughout its range in north-eastern North America 5500 years ago (14C yr 4800) (Davis 1981; Allison et al. 1986; others). Although the increase in ragweed pollen in an undisturbed forested hollow could underestimate the timing of regional agricultural clearing, it is not likely to be by more than a few decades because of the rapid rate at which the historic clearing of forests occurred in the region.

CHARRED PARTICLE ANALYSIS

The total area of macroscopic charred fragments >425 µm in sediment subsamples was determined by counting the number of 1 mm grid squares covered by charred particles in a known volume of sediment at 1.0 cm intervals. The area was summed and expressed in terms of volume of sediment (mm² charred material/cm³ sediment).

Results

The general similarity of the small-hollow pollen profiles to regional pollen records and the absence of abrupt stratigraphic changes suggest that these sediment records are continuous, with no evident hiatuses and no in situ disturbance of the sediment stratigraphies, with the exception of a possible hiatus in the middle of the core from Roque Island. Although the overall proportion of degraded charcoal is undetectably pollen in the forest-hollow sediments is higher than in most lake-sediment stratigraphies, preservation was sufficient to readily identify 300 grains per level, except in occasional sections of cores. Sections of cores that contained a high proportion of indeterminate (corroded or degraded) grains (i.e. > 15%) probably indicate episodes of drier conditions, when sediments were eroded.

The rate of pollen deposition in forest hollows is probably reasonably constant as long as stands remain forested (Hannon & Bradshaw 1989). Here, pollen concentrations vary greatly within each core (as is typical in peat stratigraphies from bogs), probably indicating temporal variability in the rate of decomposition of organic sediments, which increases as temperatures warm and as sediments become dry and aerated.

Both coastal and inland forest-hollow pollen stratigraphies indicate the presence of a spruce-tundra woodland during the early Holocene (in the older cores), and a late-Holocene increase in the abundance of spruce (in all cores). However, beyond these broad similarities, several differences among the stratigraphies are significant.

COASTAL SMALL-HOLLOW SITES

Isle au Haut (north and south sites)

Spruce has been established in both stands on Isle au Haut since the time sediment began accumulating in these hollows 4500–5000 years ago, and has remained well-established until present (Picea pollen > 80%) (Fig. 4a,b). Recent increases in spruce and alder (Alnus) pollen in both pollen stratigraphies suggest conditions that cooled and moistened 1000–1500 years ago. Large decreases in tree pollen at around 20 cm, especially at the southern site, and increases in non-arboreal pollen (NAP) corroborate historical accounts that report much of the island was cleared for sheep pasture in the 1800s.

Macrofossils of charred material occur throughout the top two-thirds of both cores, suggesting fires burned in the vicinity of both sites during the last 1500 years (north site) to 2800 years (south site). The wide, visible band of charcoal between 17 and 19 cm in the core from the south site contains an order of magnitude more charcoal and particles in a wider range of size-classes than elsewhere in the core, and could be associated with Island-wide burning around the time of European settlement at or very near the sampled hollow.

Blackwoods – Mount Desert Island

The sediment in the Blackwoods hollow is twice as deep as sediment in other hollows in this study, and radiocarbon dates indicate an unusually rapid rate of sediment accumulation in the bottom third of the core, where macrofossils were well-preserved. The vegetation history of this site is highly dynamic (Fig. 4c). Aquatic and wetland pollen types suggest that basal sediments were deposited in a small postglacial pond surrounded by a shrub fen in a spruce–tundra setting. The disappearance of aquatic macrofossils around 135 cm suggests that the pond had become open fen by 10 500 years ago. Increases in tree pollen and Sphagnum spores, and the disappearance of well-preserved macrofossils around 80–85 cm indicate that conditions became drier between 7500 and 7000 years ago and that the canopy closed in with hemlock, pine, and spruce.

The stand remained mixed softwoods and hardwoods for much of the middle Holocene, dominated by hemlock, white pine, and mixed northern hardwoods (birch, maple, and beech) and winterberry/mountain holly (Ilex/Nemopanthus) shrubs in the understory. The hemlock decline around 5500 years ago apparently coincided with a moistening trend (indicated by small increases in Picea pollen and Sphagnum-type spores). Hemlock recovered within a few centuries, while spruce percentages remain low, indicating that conditions here were apparently not yet ideally suited for spruce.
Fig. 4  (a)–(g) Lithology and summary pollen diagrams for selected taxa for (a) Isle au Haut (north site) (b) Isle au Haut (south site) (c) Blackwoods (d) Schoodic Peninsula (e) Roque Island (f) Big Reed Pond hollow, and (g) Buckley Pond hollow. Pollen percentages are based on the total terrestrial pollen count. The total area (mm$^2$) for charred material (CP) includes particles larger than 425 µm. The time-scale is in calibrated ¹⁴C years, based on AMS dates and the *Ambrosia* rise. Note different scales on X-axes. Macrofossils (at Blackwoods only) are indicated by black dots.
(4d) Schoodic Peninsula Hollow
44°27'0" lat, 68°7'30" long
analyst: M. Schaufler

Fig. 4 Continued
Although it was present, spruce did not begin to dominate the stand until around 2000 years ago, at least 1000 years earlier than the regional late-Holocene spruce rise, reaching present-day proportions only around 500 years ago.

Schoodic Peninsula

The pollen data here span most of the Holocene and indicate that spruce has been dominant in the canopy for the last 5000–6000 years (Fig. 4d). After the mid-Holocene hemlock decline, hemlock and pine were apparently replaced by spruce, birch, and fir, which have remained dominant since. An increase in the moisture balance between 2000 and 3000 years ago is suggested by increases in pollen of understorey wetland shrubs (Alnus, Ilex/Nemopanthus) at around 33 cm. The small amount of charred material suggests that major fires burned infrequently, if at all, in or near this stand. A major disturbance (the hemlock decline) combined with the development of cool conditions probably facilitated the subsequent rapid establishment of spruce and fir.

The percentage of NAP between 12 and 15 cm is 10–20%, similar to other presently forested sites known to have been open at one time (Foster et al. 1992). These high NAP values are accompanied by abrupt decreases in spruce and fir pollen and by a spike in birch pollen, suggesting significant local clearing. This possibility is supported by historic accounts of farm settlements on the north end of Schoodic peninsula in the 1800s (Smallidge 1994).

Roque Island

Spruce pollen percentages > 10% throughout the length of this core implies that spruce has dominated for the last 9500 years, probably since its initial arrival following deglaciation (Fig. 4e). Lake-sediment pollen stratigraphies elsewhere in northern New England indicate that spruce had decreased to a mid-Holocene low by around 10 000 years ago, except those in northernmost Maine and on Monhegan Island where it decreased later (Davis & Jacobson 1985). This time-frame is close enough to suggest that spruce never left the stand on Roque Island.

The constricted dates and high percentages of indeterminable (degraded) pollen between 5000 and 3000 years ago suggests there may be a mid-Holocene hiatus in this core. Spruce does not appear to increase as much around 5000 years ago here as it does at the other coastal sites, possibly because it is already abundant in the canopy (Picea pollen percentages are between 10 and 20%). However, the sharp decrease in Pinus strobus pollen, and increases in Abies pollen and Sphagnum spores are other indications that, as at the other coastal small hollows, cool and moist conditions developed around this time. Spruce apparently did not reach its present nearly 100% dominance in the canopy until around 800 years ago, when the local population increased abruptly within 200 years, indicated by a nearly three-fold increase in its pollen percentage between 25 and 30 cm.

INLAND SMALL-HOLLOW SITES

Big Reed Pond Hollow

Sediments in the stand near Big Reed Pond began accumulating around 6300 years ago under a canopy dominated by pine (sect. Pinus) and white pine, with significant amounts of hemlock and birch, and ferns (Polypodium and Osmunda) abundant in the understorey (Fig. 4f). Scattered individuals of spruce and fir were probably present, but neither was abundant; Picea pollen was less than the 6% needed to indicate significant presence in the canopy (Schauffler 1998).
The nearly five-fold increase in *Picea* pollen beginning around 1000 years ago, from its low percentages during the middle Holocene, mirrors the widespread increase in spruce seen in lake pollen records throughout north-eastern North America. Increased proportions of *Alnus*, *Hedysarum*, cedar or juniper, and sedge (Cyperaceae) pollen and *Sphagnum* spores accompany the rise in spruce, providing further evidence that conditions cooled and moistened.

The increase in *Ambrosia* and other non-arboreal pollen (NAP) at the top of the core is slight (to 4%), suggesting that there was not significant clearing in the stand when Europeans settled in the area (c. 1790 AD). Coincident abrupt decreases in tree pollen (possible indications of forest cutting) are relatively minor.

**Buckley Hollow**

During the early Holocene, spruce, shrubs (birch spp., alder and probably *Juniperus*), and sedges occupied this site. The low concentrations of pollen and high proportions of NAP (10%) indicate an open and sparsely covered landscape, which was widespread across the region following deglaciation (Davis & Jacobson 1985). Proportions of spruce began to decrease between 9000 and 8500 years ago, and by 7200 years ago a mixed canopy of white pine, birch, alder, spruce, fir and understorey ferns replaced the tundra woodland.

The pollen data suggest that this was a mixed softwood stand throughout the mid-Holocene, with a canopy of *Pinus* (sect. *Strobus*) (40–60%), *Picea, Abies* and (towards the later Holocene) *Tsuga* (Fig. 4g). *Picea* pollen remained around or slightly above 5% throughout the mid-Holocene, suggesting that spruce was present in significant amounts, and possibly codominant with other softwoods. hardwoods are less evident in this stand than in the stand near Big Reed Pond. As in other small hollow cores in this study and as in lake pollen records in the region, the proportion of *Picea* pollen at Buckley Hollow increased around 1000 years ago.

Evidence of local clearing and agricultural land-use by European settlers in the late 1700s is slight. Decreases in the pollen of dominant tree taxa are small, and the rise in NAP is gradual and increases to only 3% or less. This implies that although there may have been some cutting of scattered individual trees, the local canopy was probably not opened significantly.

The small quantity of charred material in both cores from Big Reed Preserve indicate that large fires have not often burned in these stands.

**Discussion**

**Patterns in the persistence of coastal spruce populations during the Holocene**

The five pollen records from coastal hollows provide evidence that spruce has been well-established since the mid-Holocene on the eastern coast of Maine and in some places may have persisted throughout the Holocene since its initial arrival after deglaciation (Fig. 1). Lake pollen records across northern New England provide no evidence that spruce was dominant at the landscape-scale during the mid-Holocene (Fig. 1) and the two cores from Big Reed Preserve have similarly low abundance of spruce pollen prior to 1000 years ago. One of the inland cores (Buckley Hollow), does have enough spruce pollen to suggest that it may have been codominant in the canopy, with other softwoods, suggesting that spruce existed in distinct populations not distinguishable in regional signals, with its distribution influenced by climatic variation at both regional and local scales. These populations appear to have occurred in higher density along the coast.

The longest documented continuous spruce stand is at Roque Island, the easternmost of our coastal sites, where it has been well-established for at least the last 9000 years. Mean monthly temperature data averaged over the last 78 years for Bar Harbor (Mt. Desert Island, near the Blackwoods site) and Eastport (east of Roque Island) indicate that average July temperatures are 2.6 °C lower at the more easterly station. In addition, although the entire Maine coast experiences fog during the summer, easternmost sections receive twice as many hours of fog as do regions west and south of Penobscot Bay (Fobes 1946), creating a gradient in potential evapotranspiration which decreases eastward along the coast (McMahon 1990). The cores from Roque Island and Schoodic Peninsula also contain the least amounts of charred material, further supporting the long-term presence of this trend.

Although spruce was already well-established at all five coastal stands, each of the stand-scale pollen stratigraphies indicate a further proliferation of spruce around 1000 years ago. Similar two- to six-fold increases in spruce pollen occur in the inland forest-hollow stratigraphies throughout northern New England; the ubiquity and magnitude of the increase indicates that this recent expansion of spruce was widespread and probably occurred in response to a regional climate cooling (Figs 1 and 5).

**Mid-Holocene changes in marine influence (and the persistence of steep coastal vegetation gradients, even in the face of climate change)**

Despite the differences in the timing and development of the stands, the three older records (Roque Island, Schoodic Peninsula, and Blackwoods) all indicate major vegetation changes around 5500 years ago, supported by high-level splits in Cowan dissimilarity clusters. In each one, spruce and other taxa favoured by cool conditions increased or pine decreased, or both. The two cores from Isle au Haut, although too young to show...
these vegetation changes, both began accumulating sediment between 5200 and 4500 years ago, a possible indication that conditions had become cool and wet enough to slow the rate of decomposition and form perennially wet, anaerobic sediment capable of preserving pollen. Neither of the inland cores shows evidence of a cooling in the mid-Holocene, suggesting that the mid-Holocene cooling was stronger on, and possibly restricted to, the coast.

The timing of the vegetation change between 6000 and 5000 years ago in these coastal forest stands coincides with the time-frame of other indications of cooling of the Gulf of Maine and the possible formation of foggy conditions along the eastern coast. As the sea-level rose from a minimum at 12 000 years ago (60 m below present sea-level), the shape of the semi-enclosed basin of the Gulf of Maine changed and approached natural resonance with the lunar diurnal period of tidal forcing (12.42 h) (Gehrels et al. 1995). Tidal amplitude increased rapidly between 8000 and 4500 years ago, so that by 4500 years ago it was about 78% of the present amplitude (Scott & Greenberg 1983; Gehrels et al. 1995). Shifts in the Labrador Currents may also have introduced cooler water to the Gulf of Maine during the middle Holocene (Scott & Collins 1996). Although there are no precise quantitative estimates of temperature changes in the Gulf, many lines of evidence indicate that surface waters cooled during the middle Holocene (Sanger 1975; McAlice 1981; Schnitker & Jorgensen 1990; others).

This shift to large tides in the Bay of Fundy–Gulf of Maine system by the mid-Holocene, combined with continued rise in sea-level, must have had a large influence on coastal environments. The stronger tides caused diurnal mixing of the warm surface water with cold layers below, lowering surface-water temperatures and favouring the frequent formation of fog (Schnitker & Jorgensen 1990). This would have favoured spruce and fir and discouraged pine by increasing moisture and lowering temperatures during the growing season (Davis 1966). Populations of swordfish (which prefer warm surface water temperatures and had been abundant in the Gulf) declined during the mid-Holocene (Sanger 1975), while broad tidal flats formed and shellfish populations expanded, nourished by increased productivity of the cold, well-mixed surface-water. Thus, swordfish bones disappear from the oldest midden sites around 4000 years ago and numerous shell-heap middens appear by around 3200 years ago (Sanger 1975).
Persistence of coastal spruce refugia

The long-term presence of spruce in the coastal stands suggests that the eastern coast of Maine and Canadian Maritimes, as well as in high-elevation sites elsewhere in New England (the nearest known large populations of mid-Holocene spruce) (Davis et al. 1980; Jackson & Whitehead 1991; Spear et al. 1993) provided locally favourable conditions and thus enabled spruce survival during centuries to millennia warmer mid-Holocene. This is supported by the lake data in Fig. 1 where three of the six coastal sites (Silver Lake, Shaw’s Bog, and Monhegan Island Meadow) have higher percentages of spruce pollen during the mid-Holocene than the other lakes do. Neither Ross Pond nor Little Lake, only a few kilometres from the coast, indicate significant spruce during the middle-Holocene, suggesting that the influences that permitted spruce to grow affected only a very narrow band near the shore, and perhaps even just stands on coastal islands and peninsulas. Such narrow ecological zones that harbour refugia may easily be overlooked by regional palaeoecological reconstructions.

The presence of moderately abundant spruce at Buckley Hollow throughout the Holocene suggests however, that microsites favourable for spruce also occurred inland. But because none of the inland lake stratigraphies contain much spruce pollen during the mid-Holocene and because the percentages for spruce even at Buckley are lower than in the coastal hollows, it seems likely that refugia spruce stands occurred in lower density inland, or contained spruce in lower densities, or both. Analyses from a larger suite of small-hollow and small-basin stratigraphies in both coastal and interior geographical areas are needed to test (1) the extent to which these results can be generalized to coastal and interior regions and (2) the potential contribution of other local factors besides climate to differences in vegetation histories (e.g. fire and other disturbances).

The variable histories of both the inland and coastal stands, and the length of time for which differences persisted (centuries to millennia) demonstrate that forest stands respond individually to changes in regional and extra-local climate and other factors, and that differences can persist for thousands of years (Davis et al. 1994, 1998). Differences in local factors, including soil type, local hydrology, bedrock geology, local topography and local disturbances, in addition to climate, probably have contributed to the differences in the long-term success of spruce in the coastal stands. The development of forest stands thousands of years ago, influenced by local factors, may have formed a template for the distribution of stand types in today’s forests (Frelich et al. 1993). For example, the difference in the relative proportions of hardwoods and softwoods in the two stands from Big Reed Pond Preserve have apparently persisted for thousands of years and up until the present day. Regional pollen stratigraphies provide a regional context for interpreting major changes in the forest-hollow stratigraphies; the unique presence of aquatic macrofossils and high sedimentation rate in the depression at Blackwoods during the early Holocene was probably the result of specific local hydrological conditions, which probably influenced the relatively late arrival of forest cover evident at that site compared with the establishment of forests regionally.

Insights into the mechanisms for rapid expansion of spruce

The large increase in spruce pollen in the last 500–1000 years evident in all lake and forest-hollow pollen stratigraphies across northern New England suggests that scattered refugia populations probably played a critical role in the recent and extremely rapid expansion of spruce across the region.

The long-term presence of spruce at several coastal sites raises questions about which factors most strongly influence its success. The association of increases in spruce in coastal stands with the timing of changes in the Gulf of Maine suggests that marine influences such as temperature and humidity are important, although they interact to determine potential evapotranspiration rates and are difficult to test separately in field conditions. Preliminary observations of red spruce seedlings in growing chambers, however, suggest a greater growth response to increases in humidity than to decreases in temperature (M. Day & R. Jagels personal comm.). Other studies attempting to isolate the effects of high temperatures on growth in red spruce suggest that there is a physiological decline when growing season temperatures become too warm (Vann et al. 1993; Alexander et al. 1995). Other climate-related factors, including low light-levels associated with frequent fog, direct interaction of fog with spruce needles, and the combined influences of high moisture and low temperatures on improved water-use efficiency and carbon balance, may give spruce a competitive advantage over less tolerant species in coastal settings (Jackson & Whitehead 1991; Jagels 1993; M. Day personal comm.). Further, red spruce is susceptible to winter injury, and its north-eastern maritime distribution may be influenced by moderating effects of the Gulf of Maine on extreme winter temperatures (Livingston & Day 1999, Lund & Livingston 1999).

Small-hollow pollen stratigraphies as a tool for reconstructing local vegetation dynamics

Sampling small hollows allows ecological processes to be refined spatially and, by comparison with lake pollen data, local changes can be interpreted in a regional palaeoecological context. The site-specific nature of these records (evident in the high variability among the forest-hollow stratigraphies) means that they can be used to understand edaphic and microclimate influences on the forest ecosystems, as well as the history of local disturbances.
The pollen stratigraphies from Big Reed Pond Preserve sites corroborate other evidence that major timber harvesting did not occur here (Coghill 1985; Moehs 1995), as it did along Maine’s coast. The NAP percentages at the tops of both cores from Big Reed Preserve are less than 3–4%, well below NAP percentages of 15% or more in stands in western Massachusetts that had ‘significant cutting in the canopy and sprouting of chestnut’, and where intensive extra-local clearing of land is documented (Foster et al. 1992). This is also in contrast to NAP between 10 and 20% in sediments deposited during the last two centuries at Upper South Branch Pond (Anderson et al. 1986), which suggests there was less significant harvesting in the stands in Big Reed than was characteristic elsewhere in northern interior Maine. All coastal sites had NAP > 5–10% during recent centuries, and on Isle au Haut (which historic records describe as largely cleared during the 1800s), recent NAP percentages are as high as 35% (Schauffler 1998).

Conclusions
Spruce has been well-established throughout the Holocene at several places on the eastern coast of Maine, and at least since the mid-Holocene at other sites, suggesting that local marine influences probably overwhelmed the influence of regional climate warming, if only in a narrow band and predominantly in the cooler and wetter east.

Major shifts in vegetation were coincident with archaeological and oceanographic indications of cooling of the surface waters of the Gulf of Maine and the possible increase in foggy conditions along the eastern coast between 6000 and 3000 years ago. The local coastal influence was apparently strong enough to allow the persistence of a coastal–interior environmental gradient for at least several thousand years, even in the face of a changing regional climate.

Favourable microsites also appear to have existed inland throughout the Holocene and are likely to have enabled the rapid regional expansion of spruce 1000 years ago. Lake records alone are not necessarily sufficient to describe the dynamics of vegetation change in a region, especially in areas where regional environmental gradients exist, and where local and regional influences are likely to be strong enough to compete with one another.

Acknowledgements
This work was funded primarily by the U. S. National Park Service, with assistance from The Eastern Maine Conservation Initiative and the Maine Chapter of The Nature Conservancy. Discussions with Matts Lindbladh, David Sanger, Robert Seymour, Ivan Fernandez, Ronald B. Davis, Douglas Maguire, and Shimy Sugita provided much insight. We also thank Lindsay Haddon, David R. Foster and two anonymous referees for their valuable comments.

References
Björkman, L. (1996) *The late Holocene history of beech Fagus sylvatica and Norway spruce Picea abies at stand-scale in*
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Received 2 April 2001
revision accepted 29 August 2001