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Short Paper

Analysis of hemlock pollen size in Holocene lake sediments from New England

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ABSTRACT

We explored the middle-Holocene decline of *Tsuga canadensis* by measuring the diameters of pollen grains in two lake-sediment cores from New England. We hypothesized that a drop in pollen size at the time of the decline followed by an increase in pollen diameters as *Tsuga* recovered during the late Holocene might indicate reduced abundance of *Tsuga* in the vicinity of the lake during the decline, as smaller pollen grains travel farther than larger ones. To provide context for this hypothesis, we also measured the diameters of *Tsuga* pollen grains in the surface sediments of sites spanning the modern-day gradient of *Tsuga* in New England. Both fossil records exhibited a reduction in pollen size during the interval of the middle-Holocene decline, with diameters similar to those observed in the upper sediments of those sites, yet larger than *Tsuga* pollen grains in the surface sediments of coastal sites beyond the modern range of *Tsuga*. This pattern suggests that *Tsuga* persisted in scattered, low-density populations during the middle Holocene, as it has remained on the landscape since European settlement.

Introduction

Lake-sediment pollen records from across eastern North America feature a dramatic decline of *Tsuga canadensis* (eastern hemlock; hereafter "*Tsuga*") during the middle Holocene (e.g., Bennett and Fuller, 2002). *Tsuga* pollen percentages drop abruptly at ~5500 calibrated years before present (cal yr BP), its abundance is low until ~4000–3000 cal yr BP, and then *Tsuga* recovers to nearly pre-decline levels during the late Holocene (e.g., Oswald et al., 2007). Over decades of study, these shifts in *Tsuga* abundance have been interpreted in various ways. Davis (1981) posed the intriguing hypothesis that the *Tsuga* decline was caused by a pathogen, with its eventual recovery attributable to the evolution of disease resistance. The event has subsequently been linked to insect activity (Bhiry and Filion, 1996) and climate change (e.g., Foster et al., 2006), with recent studies suggesting that the *Tsuga* decline was initiated and maintained by a series of pronounced droughts (e.g., Shuman et al., 2009).

In most records where the decline has been observed, *Tsuga* is reduced to <5% during the period of low pollen percentages (e.g., Oswald et al., 2007; Shuman et al., 2009). Clearly *Tsuga* was rare across its range for a period of more than a millennium, but determining the presence of any small, remnant populations has been difficult. The interpretation of minor amounts of *Tsuga* pollen is equivocal, as pollen-vegetation calibration studies show background levels of 0–10% *Tsuga* pollen for sites where the tree is not present on the surrounding landscape (e.g., Bradshaw and Webb, 1985). However, the pollen record from Hemlock Hollow, a small sedimentary basin in north-central Massachusetts, suggests that sizable populations of *Tsuga* did persist through the decline in some areas (Foster and Zebryk, 1993). In that record, *Tsuga* pollen percentages remain at ~5–15% during the middle Holocene, likely representing the presence of *Tsuga* stands in swampy areas surrounding the study site.

This paper presents a new approach for studying spatial patterns of past vegetation. To explore the distribution of *Tsuga* in New England during the middle-Holocene decline, we analyzed changes in the size of *Tsuga* pollen grains in Holocene-aged sediments. Pollen-percentage and influx data suggest that *Tsuga* was rare in this region during the decline (e.g., Oswald et al., 2007; Oswald and Foster, 2012), and pollen-grain size should, in theory, provide additional information about its past abundance and geographic pattern. Smaller pollen grains travel farther than larger pollen grains (e.g., Sugita, 1993), such that a shift from large to small grains would indicate that the source area for a given number of grains was expanding due to an overall decline in the number of *Tsuga* trees in the area. We analyzed *Tsuga* pollen grains in two lake-sediment records from New England: Little Pond in north-central Massachusetts (Oswald et al., 2007) and Knob Hill Pond in northern Vermont (Oswald and Foster, 2012). To test our assumption that the dispersal of *Tsuga* pollen varies by size, we also analyzed surface-sediment samples from four additional sites across the modern-day gradient of *Tsuga* abundance from inland to coastal areas of New England. Our findings illustrate the utility of this approach and provide new insights into the Holocene history of *Tsuga* in eastern North America.

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Study area

T. canadensis is found across much of eastern North America, occurring along the Appalachian Mountains from Alabama north to Nova Scotia, and west to the Great Lakes region (Little, 1971; Thompson et al., 1999). In New England it is most abundant in the inland and northern parts of the region (Cogbill et al., 2002), where winters are cold (mean January temperatures ~−5°C), summers are cool (mean July temperatures ~20°C), and mean annual precipitation is ~100 cm, distributed evenly throughout the year (Easterling et al., 1996). *Tsuga* co-occurs with *Pinus strobus*, *Acer saccharum*, *Acer rubrum*, *Fagus grandifolia*, *Betula alleghaniensis*, *Betula papyrifera*, *Quercus rubra*, and *Prunus serotina* (e.g., Nichols, 1935).

Methods

We analyzed pollen in lake-sediment cores from two sites located in the area of New England where *Tsuga* is abundant (Fig. 1): Little Pond in the town of Royalston in north-central Massachusetts (42.675 °N, 72.192 °W, 302 m elevation) and Knob Hill Pond in the town of Marshfield in northern Vermont (44.361 °N, 72.374 °W, 370 m elevation). Details of the study sites, fieldwork, ^{14}C dating, and other laboratory analyses are described elsewhere (Oswald et al., 2007; Oswald and Foster, 2012).

For each study site, we analyzed *Tsuga* pollen grains at 16 depths: five each in the intervals before, during, and after the *Tsuga* decline, plus the surface sediment (0–1 cm depth). For each of those samples, we measured the diameters of 50 grains using image-analysis software (Scion Image; Scion Corporation, Frederick, MD). For each record, the *Tsuga*-decline samples were compared with the five samples from the preceding and subsequent intervals using one-way analysis of variance.

We also conducted the same pollen-size measurements for surface-sediment samples (collected with a plastic tube fitted with a piston) from four lakes located in coastal New England, outside the area of abundant *Tsuga* (Fig. 1). Mary's Lake and Blaney's Pond (Oswald and Foster, unpublished data) are located on Naushon Island, just offshore from Woods Hole on southwestern Cape Cod; Harlock Pond (Foster et al., 2002) and Black Pond (Oswald and Foster, unpublished data) are located on the island of Martha's Vineyard. We measured the diameters of 30 *Tsuga* pollen grains for Mary's Lake, Harlock Pond, and Black Pond, but only 15 for Blaney's Pond due to low pollen concentrations.

Results

In the Knob Hill Pond record, the diameter measurements of *Tsuga* pollen grains track the pattern observed in the pollen percentages and influx data, with relatively low values during the *Tsuga* decline and in the uppermost sample (Fig. 2). Median diameter values are 63.6–67.8 μm before the *Tsuga* decline, 58.4–61.6 μm during the decline, 62–64.6 μm in the late Holocene, and 54.5 μm in the surface sediments. The Little Pond record features a similar pattern: pre-*Tsuga*-decline median diameters are 62.6–64 μm, middle-Holocene values are 60.2–61.8 μm, post-decline values are 63.6–65 μm, and the surface-sediment median value is 59.2 μm. In both records, *Tsuga*-decline samples are significantly smaller than those from the pre-decline and post-decline intervals (Knob Hill Pond $F(14, 735) = 9.38$, $p < 0.001$; Little Pond $F(14, 735) = 5.59$, $p < 0.001$).

Tsuga pollen grains tend to be even smaller in the surface sediments of coastal sites. The Naushon Island sites have median values of 55.2 μm (Blaney's Pond) and 58 μm (Mary's Pond), while the Martha's Vineyard sites have median values of 50 μm (Black Pond) and 52.2 μm (Harlock Pond).

Discussion

The *Tsuga* pollen data from Knob Hill Pond and Little Pond show shifts in pollen-grain size that appear to represent changes in the abundance and spatial distribution of *Tsuga* during the Holocene. The occurrence of relatively large pollen grains in the early- and late-Holocene intervals of both records and significantly smaller grains during the *Tsuga* decline suggests that during the middle-Holocene period of low *Tsuga* abundance large populations of *Tsuga* were far enough away from the study sites that the proportion of small *Tsuga* grains in the

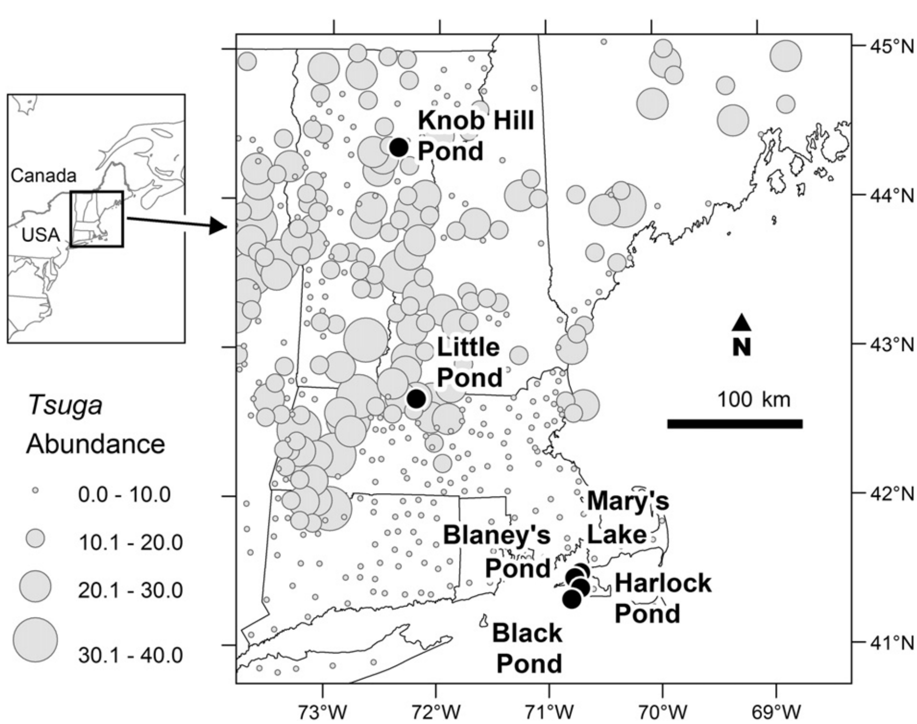

Figure 1. Map of New England showing locations of study sites and pre-settlement relative abundance (percentage values in witness-tree data set) of *Tsuga canadensis* (Cogbill et al., 2002).

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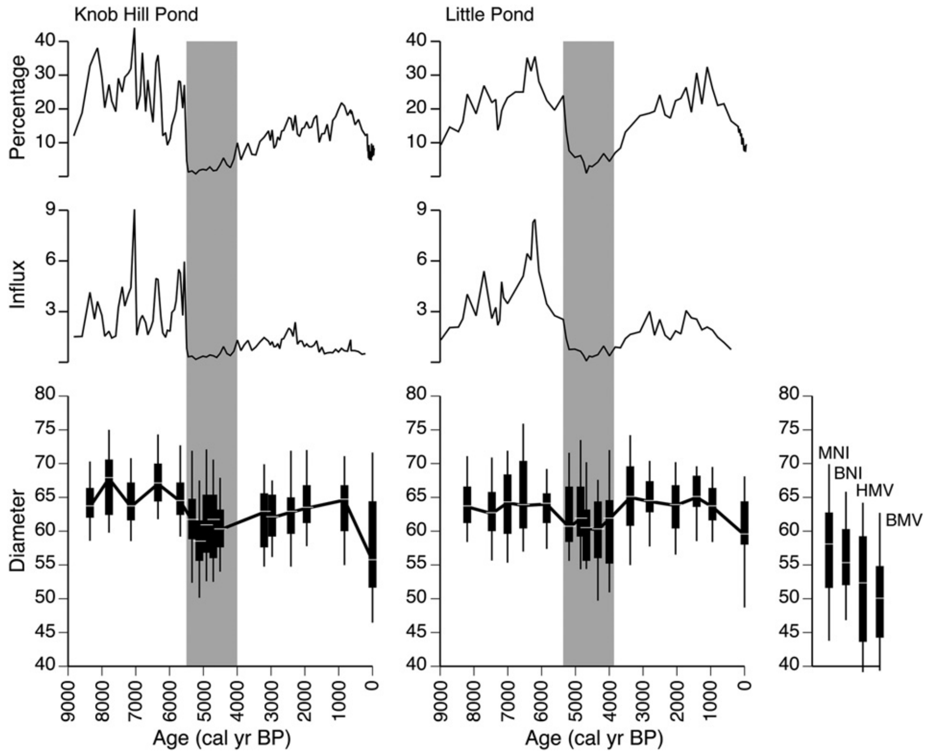

Figure 2. Fossil-pollen data from Knob Hill Pond and Little Pond, including *Tsuga* percentages, influx (grains cm^{-2} yr^{-1}), and pollen-grain diameters (μm) compared with *Tsuga* pollen-grain diameters in surface sediments from Mary's Pond, Naushon Island (MNI), Blaney's Pond, Naushon Island (BNI), Harlock Pond, Martha's Vineyard (HMV), and Black Pond, Martha's Vineyard (BMV); boxes = 25–75th percentile, whiskers = 5–95th percentile, and white line = median.

pollen rain increased. Our analyses of surface-sediment samples are consistent with this interpretation, as there is a progressive decline in the size of *Tsuga* pollen grains across the modern-day gradient of *Tsuga* abundance. Pollen-grain diameters were largest at the inland sites where *Tsuga* is common today (median diameter ~55–59 μm), slightly smaller along the coast (e.g., Naushon Island) where *Tsuga* is rare (~55–58 μm), and smallest offshore on Martha's Vineyard where *Tsuga* does not occur (~50–52 μm).

The pollen-grain measurements for the *Tsuga* decline (median diameter ~58–62 μm) are fairly similar to those of the present-day samples from Knob Hill Pond and Little Pond, and larger than the values of the coastal surface samples. That pattern suggests that *Tsuga* populations were not entirely decimated by the environmental and/or biological stressors of the middle Holocene. Instead, scattered or low-density populations of *Tsuga* persisted through the decline, just as *Tsuga* has remained upon the landscape since the period of European settlement and forest clearance (e.g., Hall et al., 2002). If the *Tsuga* decline were initiated and sustained by dry conditions (e.g., Foster et al., 2006; Shuman et al., 2009), the relict populations of *Tsuga* likely occurred in relatively moist areas of the landscape, as proposed by Foster and Zebryk (1993).

Although climate change appears to have been the primary driver of the hemlock decline (e.g., Foster et al., 2006), it is possible that drought-stressed trees ultimately succumbed to insects or disease, and any or all of these factors might have brought about an evolutionary change in *Tsuga*, as proposed by Davis (1981). Theoretically, variations in pollen-grain size could serve as indirect evidence for the evolution of *Tsuga* during the Holocene, as pollen traits may be influenced by the strong selective forces involved in reproduction (e.g., Erdtman, 1952; Nowicke and Skvarla, 1979). However, given the gradient of *Tsuga* pollen size observed in modern lake sediments, it seems reasonable to interpret the Holocene variations as reflecting changes in the abundance and distribution of *Tsuga* through time. On the other hand, our results do not preclude the possibility that *Tsuga* experienced evolutionary changes in response to the various selective pressures that it may have faced in the middle Holocene. Perhaps genetic analyses of fossil plant remains or sediments will shed additional light on this issue in the future.

This study represents the initial application of a new approach to a long-standing paleoecological question. The shifts in *Tsuga* pollen-grain size in these New England lake-sediment records suggest that *Tsuga* persisted through the middle-Holocene decline in scattered, low-density groups, but sizeable populations of *Tsuga* were not present near the study sites during the decline. A next step would be to carry out these analyses at a larger number of study sites in New England and across the range of *Tsuga* in eastern North America, perhaps allowing the locations of any larger, remnant *Tsuga* populations to be determined. It may also be possible to apply this pollen-size approach to the reconstruction of past spatial patterns for other taxa in other regions.

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