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Evaluating the role of insects in the middle-Holocene *Tsuga* decline

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Abstract. The middle-Holocene decline of *Tsuga canadensis* (L.) Carrière (eastern hemlock) across eastern North America has been attributed to various causes, including the widespread outbreak of an insect pest, such as *Lambdina fiscellaria* (hemlock looper). We tested this hypothesis by searching for insect remains in sediment cores from Hemlock Hollow, a small basin in north-central Massachusetts. Previous analyses of this site demonstrated that it has been surrounded by *Tsuga* forest for the past 10,000 yr. We found the remains of chironomids and beetles in the cores but not in sediments dating to the interval of low *Tsuga* abundance; remains of *Lambdina fiscellaria* were not encountered. These results are consistent with the interpretation that the decline of *Tsuga* at Hemlock Hollow was not caused solely by an insect outbreak. The presence of *Lambdina fiscellaria* remains in middle-Holocene sediments at other sites in the region may reflect local outbreaks, perhaps facilitated by drought or other changes in climate that stressed *Tsuga* populations.

Key words: hemlock, Holocene, New England, paleoecology, pollen


This uncertainty about the role of insects in the *Tsuga* decline prompted us to design a project to search purposefully for insect remains in association with this event. In this study, we performed detailed analyses of sediment cores from Hemlock Hollow, a small basin known to have been surrounded by *Tsuga* forest since approximately 10,000 cal yr BP (Foster and Zebryk 1993).

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Materials and Methods. Hemlock Hollow (42.538°N, 72.179°W, 360 m elevation) is a vernal pool located on the Prospect Hill Tract of the Harvard Forest in the north-central Massachusetts town of Petersham (Fig. 1). The approximately 60-m² pool features two basins separated by a shallow area; the southern basin is slightly deeper than the northern basin. The pool has no aboveground inlets or outlets. *Ilex verticillata* (L.) A. Gray and *Vaccinium corymbosum* L. grow in the shallow center of the pool, and *Picea rubens* Don., *Osmunda cinnamomea* L., and *Sphagnum* sp. occur around the margins. The stand surrounding Hemlock Hollow is dominated by *Tsuga canadensis* but also includes *Pinus strobus* Douglas ex D. Don, *Picea rubens* Sarg., *Betula alleghaniensis* Britton, *Fagus grandifolia* Ehrh., and *Acer rubrum* L. This stand remained forested throughout the period of European settlement in the late 18th and early 19th centuries, although it was used as a woodlot and source of tanbark (Raup and Carlson 1941, Foster et al. 1992). *Tsuga* trees in the forest surrounding Hemlock Hollow are currently declining because of *Adelges tsugae* (hemlock woolly adelgid); it was first observed in this stand in 2008 common era (CE).

A 72-cm-long sediment core was collected from Hemlock Hollow in 1988. That core was analyzed for pollen, charcoal, and organic content, and an age-depth model was developed by pollen-stratigraphic correlation with a 14C-dated pollen record (Foster et al. 1984) to collect cores from nine locations (sites A–I) across the basin, including six sites (A–F) in the vicinity of the 1988 core, at the southern end of the pool where the water is deepest (27 cm at the time of coring) (Oswald et al. 2014). The cores were extruded horizontally in the field and wrapped in plastic and aluminum foil. All samples were subsequently refrigerated. The cores ranged in length from 33 cm to 94 cm, and we selected the two longest cores (E and F, 94 and 93 cm long, respectively) for further analysis.

Cores E and F were subsampled at 1-cm depth intervals, and organic content was estimated for 1-cm³ samples at all depths via the percentage of weight loss on ignition (LOI) at 550°C. To define the depth range of the low-*Tsuga* interval in core E, 16 sediment samples (1 cm³ each) between 46 cm and 16 cm were prepared for pollen analysis following standard procedures (Faegri and Iversen 1989). Pollen residues were mounted in silicone oil and analyzed at 400× magnification. At least 500 pollen grains and spores of upland plant taxa were counted for each sample, and pollen percentages were calculated relative to that sum. For insect analysis, 15-cm³ subsamples (0–94 cm for core E; 0–55 cm for core F) were soaked in potassium chloride and washed through a 180-μm sieve, and the > 180-μm fraction was analyzed at 40× magnification. Chronological control for core E was provided by accelerator mass spectrometry radiocarbon (14C) analysis of six plant macrofossils. 14C dates were converted to calibrated years before present using the IntCal13 calibration curve (Reimer et al. 2013).

Results and Discussion. The 14C dates obtained for Hemlock Hollow core E do not occur in chronological order (Table 1). The dates at 13–14 cm (modern age), 32–33 cm (291 cal yr BP), and 51–52 cm (438 cal yr BP) are substantially younger than would be expected based on the other 14C dates and the pollen data. Given that neither the pollen nor the organic-content data indicated substantial mixing of the sediments (see below), the dating reversals may be attributable to

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Laboratory No.</th>
<th>14C mean age ± SD</th>
<th>δ13C</th>
<th>Calibrated age range(s)</th>
<th>Median calibrated age</th>
</tr>
</thead>
<tbody>
<tr>
<td>9–10</td>
<td>OS-107715</td>
<td>525 ± 20</td>
<td>-26.49</td>
<td>514–553; 612–619</td>
<td>535</td>
</tr>
<tr>
<td>13–14</td>
<td>OS-107623</td>
<td>65 ± 25</td>
<td>-27.90</td>
<td>Modern age</td>
<td>Modern</td>
</tr>
<tr>
<td>23–24</td>
<td>OS-107716</td>
<td>3,240 ± 30</td>
<td>-31.08</td>
<td>3,389–3,514; 3,524–3,559</td>
<td>3,460</td>
</tr>
<tr>
<td>32–33</td>
<td>OS-107717</td>
<td>240 ± 20</td>
<td>-27.19</td>
<td>0–3; 153–169; 282–308</td>
<td>291</td>
</tr>
<tr>
<td>39–40</td>
<td>OS-107624</td>
<td>4,320 ± 30</td>
<td>-25.65</td>
<td>4,840–4,962</td>
<td>4,873</td>
</tr>
<tr>
<td>51–52</td>
<td>OS-108078</td>
<td>415 ± 110</td>
<td>-26.81</td>
<td>0–9; 151–173; 275–654</td>
<td>438</td>
</tr>
</tbody>
</table>
plant macrofossils being pushed downward through the sediment by the corer. The other three 14C dates, however, are generally consistent with the pollen data from the 1988 core and core E, thus providing some age control for the record (Fig. 2).

In Hemlock Hollow core E, Tsuga pollen abundance drops from > 40% at 38 cm to < 10% at 30 cm, a percentage decline similar to that observed in the 1988 core (Foster and Zebrzyk 1993). Tsuga percentages then increase to > 30% at 20 cm (Fig. 2). The similarity of the pollen records from core E and the 1988 core suggests that the sediments have not experienced substantial disturbance or bioturbation. The 14C results do not provide a clear age for the Tsuga decline at Hemlock Hollow, but the dates of approximately 4,870 and 3,460 cal yr BP, near the beginning and end of the low-Tsuga interval, respectively, are generally consistent with other pollen records from the region (e.g., Oswald et al. 2007; Oswald and Foster 2012).

The organic-content (LOI) profiles are similar for the three cores (Fig. 2). In the longer cores, E and F, LOI values are < 10% below 75 cm, slightly elevated (10–20%) at 70–75 cm, and then < 10% from 70 cm to 60 cm. All three cores feature rising LOI values between 60 cm and 50 cm, relatively stable LOI (20–25%) from 50 cm to 40 cm, and then a peak in organic content at 39–40 cm. In the 1988 core, LOI values increase from 30% to 45% during the low-Tsuga interval (35–28 cm). Cores E and F, on the other hand, have a somewhat different pattern of LOI during and following the Tsuga decline. LOI values are 30–40%, with the exception of two units with reduced organic content. These declines in LOI occur at 37 cm and 28 cm in core E, and at 37 cm and 30 cm in core F. These low-LOI values may represent reduced water depth in Hemlock Hollow during the middle-Holocene drought events identified in lake-sediment records from multiple sites in southern New England (Shuman et al. 2009, Marsicek et al. 2013, Newby et al. 2014), or they may reflect soil disturbance associated with Tsuga mortality in the surrounding stand. Following the interval of low-Tsuga abundance, LOI values increase to reach 60–70% in the uppermost sediments.

Our efforts to locate insect remains yielded 11 chironomid head capsules (0, 3, 6, 12, 14, 18, 42, and 50 cm in core E; 0, 1, and 3 cm in core F) and two head capsules of adult beetles (11 cm in core E; 20 cm in core F). No lepidopteran (e.g., Lambdina fiscellaria) remains were encountered, and none of the insect remains fell within the depths of the low-Tsuga interval. One of the beetle head capsules was well preserved and identifiable as an aleocharinae staphylinid. The other beetle head capsule was damaged and partially collapsed; it appeared to come from either a staphylinid or a fungus beetle. Based on the sizes of the head capsules (0.43 mm and 0.39 mm in width, respectively), we estimate that the body lengths of the beetles were < 3 mm. Most staphylinid are
predaceous, although a few lineages are known to be phytophagous or consume algae.

Systematic searches for the remains of attack beetles (*i.e.* *Dendroctonus* species) in lake-sediment cores from across western North America have had limited success (Morris *et al.* 2015), with past outbreaks detected at only a small proportion of study sites (e.g., Brunelle *et al.* 2008). The absence of beetle remains, even in locations with known histories of major outbreaks, may be attributable to various processes, including the deposition of insect carcasses into littoral sediments, rather than into the deeper lake centers, where sediment cores are typically collected; dissolution of chitinous remains in alkaline lake water; and the consumption of the insects by fish (Morris *et al.* 2015). Given the small size of Hemlock Hollow and the low soil pH of *Tsuga* forests (e.g., Finzi *et al.* 1998), it seems unlikely that insect remains from an outbreak near Hemlock Hollow would be subject to the same processes that affect the taphonomy of beetle carcasses in the larger lakes studied in western North America. That said, the absence of insect remains from the low-*Tsuga* interval of Hemlock Hollow cores E and F could represent a change in environmental conditions that resulted in reduced preservation. For instance, if the basin dried out during the droughts that occurred during the middle Holocene (e.g., Newby *et al.* 2014), insect remains that were deposited into Hemlock Hollow at that time might have been destroyed. However, the condition of the pollen grains, which is very good overall, did not change during the period of reduced *Tsuga* abundance, suggesting that preservation conditions did not vary substantially through time.

The lack of *Lambdina fiscellaria* remains in the sediments of Hemlock Hollow does not necessarily mean that this species did not occur in the vicinity of the study site during the Holocene, nor does the absence of subfossil insects from the interval of low-*Tsuga* abundance preclude the possibility that insects or disease were involved to some degree in the mortality of *Tsuga* during its middle-Holocene decline. However, if a major outbreak of an insect pest, such as *Lambdina fiscellaria*, had an important role in the *Tsuga* decline, it would be reasonable to expect that a small basin like Hemlock Hollow, located beneath the canopy of a large *Tsuga* stand, would be an optimal location for the preservation of insect remains. Thus, the fact that insect remains were encountered at various depths in the Hemlock Hollow sediments, but not during the interval of low-*Tsuga* abundance, suggests that it was unlikely that *Lambdina fiscellaria*, or other insects, had a major role in the decline of *Tsuga* at Hemlock Hollow. Accordingly, the insect remains found in middle-Holocene sediments at other sites (Anderson *et al.* 1986, Bhiry and Filion 1996) may reflect local outbreaks of *Lambdina fiscellaria*, perhaps facilitated by drought or other changes in climate that stressed *Tsuga* populations (Shuman *et al.* 2004, Foster *et al.* 2006, Zhao *et al.* 2010, Marsicke *et al.* 2013).

**Literature Cited**


