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Evaluating the role of insects in the middle-Holocene *Tsuga* decline[1]

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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

Numerous paleoecological studies have explored the middle-Holocene decline of *Tsuga canadensis* (L.) Carrière (eastern hemlock; hereafter *Tsuga*) across eastern North America (Davis 1981, Webb 1982, Allison *et al*. 1986, Foster and Zebryk 1993, Hall and Smol 1993, Bhiry and Filion 1996, Yu *et al*. 1997, Fuller 1998, Foster 2000, Haas and McAndrews 2000, St. Jacques *et al*. 2000, Bennett and Fuller 2002, Calcote 2003, Shuman *et al*. 2004, Foster *et al*. 2006, Heard and Valente 2009, Zhao *et al*. 2010, Booth *et al*. 2012, Oswald and Foster 2012, Day *et al*. 2013, Marsicek *et al*. 2013, Oswald and Foster 2014, Oswald *et al*. 2014). *Tsuga* declined dramatically at approximately 5,500 calibrated years before present (cal yr BP), and its abundance remained low until about 4,000–3,500 cal yr BP. For many years, the *Tsuga* decline was attributed to a pathogen or insect outbreak (*e.g*., Davis 1981), and remains of *Lambdina fiscellaria* (hemlock looper) were found in sediments dating to the low-*Tsuga* interval (Anderson *et al*. 1986, Bhiry and Filion 1996). Subsequent studies linked this widespread ecological event to climate change (Shuman *et al*. 2004, Foster *et al*. 2006, Zhao *et al*. 2010, Marsicek *et al*. 2013), but the synchrony of the *Tsuga* decline and climate change has been questioned (Booth *et al*. 2012), and the possibility that *Tsuga* mortality was caused by the combined effects of climate change and insects or another biological agent has been raised (Shuman *et al*. 2004, Foster *et al*. 2006). 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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Table 1. Radiocarbon-dating results for Hemlock Hollow (Petersham, MA).

Depth (cm)	Laboratory No.	^{14}C mean age ± SD	δ^{13}C	Calibrated age range(s)	Median calibrated age
9–10	OS-107715	525 ± 20	−26.49	514–553; 612–619	535
13–14	OS-107623	65 ± 25	−27.90	Modern age	Modern
23–24	OS-107716	3,240 ± 30	−31.08	3,389–3,514; 3,524–3,559	3,460
32–33	OS-107717	240 ± 20	−27.19	0–3; 153–169; 282–308	291
39–40	OS-107624	4,320 ± 30	−25.65	4,840–4,962	4,873
51–52	OS-108078	415 ± 110	−26.81	0–9; 151–173; 275–654	438

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-m^2 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 Cyperaceae, Poaceae, *Osmunda cinnamomea* L., and *Sphagnum* sp. occur around the margins. The stand surrounding Hemlock Hollow is dominated by *T. 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 ^{14}C-dated pollen record from Black Gum Swamp, a forested wetland located about 50 m west of Hemlock Hollow (Foster and Zebryk 1993). The pollen data suggest that *Tsuga* arrived at Hemlock Hollow at about 10,000 cal yr BP, and the middle-Holocene interval of low *Tsuga* abundance is a prominent feature of the record, spanning 35–28 cm in the core.

We returned to Hemlock Hollow in June 2012 and used a modified Livingstone piston sediment sampler (Wright *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-cm^3 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 cm^3 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-cm^3 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 (^{14}C) analysis of six plant macrofossils. ^{14}C dates were converted to calibrated years before present using the IntCal13 calibration curve (Reimer *et al*. 2013).

Results and Discussion. The ^{14}C 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 ^{14}C 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

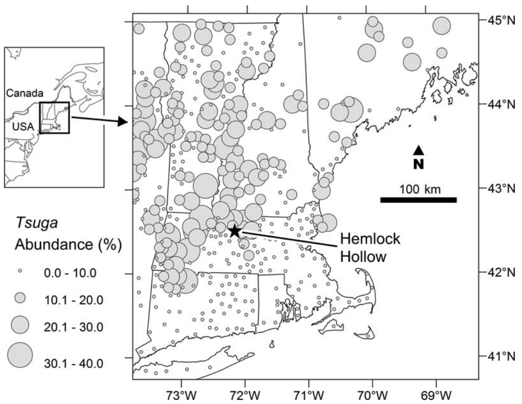

FIG. 1. Map of New England showing location of Hemlock Hollow and presettlement relative abundance (percentage values in witness-tree data set) of *Tsuga canadensis* (Cogbill *et al*. 2002).

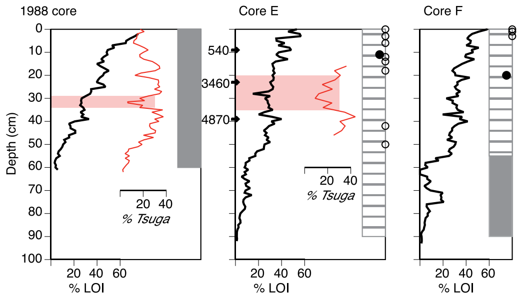

FIG. 2. Data from the 1988 core (Foster and Zebryk 1993) and cores E and F (this study) from Hemlock Hollow, including organic content (percentage of weight loss on ignition [% LOI]); *Tsuga* pollen percentages (1988 core and core E; shading highlights period of low [< 30%] *Tsuga* abundance); the intervals for which insect remains were analyzed (horizontal lines, cores E and F); calibrated radiocarbon (^{14}C) ages (arrows, core E); and the locations of insect remains (open circles are chironomid head capsules; black circles are beetle head capsules).

plant macrofossils being pushed downward through the sediment by the corer. The other three ^{14}C 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 Zebryk 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 ^{14}C 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, Marsicek *et al*. 2013).

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