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Decomposing the mid-Holocene *Tsuga* decline in eastern North America

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Abstract. The mid-Holocene decline of *Tsuga canadensis* (hereafter *Tsuga*) populations across eastern North America is widely perceived as a synchronous event, driven by pests/pathogens, rapid climate change, or both. Pattern identification and causal attribution are hampered by low stratigraphic density of pollen-sampling and radiometric dates at most sites, and by absence of highly resolved, paired pollen and paleoclimate records from single sediment cores, where chronological order of climatic and vegetational changes can be assessed. We present an intensely sampled (contiguous 1-cm intervals) record of pollen and water table depth (inferred from testate amoebae) from a single core spanning the *Tsuga* decline at Irwin Smith Bog in Lower Michigan, with high-precision chronology. We also present an intensely sampled pollen record from Tower Lake in Upper Michigan. Both sites show high-magnitude fluctuations in *Tsuga* pollen percentages during the pre-decline maximum. The terminal decline is dated at both sites ca. 5000 cal yr BP, some 400 years later than estimates from other sites and data compilations. The terminal *Tsuga* decline was evidently heterochronous across its range. A transient decline ca. 5350 cal yr BP at both sites may correspond to the terminal decline at other sites in eastern North America. At Irwin Smith Bog, the terminal *Tsuga* decline preceded an abrupt and persistent decline in water table depths by ~200 years, suggesting the decline was not directly driven by abrupt climate change. The *Tsuga* decline may best be viewed as comprising at least three phases: a long-duration pre-decline maximum with high-magnitude and high-frequency fluctuations, followed by a terminal decline at individual sites, followed in turn by two millennia of persistently low *Tsuga* populations. These phases may not be causally linked, and may represent dynamics taking place at multiple temporal and spatial scales. Further progress toward understanding the phenomenon requires an expanded network of high-resolution pollen and paleoclimate chronologies.

Key words: abrupt change; causal attribution; Eastern North America; Holocene; Michigan; paleoecology; temporal precision; *Tsuga* decline; vegetation dynamics.

INTRODUCTION

Abrupt ecological transitions, particularly in response to gradual or abrupt climatic changes, command increasing attention and concern in both ecological theory and application. The theory of complex adaptive systems predicts that ecological and other systems may reach critical thresholds, whereupon existing systems collapse and are quickly replaced by systems with contrasting properties (Holling 1992, Folke et al. 2004, Scheffer 2009). Considerable research effort is being devoted to documenting specific cases and identifying “leading indicators” or “early warning” signs (Carpenter and Brock 2006, Biggs et al. 2009, Hastings and

Wysham 2010). Parallel concerns have developed from empirical studies of climatic and ecological history, which indicate climatic and ecological transitions of varying magnitudes and rates during the past 100 000 years (NRC 2002, Williams et al. 2002, 2011, Foley et al. 2003, Alley and Ágústsdóttir 2005, Harrison and Sanchez Goñi 2010). Paleocological records offer a rich source of information on past ecological transitions, and understanding their causes and circumstances can help assess risks of loss or transformation of ecological goods and services in the future under a rapidly changing climate. Assessment of causation, however, as well as such fundamental phenomenological properties as synchrony, spatiotemporal pattern, and rate of change, requires detailed examination of paleocological records, with temporal, spatial, and taxonomic precision higher than routinely achieved in paleocological studies.

The mid-Holocene *Tsuga* decline in eastern North America is one of the most intensely studied and

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discussed ecological events of the Holocene. It is marked at individual sites by several centuries of high *Tsuga* pollen percentages, followed by a steep decline to low or trace levels that persist for at least two millennia (Davis 1981). Plant macrofossil sequences show similar patterns (Anderson et al. 1986, Jackson 1989, Spear et al. 1994, Reeves 2006), confirming that the *Tsuga* decline represents a reduction in population size rather than pollen productivity. The decline at individual sites appears to have occurred in less than a century, possibly less than a decade (Allison et al. 1986).

First recognized in pollen sequences from New England (Deevey 1939), the *Tsuga* decline drew particular attention with Margaret Davis's synthesis and summary (Davis 1981), in which she observed that the decline was apparently synchronous across the entire species range. In an elegant application of "strong inference" (Chamberlin 1890, Platt 1964) to paleoecology, Davis argued that the event was caused by a pest or pathogen outbreak by evaluating and rejecting a series of alternative hypotheses and by drawing analogies to the 20th century pathogen-driven *Castanea* and *Ulmus* declines in the same region (Davis 1981, Allison et al. 1986).

Although the pathogen hypothesis was widely accepted in the following decades (Webb 1982), new evidence suggests that climate change, an alternative hypothesis rejected by Davis, played a critical role in the decline. Lake level records indicate drawdown, rapid at some sites, approximately coincident with the *Tsuga* decline at sites in New England and the central Great Lakes (Yu et al. 1997, Haas and McAndrews 2000, Shuman et al. 2004, 2009b). Coastal areas of southern New England show a nearly concurrent rapid decline in *Quercus*, suggesting a common mechanism (Foster et al. 2006). Although a role for pests or pathogens has not been ruled out, several recent papers argue that the *Tsuga* decline resulted from abrupt climate change (Shuman et al. 2009b, Zhao et al. 2010b, Oswald and Foster 2011).

Recent high-resolution paleoecological and paleoclimatic studies indicate that long-term ecological dynamics are often temporally fine grained, whereby climatic change and variability across a range of time scales interact to induce ecological responses that also occur across a wide range of scales (Gray et al. 2006, Jackson et al. 2009, Shuman et al. 2009a, b, Booth et al. 2012). This complexity poses a central challenge for causal attribution in interpreting paleoecological records, particularly given the low sampling densities typical for pollen sequences, time-averaging of lake sediments, and imprecision of age estimates. Uncertainties are compounded in trying to compare records among different sites.

Understanding of the *Tsuga* decline is particularly hampered by three deficiencies in current knowledge and data. First, although the *Tsuga* decline has been treated as a synchronous event within the error limits of ^{14}C dating (Davis 1981, Webb 1982, Bennett and Fuller

2002), it remains unclear whether the event was truly synchronous across the entire region. A compilation and analysis of data from 60 sites places the age of the event at 5450 yr BP (Bennett and Fuller 2002), but dates at individual sites are spread over a period spanning >2000 years (Haas and McAndrews 2000, Bennett and Fuller 2002, Shuman et al. 2009b). (All ages reported in this paper [yr BP] are expressed as calendar years Before Present [1950 CE datum], unless specifically noted otherwise.) This variation might derive from errors in age estimation, but it may also indicate heterochrony.

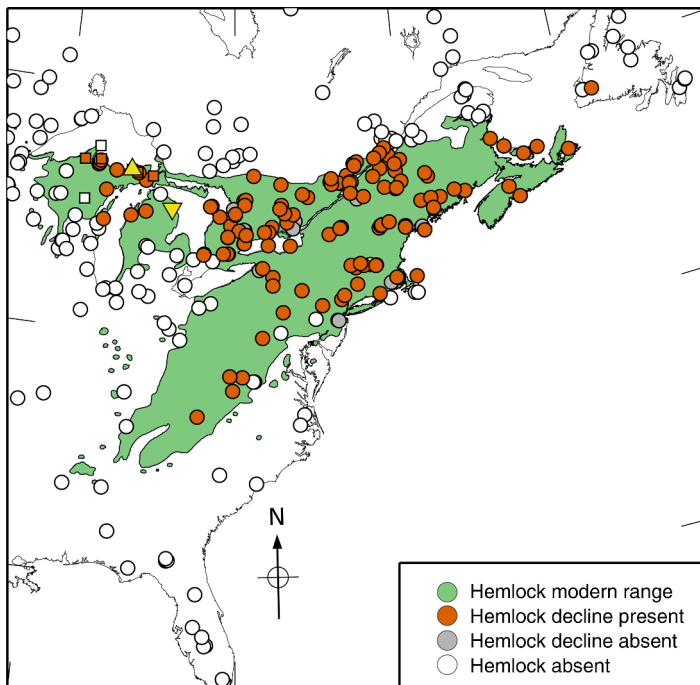
Second, the final *Tsuga* decline at some sites was preceded by transient declines in *Tsuga* pollen, followed by rebound to high percentages (e.g., Fuller 1998, Haas and McAndrews 2000, Foster et al. 2006, Oswald and Foster 2011). These fluctuations, absent in most low-density pollen sequences, might represent local disturbances, but may also indicate dynamic responses to climate variability or pathogen outbreaks preceding the final decline. The pre-decline fluctuations are poorly dated, and require careful assessment using high-frequency sampling and precise dating to assess their extent and synchrony.

Finally, currently available independent paleoclimate records are mostly from different sites or cores than those with pollen records of the *Tsuga* decline (Haas and McAndrews 2000, Foster et al. 2006, Shuman et al. 2009b). Although significant climate changes occurred between 6000 and 5000 yr BP, causal attribution is uncertain in the absence of clear demonstration that the *Tsuga* decline was coincident with, or immediately preceded by, a rapid climate transition. This is not a trivial task: uncertainties in age estimation at individual sites compound to greater uncertainties in correlating among sites or cores, and hence assessment of the relative timing of the *Tsuga* decline and climatic changes is rendered difficult.

All three deficiencies can be resolved by developing records with precisely dated, high-resolution pollen sequences associated with sensitive, independent, and precisely dated paleoclimate records. Ideally, the paleoclimate and pollen records should derive from the same sediment cores, allowing direct comparison of timing and sequence of events. In addition, recent developments in age modeling (Parnell et al. 2008, Blaauw and Christen 2011) can now support probabilistic approaches to dating the *Tsuga* decline, comparing it among sites, and correlating it with other paleoenvironmental changes.

We present results of a precisely dated, intensively sampled pollen sequence from an ombrotrophic peatland, Irwin Smith Bog, in the Lower Peninsula of Michigan. We compare that record with a paleohydrological record from the same sediment core, inferred from testate amoeba assemblages, which are sensitive to summer moisture deficit (Charman et al. 2000, Booth 2010). We also present an intensively sampled pollen sequence from a small lake, Tower Lake, in the Upper Peninsula of Michigan with moderately precise dating to

FIG. 1. Spatial distribution of the mid-Holocene *Tsuga* decline in eastern North America. The green-shaded area represents the modern distribution of hemlock, *Tsuga canadensis* (adapted from Little 1971). Individual symbols represent paleoecological sites. The two sites described in this paper are also shown: Irwin Smith Bog (inverted yellow triangle) and Tower Lake (yellow triangle). Circles represent sites from the Neotoma Database; squares represent other sites (S. T. Jackson, R. K. Booth, J. J. Andersen, T. A. Minckley, K. Reeves, *unpublished data*). Sites are classified as follows: *Tsuga* present in pollen record, and decline identified (red); *Tsuga* present in pollen record, but no decline identified (gray); *Tsuga* absent from pollen record (white). See the methodological details in Appendix A.



compare with the Irwin Smith Bog record. We use these records to address the following questions: When did the *Tsuga* decline occur in the region? Was the timing of the decline synchronous between the two sites, and was it synchronous with records from elsewhere in eastern North America? Were pre-decline fluctuations in *Tsuga* pollen abundance synchronous between the two sites, and with other sites in eastern North America? Was the *Tsuga* decline driven by a rapid transition toward persistent dry conditions? Our results indicate that the *Tsuga* decline was a more complex phenomenon than has been commonly assumed, and we prescribe a research strategy for effective understanding of the nature of the decline and its driving mechanisms.

METHODS

Irwin Smith Bog (informal name; 45°1'55" N, 83°37'5" W, 223 m elevation) is an ombrotrophic peatland located near Lake Huron in northwest Lower Michigan, USA (Fig. 1). The bog covers ~65 ha, but may have been larger before agricultural development of the surrounding landscape. *Sphagnum* mosses, various graminoids (mainly *Carex* spp.), low-growing ericaceous shrubs (*Kalmia polifolia*, *Chamaedaphne calyculata*), and scattered trees (*Larix laricina*, *Picea mariana*, *Pinus strobus*) characterize the hummock-hollow topography of the bog surface. Regional vegetation before 19th century land clearance comprised a mosaic of mixed conifer/hardwood forests (*Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, *P. strobus*, *Tsuga canadensis*), pine forests (*P. strobus*, *P. resinosa*, *P. banksiana*), and conifer swamps (*Picea mariana*, *Larix*

laricina, *P. strobus*, *T. canadensis*) (Albert and Comer 2008).

Tower Lake (informal name; 46°32'31" N, 86°2'13" W, 261 m elevation), is a small (2.6 ha) endorheic kettle pond on sandy glacial till 250 km northwest of Irwin Smith Bog in the eastern Upper Peninsula of Michigan (Reeves 2006) (Fig. 1). Surrounding second-growth forests are dominated by *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, *Pinus strobus*, and *Tsuga canadensis*, generally similar in composition to those before 19th century logging.

Sediment cores were obtained in summer 2004, using a modified Livingstone piston corer (10 cm diameter at Irwin Smith Bog; 7.5 cm diameter at Tower Lake) and a 7.6 cm diameter vibracorer for the lowermost sediments at Irwin Smith Bog. In this study, we concentrated on sediments dating between 7000 and 4000 yr BP. At Irwin Smith Bog, sediments dating between 6600 and 4000 yr BP were captured in a single drive with the piston corer, whereas sediments between 7000 and 6600 yr BP represented the upper 40 cm of the vibracore sediments. The upper portion of the Irwin Smith sequence has been reported elsewhere (Booth et al. 2012), and a Holocene pollen and macrofossil sequence from Tower Lake is described by Reeves (2006). Sediments dating between 7000 and 4000 yr BP comprise *Sphagnum* peats at Irwin Smith Bog and moderately compact, macrofossil-rich gyttja at Tower Lake.

At Irwin Smith Bog, we obtained subsamples (2 cm³) at contiguous 1-cm intervals along the length of the sediment core for pollen and testate amoeba analysis. Samples were prepared using standard techniques for

testate amoeba analysis, including boiling and nested sieving (Booth et al. 2010). The sieve fraction $\leq 355 \mu\text{m}$ and $\geq 15 \mu\text{m}$ was retained, stained with Safranin O dye, and stored in glycerol. These residues were used for both pollen and testate amoeba analysis. Testate amoebae were analyzed at 1-cm intervals between 7000 and 4000 yr BP, and pollen was analyzed at 1-cm intervals between 6800 and 4000 yr BP. Testate amoeba were identified and tallied at $400\times$ magnification to a minimum sum of 150 tests (for a few samples this count total was not possible), following taxonomy of Charman et al. (2000), except as noted by Booth (2008). For Tower Lake, we obtained sediment subsamples (1 cm^3) at contiguous 1-cm intervals and prepared them for pollen analysis using standard chemical digestion techniques (Jackson 1999). Samples from Tower Lake were counted at 1-cm intervals between 6100 and 4590 yr BP, and at minimum 5-cm intervals between 7000 and 6100 yr BP and between 4590 and 4000 yr BP. Between 200 and 300 arboreal pollen grains were typically counted in each sample at both sites, with some count totals higher. Pollen percentages were calculated based on a sum of arboreal pollen types.

A transfer function developed from modern testate amoeba communities and water table depth data collected from 650 sites within North American peatlands was used to infer water table depth from fossil testate amoeba assemblages (Booth 2008). The transfer function provides an estimate of the mean depth of the water table during the growing season. A simple weighted-average model was used, and standard leave-one-out cross-validation suggests an error of about ± 8 cm. Bootstrapping techniques were used to estimate sample-specific errors for the Irwin Smith Bog assemblages ($n = 1000$). Reconstructions were not performed for samples if < 50 testate amoebae were counted ($n = 5$) (Payne and Mitchell 2007).

Dense arrays of AMS (accelerator mass spectrometry) ^{14}C dates were obtained from the two sites (Appendix B: Tables B1 and B2), with most dates positioned at or immediately below the depth of the *Tsuga* decline. At Irwin Smith Bog, 14 AMS ^{14}C dates were obtained between 7000 and 4000 yr BP, with six dates positioned within 10 cm and 11 dates within 20 cm of the *Tsuga* decline. At Tower Lake, seven AMS ^{14}C dates were obtained between 7000 and 4000 yr BP; of these, two were within 10 cm and five within 25 cm of the *Tsuga* decline. *Sphagnum* or terrestrial macrofossils were used for all ^{14}C dates (Appendix B: Tables B1 and B2). Age models were fit using a Bayesian approach developed by Blaauw and Christen (2011), which uses realistic estimates of sediment accumulation and the autocorrelation of this accumulation to relate the depth of any given pollen sample to calibrated AMS dates. Plots of the age models, together with information on prior and posterior distribution of the parameters used, are given in Appendix C: Figs. C1 and C2.

We identified the *Tsuga* decline at both sites using two complementary approaches: (1) identifying the sample at which *Tsuga* pollen percentages were halved from the preceding sample (Bennett and Fuller 2002), and (2) Bayesian change-point analysis (Barry and Hartigan 1993, Blois et al. 2011). In the latter method, we partitioned the sequence of *Tsuga* pollen percentages into sections with constant means, and calculated the posterior probability that each sample is a break point between two sections. We retained as break points only those samples where the posterior probability exceeded 0.90. Although both methods identified a series of samples through the cores (Appendix D: Figs. D1 and D2), each method identified precisely identical stratigraphic levels for the final *Tsuga* decline at both sites. We also used these methods to identify transient *Tsuga* declines that preceded the terminal *Tsuga* decline at our sites (Appendix D: Figs. D1 and D2).

We tested for differences in timing of the *Tsuga* decline between our study sites using the probability density function (PDF) of ages for the decline at each site. We first calculated the overlap between the two age PDFs using the overlap method of Schmid and Schmidt (2006), and then used pairwise comparisons of dates randomly extracted from the two age PDFs (Parnell et al. 2008) to study potential diachroneity. We used 10 000 random sets of dates, and constructed the distribution of differences. Because our test was for diachroneity, the null hypothesis was that the age of the *Tsuga* decline did not differ between the sites. We also used this method to estimate the age difference between the *Tsuga* decline and the reduction in water table depth at Irwin Smith Bog, with the modification that the dates must increase monotonically with depth (Parnell et al. 2008). Finally, we used the method of Parnell et al. (2008) to test for diachroneity among the terminal declines at each site and transient declines preceding the terminal decline.

RESULTS

Tsuga pollen at Irwin Smith Bog increased from trace levels ca. 7100 yr BP, following a sawtooth pattern with high-magnitude, high-frequency fluctuations superimposed on a trend of steadily increasing maxima until ca. 5300 yr BP, when it attained its highest level of 40% (Fig. 2; Appendix E: Fig. E1; Appendix F: Fig. F1). It underwent particularly sharp declines ca. 6790, 6370, 5700, and 5340 yr BP, rebounding each time to a transient maximum. The final decline, from a maximum of 35% ca. 5050 yr BP, was followed by low *Tsuga* pollen percentages ($\leq 10\%$) (Fig. 2a) that persisted until ca. 3100 yr BP (Appendix E: Fig. E1). Our best estimate of the timing of the terminal *Tsuga* decline at Irwin Smith Bog is 5025 yr BP, with an estimated uncertainty range (95% confidence intervals) of 4895–5160 yr BP (Fig. 2a).

At Tower Lake, the initial *Tsuga* increase commenced ca. 6000 yr BP, reaching an initial maximum ($> 25\%$) ca. 5600 yr BP (Fig. 2b; Appendix E: Fig. E2; Appendix F: Fig. F2). During and after this initial increase, *Tsuga*

percentages show fluctuations similar to those at Irwin Smith Bog, though of lesser magnitude. The most visible one is centered at ca. 5390 yr BP (Fig. 2b), and was clearly identified by change-point analysis (Appendix D: Fig. D2). The final decline was followed by persistent low percentages ($\leq 5\%$) until ca. 3000 yr BP (Appendix E: Fig. E2). Our age estimate for the terminal decline at Tower Lake is 4887 yr BP, with estimated range of 4855–5270 yr BP (Fig. 2b).

The probability distributions for our age estimates of the terminal *Tsuga* decline at Irwin Smith Bog and Tower Lake overlap by 68% (Appendix G: Fig. G1). Pairwise comparison of dates (Parnell et al. 2008) shows that zero difference (i.e., synchronicity) is contained within the 95% highest posterior density range (HDR) of these differences (Appendix G: Fig. G2), and hence we are unable to reject the null hypothesis that the age of the terminal *Tsuga* decline did not differ between the two sites.

Pairwise comparison of dates between both *Tsuga* declines at Tower Lake (the terminal decline and the preceding transient decline) and the four identified declines at Irwin Smith Bog (terminal decline and three transient declines) indicate that all pairs of events were diachronous between sites except two: the terminal decline discussed above, and a transient decline centering on 5340 yr BP at Irwin Smith Bog and 5385 yr BP at Tower Lake (Appendix G: Figs. G1 and G2; Appendix H: Fig. H1).

The record of water table depth (WTD) from Irwin Smith Bog shows WTDs near the surface of the peatland (moist conditions) between ca. 7200 and 6200 yr BP, with overall moist but fluctuating conditions between 6200 and 5000 yr BP (Fig. 3; Appendix I: Fig. I1). Rapid but transient moisture declines occur ca. 6100, 5700, and 5600 yr BP, but none correspond to the transient *Tsuga* declines at the site (Fig. 3). The WTD record shows a moisture decline rapidly after 5000 yr BP, with persistent low moisture until ca. 3000 yr BP (Fig. 3; Appendix J: Fig. J1). Onset of drier conditions occurs well after the terminal *Tsuga* decline (Fig. 3), with a lag of nearly 200 years (Appendix J: Fig. J1). Our estimate for the timing of the WTD decline (defined by change point analysis) is 4858 yr BP, with a 95% confidence interval range of 4951–4590 yr BP. Probability distributions for our age estimates of the WTD decline and the *Tsuga* decline at Irwin Smith Bog overlap by only 6% (Appendix J: Fig. J1), and pairwise comparison of dates indicate the ages of the two events are significantly different (Appendix J: Fig. J2). The age of the Irwin Smith WTD decline is closer to the estimated age of the *Tsuga* decline at Tower Lake (Appendix J: Fig. J3), and we cannot conclude that the ages are significantly different (Appendix J: Fig. J4). However, age uncertainties are greater than for the comparison within Irwin Smith Bog; we are more confident about the stratigraphic offset within a single core than marginal overlap in age distributions between two sites.

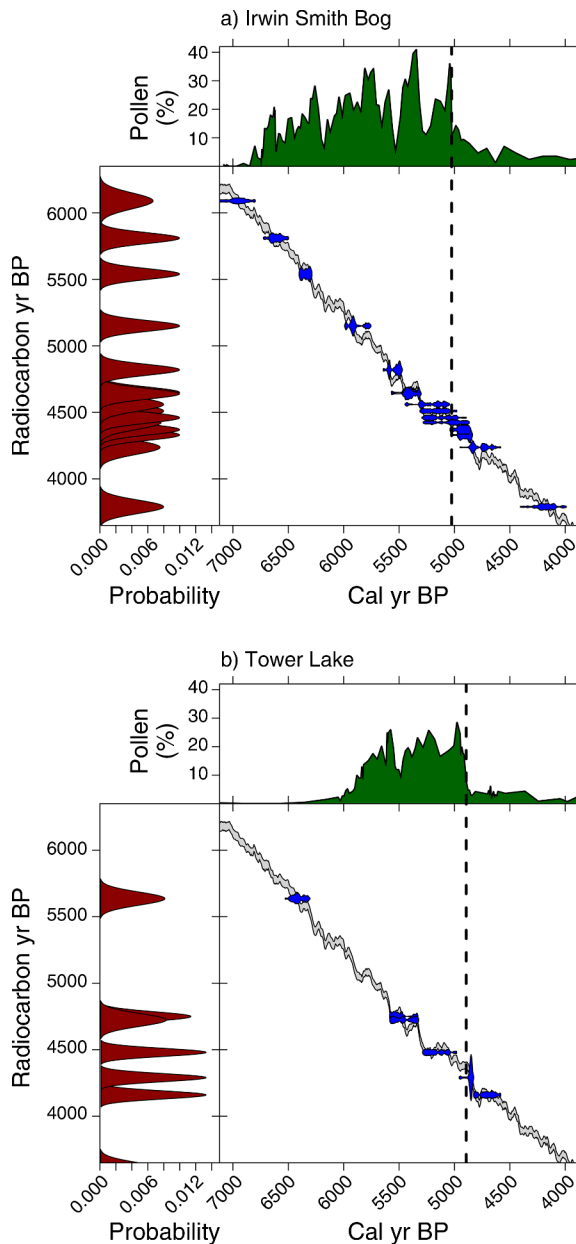


FIG. 2. Estimation of the timing of the *Tsuga* decline at (a) Irwin Smith Bog and (b) Tower Lake. The upper panel in each set of graphs shows *Tsuga* pollen percentages (green) at the respective site between ca. 7000 and 4000 yr BP. The left-hand panel in each set of graphs shows the 2σ distribution for each AMS (accelerator mass spectrometry) ^{14}C age obtained from the core (red), expressed in ^{14}C yr BP. The central graphs portray the ^{14}C -calendar year calibration curve (Reimer et al. 2009) between ca. 7000 and 4000 yr BP (gray curve, calibrated years BP), and the probability density functions (PDF) for the calendar year age estimate corresponding to each ^{14}C date (blue). The vertical dashed line shows the estimated location of the terminal *Tsuga* decline. The PDFs for the individual ages place constraints on the age estimates for the terminal *Tsuga* decline and other events, and they provide the basis for statistical assessment of synchronicity or diachroneity of events.

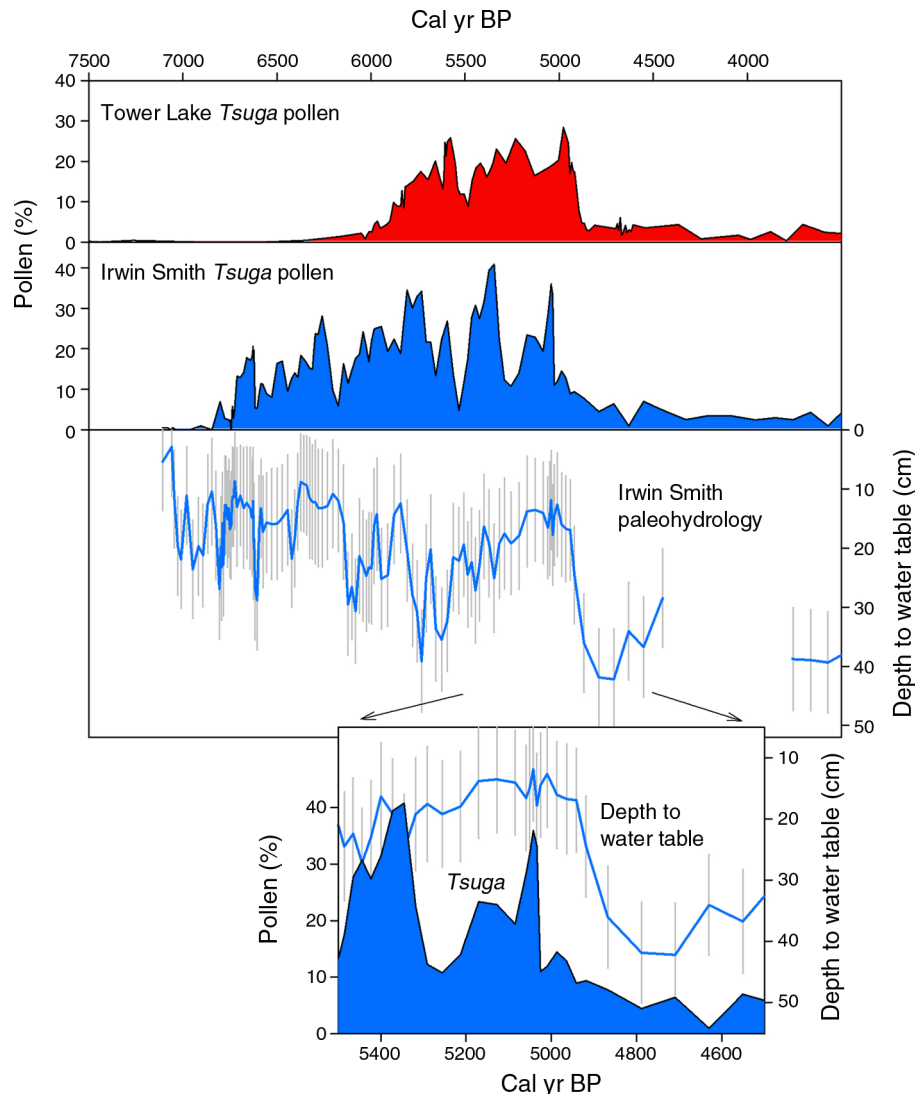


FIG. 3. Temporal relationship between *Tsuga* pollen percentages at Tower Lake (red) and Irwin Smith Bog (blue) and estimated depth to water table (DWT) at Irwin Smith Bog (blue line). The inset shows a detailed comparison between *Tsuga* pollen percentages and DWT at Irwin Smith Bog between 5500 and 4500 yr BP. Vertical bars denote bootstrapped error estimates ($n = 1000$). The gap in the DWT reconstructions between 4400 and 3800 yr BP represents a period of very low sediment accumulation rates, highly humified peat, and poor preservation of testate amoebae (Appendix I: Fig. 11).

DISCUSSION

One event, or many?

Our age estimates for the *Tsuga* decline at Irwin Smith Bog and Tower Lake postdate a statistical estimate from compiled records (Bennett and Fuller 2002) by ~ 400 years. However, the latter compilation yielded a multimodal age distribution pattern, in part because of irregularities in the radiocarbon calibration curve, and in part because of the broad distribution of ^{14}C age estimates for the *Tsuga* decline (Bennett and Fuller 2002). The estimated age of 5450 yr BP (Bennett and Fuller 2002) falls entirely outside the age PDFs for the *Tsuga* decline at both our sites. However, age estimates

at our sites fall close to one of the alternate modes identified in that analysis, centering on 5100 yr BP.

Two potential explanations arise for the discrepancy between the age estimates for our sites and those of Bennett and Fuller (2002). First, if the *Tsuga* decline across eastern North America was indeed a single event, effectively synchronous to within a century, aliasing (distortion) may have arisen in site aggregations owing to a combination of age uncertainties at individual sites, irregularities in the radiocarbon-calibration curve in the centuries bracketing the event, low pollen-sampling density in individual cores, and effects of the pre-decline fluctuations (particularly troughs) in *Tsuga* pollen.

Simulations and analyses using the Irwin Smith Bog and Tower Lake pollen sequences indicate that stratigraphic placement and age estimates for the *Tsuga* decline are sensitive to stratigraphic pollen-sampling density, and are amplified by pre-decline troughs in *Tsuga* pollen (Liu et al. 2012).

Alternatively, the *Tsuga* decline, although a singular event at individual sites, may not have been a uniform, synchronous event at regional or subcontinental scales (Shuman et al. 2009b). The event may have been time transgressive, occurring as a continuous, subcontinental wave spanning several centuries, or it may have been episodic, with multiple declines at different sites and in different regions, with or without spatial and temporal coherence. One or more of the pre-decline excursions at Irwin Smith Bog and Tower Lake may have been synchronous with the final decline at other sites; in particular, the negative anomalies ca. 5340 yr BP (Irwin Smith Bog) and 5390 yr BP (Tower Lake) are close to the modal age (5450 yr BP) estimated by Bennett and Fuller (2002).

Although aliasing may account for some differences in age estimates among sites, the preponderance of evidence suggests that the terminal *Tsuga* decline was heterochronous among sites. The modal estimate of 5450 yr BP (Bennett and Fuller 2002) seems robust in view of the number of chronologies that converge on that date, and dating and sampling density at the most intensively studied individual sites (e.g., Fuller 1998, Oswald and Foster 2011) are inconsistent with a younger age for the decline. We are currently investigating synchrony and spatial patterns of *Tsuga* fluctuations at sites across eastern North America using the Neotoma database ([available online](http://www.neotomadb.org))⁷ and statistical approaches similar to those in the current paper. However, density of ¹⁴C dating and pollen sampling at most published sites are inadequate to provide precise estimates of synchrony and number of terminal events. Additional high-density pollen records with high-precision chronologies and quantified uncertainties are needed from sites across the *Tsuga* decline region (Fig. 1). Assessment of mechanisms underlying the decline will remain difficult until its spatial and temporal patterns are more precisely characterized.

Did abrupt climate change drive the Tsuga decline?

Evidence is now strong that eastern North America experienced climatic changes between 6000 and 4500 yr BP, coinciding with the *Tsuga* decline interval. The changes involved a net transition from relatively wet to relatively dry conditions (Yu et al. 1997, Newby et al. 2000, 2011, Shuman et al. 2001, 2004, 2009b, Booth et al. 2002, 2004, Foster et al. 2006), possibly accompanied by cooling (Kirby et al. 2002, Zhao et al. 2010b). A climatic or hydrological transition, often rapid, oc-

curred at many sites during this interval (e.g., Fig. 3), suggesting that the abrupt decline in *Tsuga* was driven by an abrupt climatic transition (Foster et al. 2006, Shuman et al. 2009b). However, most of the evidence for climatic change is only loosely associated in time with the *Tsuga* decline, owing in part to imprecision in age estimates and uncertainties in correlating events among diverse cores and sites. Attribution of the decline to a climate driver, gradual or abrupt, will be strengthened by direct evidence that the decline at individual sites either coincided with or was preceded closely by a climate transition. To date, only a few records have pollen data associated directly with independent paleoclimate proxies from the same core, where the timing of the decline relative to climate change can be assessed.

In some cases, the *Tsuga* decline precedes the change in the paleoclimate proxy. At Irwin Smith Bog, the *Tsuga* decline precedes the hydrological transition to drier conditions by 178 years with a 95% HDR range of 76 to 398 years (Fig. 3; Appendix J: Figs. J1 and J2). At Crawford Lake in southern Ontario, the *Tsuga* decline precedes a lithological transition (marl to organic marl) interpreted as indicating lower lake levels (Yu et al. 1997). Carbonate $\delta^{18}\text{O}$ values at Crawford Lake are higher before the *Tsuga* decline than after it, but sampling density is too low to assess whether the isotopic transition preceded, coincided with, or followed the *Tsuga* decline. At Wildwood Lake in coastal Long Island (New York), the *Tsuga* decline precedes a sediment organic-content excursion suggestive of draw-down (Foster et al. 2006). A temporally dense carbonate $\delta^{18}\text{O}$ record at Lake Grinnell in northern New Jersey shows steadily decreasing (cooling) values between ca. 5800 and 3000 yr BP, spanning the *Tsuga* decline period (Zhao et al. 2010a, b). The $\delta^{18}\text{O}$ values fluctuate at roughly centennial scales during this period, but no clear transition is apparent at the time of the local *Tsuga* decline (Zhao et al. 2010b).

Other sites indicate mid-Holocene climate transitions, but timing relative to *Tsuga* pollen patterns is obscure. A transition from lacustrine sediment to peat in a swamp in southeast Massachusetts is dated at 5600 yr BP, but *Tsuga* pollen percentages are very low and the *Tsuga* decline is subtle; its timing relative to the sediment transition is not clear (Newby et al. 2000). A nearby lake shows mid-Holocene drawdown (ca. 5400 yr BP), coinciding more closely with the *Tsuga* decline, but sampling density is low (Shuman et al. 2001). A densely sampled lacustrine-calcite $\delta^{18}\text{O}$ record from central New York shows a relatively rapid mid-Holocene transition, which may indicate either decreasing temperatures or a shift in precipitation seasonality (Kirby et al. 2002). This transition is dated between 5400 and 4800 yr BP, but the chronology is based on interpolation between two ¹⁴C samples spanning several lithological transitions, and one date is based on moss peat, potentially subject to carbonate error. In Upper Michigan, a kettle basin 5 km

⁷ www.neotomadb.org

northeast of Tower Lake converted from sedge fen to near-ombrotrophic *Sphagnum* peatland ca. 5100 yr BP, but the brief *Tsuga* maximum at the site (and the decline) follows the sediment transition (Booth et al. 2004). Mid-Holocene sediment transitions are recorded at other sites in the region (e.g., Booth et al. 2002, Shuman et al. 2004).

It is conceivable that the *Tsuga* decline occurred as an immediate mass-mortality response to abrupt climate change, while the paleoclimate-proxy responses at Irwin Smith Bog and other sites were delayed by various hydrological, geochemical, or biological processes. Such a lag is unlikely in the case of Irwin Smith Bog. Ombrotrophic peatlands are hydrologically sensitive to changes in available moisture, particularly summer moisture deficit, spanning a few years (Charman 2002), and testate amoeba records reliably record both transient and persistent hydrological changes at sub-decadal to decadal scales (Charman 2007, Booth 2010). The time lag, on the order of two centuries, between the *Tsuga* decline and the paleoclimate proxy at Irwin Smith Bog suggests that abrupt climate change was not the proximal driver of the population decline. However, it remains conceivable that a proximal climate driver, perhaps related to winter precipitation, went unrecorded in the Irwin Smith proxy records.

The transient *Tsuga* declines recorded in the millennium preceding the final decline at many sites (e.g., Fig. 2) may represent responses to transient drought events preceding the final decline (Haas and McAndrews 2000, Oswald and Foster 2011). Brief drought events, apparently multidecadal in duration, are recorded at Irwin Smith Bog (Fig. 2) and at other sites in the region both before and after the final *Tsuga* decline (Booth et al. 2004, 2005, Shuman et al. 2009b). No clear temporal correspondence is apparent between pre-decline droughts and either *Tsuga* pollen percentages (Fig. 2) or accumulation rates (Appendix F: Fig. F1) at Irwin Smith Bog. Although the Irwin Smith Bog record suggests that pre-decline variations in *Tsuga* populations were not driven by drought variability, additional studies pairing high-density pollen records with climate-sensitive proxies from the same cores are desirable to resolve the question.

*Was the Tsuga decline a phenomenon,
or an epiphenomenon?*

In most discussions to date, the *Tsuga* decline has been treated as a single entity, wherein the explanation for the decline itself has been identical or closely linked to the explanation for the extended post-decline period of low *Tsuga* abundance. In order to better understand the decline, its underlying properties and mechanisms, and its implications for ecology and conservation, it may be beneficial to decouple the various elements of the event and consider each separately. We suggest that the *Tsuga* decline in the traditional sense may be an epiphenomenon, consisting of at least three phases,

which may or may not have been closely linked from a causal standpoint.

The first phase comprises the pre-decline *Tsuga* maximum, during which *Tsuga* attained higher populations in many regions than at any time in the late Holocene. This period displays high-magnitude fluctuations in *Tsuga* pollen spaced a few centuries apart (e.g., Figs. 2 and 3). These fluctuations appear at multiple sites, including all sites with high-density pollen sampling (e.g., Anderson et al. 1992, Fuller 1998, Oswald and Foster 2011). These fluctuations might have been driven by widespread disturbances, including pest or pathogen outbreaks, or by transient climate events (e.g., decadal or multidecadal droughts). The Irwin Smith Bog record reveals decadal to multidecadal hydrological anomalies during this period, but they show no consistent temporal relationship with the *Tsuga* excursions (Fig. 3). Alternatively, the *Tsuga* fluctuations might represent periodic regional scale disturbances. Charcoal records show no corresponding fire events at Irwin Smith Bog (Appendix E: Fig. E1) or Tower Lake (C. Long, *personal communication*). Pest or pathogen outbreaks remain viable as a mechanism, albeit with limited direct evidence (e.g., Bhiry and Filion 1996). Critical questions for this period include: Why were *Tsuga* populations so high across the region? Did high-frequency population fluctuations occur across its range? Were these fluctuations synchronous within or among regions? What factor(s) drove the transient declines, and the rapid rebounds to former high levels? Was there a common driver for these fluctuations? Immediate future work should focus on assessing synchrony of these fluctuations among sites and regions, and on developing additional records linking sensitive, temporally precise paleoclimate proxies with pollen sequences.

The second phase comprises the terminal decline itself. At individual sites, the terminal decline may simply represent the last of a series of negative excursions (i.e., it is causally related to the earlier declines). Alternatively, it may be a singular event unrelated to previous fluctuations. Although the available evidence (discussed in the preceding paragraphs) does not currently support abrupt climate change as a driver of the decline itself, additional tests involving sensitive proxies should be sought. Critical remaining questions include: Was the decline truly synchronous, or heterochronous? If, as appears, the terminal decline was heterochronous, how many terminal events were there? Do they display coherent structure in space and time? Were terminal declines at some sites synchronous with pre-decline fluctuations at others? How rapidly did populations collapse at individual sites? What was the relationship (order and timing) between the decline and climate transitions at individual sites and regions? Was the terminal decline driven by rapid climate change in some regions but not in others?

The third and final phase consists of the persistent post-decline *Tsuga* minimum, spanning two or more millennia at most sites. This period coincides generally with an extended dry period (e.g., Fig. 3; Appendix I: Fig. 11). *Tsuga* populations increased across much of its range during a trend toward cooler and moister conditions 3000 to 2000 yr BP (Williams et al. 2004). However, significant wet periods are recorded between 5000 and 3000 yr BP in New England (Shuman et al. 2009b) and in parts of the Great Lakes region (Booth et al. 2004), well before *Tsuga* populations increased again. Did those wet periods comprise a seasonal moisture regime unsuitable for *Tsuga*, unlike that during the pre-decline period (Shuman et al. 2009b)? *Tsuga* populations declined or disappeared across a broad elevational gradient in the Adirondack and White Mountains, including sites up to 200 m above its current elevational limits (Jackson 1989, Jackson and Whitehead 1991, Spear et al. 1994). Other low-elevation species (*Pinus strobus*, *Betula alleghaniensis*) persisted above their modern limits until as recently as 3000–2000 yr BP. Failure of *Tsuga* to recolonize moist, high-elevation sites after the decline suggests that moisture per se was not the critical or sole factor limiting its populations after the decline, although seasonal moisture or moisture–temperature interactions may have been involved.

The terminal decline and persistent trough may have arisen from interaction of dynamics operating at different temporal and spatial scales. Did a rapid climate transition following a few decades after the terminal decline (e.g., Fig. 3) set in motion a contingent series of ecological processes (Jackson et al. 2009), whereby *Tsuga* populations were unable to rebound after a collapse? Does the lack of recovery represent a cross-scale interaction (Holling 1992, Peters et al. 2007) between high-frequency ecological dynamics (e.g., pest or pathogen outbreaks) and lower-frequency climate change? A regional decline in *Fagus grandifolia* populations associated with multidecadal droughts of the Medieval Climate Anomaly shows a series of fluctuations in pollen percentages, but the time series shows a ramp-down pattern in which each successive peak (“recovery”) was at a generally lower level than the preceding peak (Booth et al. 2012). The mid-Holocene *Tsuga* pattern shows no such ramp-down, with successive peaks similar to or even exceeding preceding peaks, until the final decline (Fig. 2). This contrasting pattern may represent a different set of mechanisms or responses. Comparison of mid-Holocene *Tsuga* behavior with population fluctuations and declines of other species at other times may reveal a suite of patterns and mechanisms.

Although it is tempting to speculate on the implications of the *Tsuga* decline for future global change, and to link it to threshold dynamics and critical-transition theory, it may be premature to do so in the absence of better understanding of the precise nature and timing of the various phenomena associated with the *Tsuga*

decline. Whether it was a singular set of events arising from concatenation of dynamics at multiple temporal and spatial scales, or a relatively simple force-and-response causal chain, has a strong bearing on its ecological and conservation implications. At the minimum, however, it represents an important case study in which a widespread and abundant species underwent locally rapid and persistent population decline across its range, indicating finite risk that other species might undergo similar declines in the future. Better understanding of the dynamics underlying the *Tsuga* decline will provide a better basis for assessing risks and vulnerabilities of such events in the future.

CONCLUSIONS

The mid-Holocene *Tsuga* decline has been recognized for three decades as a prominent feature of pollen sequences across much of eastern North America. Its singular features, including its apparent rapidity, synchrony, and persistence, have rendered it an important and fertile paleoecological platform for hypothesis testing and mechanistic explanation. The event’s apparent simplicity may be illusory, however. The event may comprise three distinct phases, each with features at different spatial and temporal scales and each with potentially different mechanisms. The terminal mid-Holocene decline of *Tsuga* at individual sites was certainly rapid, compared to other Holocene transitions, and was likely on the order of one or a few decades. However, more precise determinations of the rapidity of the decline are required at multiple sites to help assess mechanisms. Although the event was roughly synchronous, insofar as age estimates for most individual sites fall within a 1000-year time window and many cluster within narrower windows, precise synchrony remains unclear. At many sites the terminal decline was preceded by abrupt declines in *Tsuga* populations, followed by rapid rebounds. One or more of these events at some sites may coincide with the terminal decline at others. Finally, the event was persistent, in that *Tsuga* populations remained at very low levels for 1000–2000 years after the terminal mid-Holocene decline. The low *Tsuga* populations between ca. 5000 and 3000 yr BP may be the most important feature held in common by multiple sites, and seems most clearly related to climate. The mechanisms underlying the post-decline population trough may not be related to the mechanisms driving the decline itself, nor to those responsible for the pre-decline fluctuations in *Tsuga*.

Further progress in understanding the *Tsuga* decline will depend on development of a network of high-density, temporally precise pollen records across the region, together with additional sequences where pollen records can be compared directly and precisely to independent paleoclimate records. The *Tsuga* decline may appear enigmatic, but poses an important and soluble challenge for paleoecology. Decoupling the elements of the event and delineating its spatial and

temporal patterns should constrain and refine the underlying mechanisms.

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SUPPLEMENTAL MATERIAL

Appendix A

Methodology used to identify the *Tsuga* decline in Fig. 1 (*Ecological Archives* E093-163-A1).

Appendix B

Radiocarbon dates (*Ecological Archives* E093-163-A2).

Appendix C

Age–depth models (*Ecological Archives* E093-163-A3).

Appendix D

Identification of *Tsuga* decline at individual sites (*Ecological Archives* E093-163-A4).

Appendix E

Pollen-percentage diagrams for study sites (*Ecological Archives* E093-163-A5).

Appendix F

Pollen-accumulation-rate diagrams for study sites (*Ecological Archives* E093-163-A6).

Appendix G

Comparison of age estimates for the *Tsuga* decline between study sites (*Ecological Archives* E093-163-A7).

Appendix H

Comparison of timing of early *Tsuga*-decline events among sites (*Ecological Archives* E093-163-A8).

Appendix I

Paleohydrological records from Irwin Smith Bog (*Ecological Archives* E093-163-A9).

Appendix J

Comparison of age estimates between the *Tsuga* decline and the water-table decline at Irwin Smith Bog (*Ecological Archives* E093-163-A10).