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Note

Eastern hemlock (*Tsuga canadensis*) as an alternate host for spruce budworm (*Choristoneura fumiferana*): dendrochronological evidence from Maine, USA

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Abstract

In northeastern North America, episodic eastern spruce budworm (*Choristoneura fumiferana*) outbreaks extensively defoliate balsam fir (*Abies balsamea*) and spruces (*Picea glauca, Picea rubens, Picea mariana*). We investigated eastern spruce budworm defoliation in eastern hemlock (*Tsuga canadensis*), a reported alternate host species, during previously documented outbreaks in Maine, USA. We compiled red spruce and hemlock tree-ring series from nine sites, seven of which showed synchronous radial growth reductions in spruce and hemlock during documented budworm outbreaks. Outbreak evidence varied among sites, but growth reductions were observed in six study sites during a 1914 outbreak. Synchronous growth reductions between spruce and hemlock suggest that when budworm defoliation occurred in spruce at a given site, hemlock typically experienced at least some level of defoliation. Relative budbreak synchrony with preferred host species may contribute to hemlock's suitability as a host. This research is timely given the recent spruce budworm population increase in this region.

Key words: dendroecology, dfoliatR, forest disturbance, host-nonhost analysis, insect defoliation, red spruce

Introduction

Eastern spruce budworm (*Choristoneura fumiferana* (Clem.), Lepidoptera; hereafter budworm) is a tenacious defoliator of conifer forests in northern New England and the Great Lakes region (USA) and eastern Canada, where its preferred host species are (in descending order) balsam fir (*Abies balsamea*) and white (*Picea glauca*), red (*Picea rubens*), and black (*Picea mariana*) spruce (Mattson et al. 1988). Budworm feeds on buds and new foliage of these species, reducing capacity to photosynthesize over the growing season and causing subsequent growth reductions and potential mortality. Outbreaks occur roughly every 40 years in eastern Canada (Boulanger et al. 2012) but are more episodic in New England (Fraver et al. 2007). The ecological and economic impacts of budworm infestations on preferred host species are well documented (e.g., MacLean 1980). However, much less is known about impacts on alternate budworm host species, including eastern larch (*Larix laricina*), eastern white pine (*Pinus strobus*), and eastern hemlock (*Tsuga canadensis*) (Kucera and Orr 1981).

Eastern hemlock is an ecologically important species in eastern North America. Its longevity and deep shade tolerance create unique habitats, microclimates, and nutrient cycling patterns throughout its range (Ellison 2014). The wood is used commercially for pulpwood, dimension lumber, boards, and construction and landscape timbers. Eastern hemlock is the fifth most abundant tree species in Maine, USA, in terms of growing stock volume (Woodall et al. 2022), at times co-occurring with red spruce, balsam fir, and northern hardwoods. Several insects are recognized to impact health and productivity of eastern hemlock, such as hemlock looper (*Lambina fiscellaria*), hemlock borer (*Melanophila fulvoguttata*), hemlock scale (*Hemiberlesia ithacae*), spongy moth (*Lymantria dispar dispar*), and hemlock woolly adelgid (*Adelges tsugae),* in addition to budworm.

A recent dendrochronological project analyzing eastern hemlock from Howland Research Forest in central Maine revealed dramatic radial growth reductions dating to the late 1910s, coinciding with a known budworm outbreak beginning in 1914 (Fraver et al. 2007). A search of the refereed budworm literature revealed little information regarding eastern hemlock defoliation. However, eastern hemlock was mentioned as a budworm host species in Maine in the gray literature as early as 1919 (Colby 1919), and a 1988 report on the 1970s spruce budworm outbreak in Maine describes hemlock and red spruce succumbing to spruce budworm in Maine's southeast coastal region in 1982 (Irland et al. 1988). Additional reports suggest that eastern hemlock defoliation occurs in mixed-species stands following extensive defoliation of preferred species such as balsam fir and spruce (Godman and Lancaster 1990; MacLean and Clark 2021). Despite these mentions in the literature, the nature of budworm defoliation on eastern hemlock—including severity and temporal patterns—is largely unknown.

These initial observations presented an opportunity to utilize a network of tree-ring records of co-occurring host and alternate host species to more systematically examine the extent to which eastern hemlock serves as an alternate budworm host. We used tree-ring data from both red spruce (a known host) and eastern hemlock, collected from nine mixed-species sites across Maine. An existing dendrochronological record of budworm outbreaks in northern Maine, based on red spruce (Fraver et al. 2007), identified five defoliation events spanning back to 1709. Our specific objective was to determine whether eastern hemlock tree-ring series show substantial growth reductions concomitant with those of red spruce during these outbreaks, providing evidence in support of earlier reports that eastern hemlock is an alternate budworm host. This research question is especially timely given the ongoing budworm outbreaks in Quebec and New Brunswick (Canada) and growing budworm hotspots across northern Maine (Spruce Budworm Task Force 2023 Update 2023)

Methods

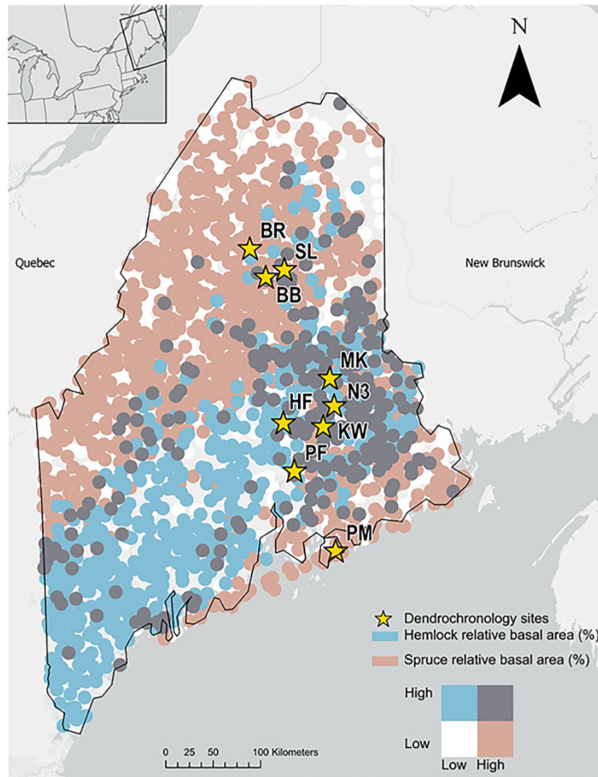
Budbreak phenology assessment

Because budworm feeds primarily on expanding buds and emerging needles, we first sought to determine whether budbreak in eastern hemlock coincided with those of other known host species. A substantial mismatch between eastern hemlock and other host species could call into question our ability to link radial growth reductions to budworm outbreaks. To this end, we analyzed eastern hemlock and spruce budbreak data from the USA-National Phenology Network (NPN) to assess budbreak synchrony between eastern hemlock and other budworm hosts (USA National Phenology Network 2025). We selected USA-NPN individual phenometric observations of eastern hemlock, red spruce, white spruce, and balsam fir budbreak in northern New England (Vermont, New Hampshire, and Maine) where these species commonly co-occur. We compiled phenometric observations from 2000 to 2024 and assessed budbreak probability density functions for each of the four species.

Site selection and metrics

We then compiled nine eastern hemlock and seven red spruce tree-ring measurement series for a total of 16 chronologies across nine sites in Maine (Fig. 1). These datasets represent results of several previous studies, which differed in terms of tree selection; however, all produced robust records of tree growth well suited for our work. Site descriptions follow; Table 1 provides additional details.

Fig. 1. Location of nine dendrochronology sites and distribution of eastern hemlock and red spruce in Maine. Distribution data are represented by fuzzed U.S.D.A. Forest Inventory and Analysis plot locations. High joint relative basal areas of both eastern hemlock and red spruce occur in the east-central part of the state, where many of our study sites are located. For site codes see Table 1. Figure was created using ArcGIS Pro version 3.4.0 and assembled from the following data sources: U.S. States (Esri), Forest Inventory and Analysis (U.S.D.A.). Base map from Esri.



Big Reed Forest Reserve: This old-growth site in northern Maine contains a range of forest types and conditions. Cores collected ca. 2000 have been used to reconstruct historical budworm outbreaks (Fraver et al. 2007) and to characterize natural disturbance regimes and age structures (Chokkalingam and White 2001).

Scraggly Lake: This eastern hemlock-dominated site is located within Scraggly Lake Public Reserved Land of northern Maine. Eastern hemlocks were sampled in 2022 as part of an ongoing project reconstructing long-term disturbance histories throughout the region. We were unable to obtain a red spruce chronology for this site.

Boody Brook Natural Area: This old-growth mixed-species reserve is located within the Baxter State Park Scientific Forest Management Area. Red spruce and eastern hemlock cores collected in 2009 were used to characterize stand dynamics and disturbance regimes (Birch 2010).

Mattawamkeag: This old-growth red spruce-eastern hemlock site is located in central Maine. Eastern hemlocks were cored for use in climate reconstruction and more recently

Table 1. Site codes, stand basal areas (BA; $m^2\ ha^{-1}$), tree densities (trees ha^{-1}), number of hemlock and red spruce tree-ring series, and eastern hemlock and red spruce tree-ring inter-series correlations (Int.Corr.) for each of the nine study sites in Maine.

Site	Code	BA	Density	No. Hemlock	Hemlock Int.Corr	No. Spruce	Spruce Int.Corr
Big Reed Forest Preserve	BR	32	618	57	0.60	755	0.53
Scraggly Lake	SL	44	432	24	0.57	–	–
Boody Brook	BB	33	543	21	0.45	124	0.54
Mattawamkeag	MK	55	831	49	0.61	54	0.57
Number 3 Pond	N3	–	–	19	0.59	–	–
Howland Research Forest	HF	46	1271	108	0.51	105	0.53
Kanoti Woodlot	KW	51	1087	31	0.51	27	0.53
Penobscot Exp. Forest	PF	43	624	115	0.53	36	0.49
Pemetic Mountain	PM	49	885	23	0.53	30	0.53

Note: No red spruce chronologies were available for the Scraggly Lake or Number 3 Pond sites. No site data were available for the Number 3 Pond site.

cored in 2009 to update the chronology (Cook 2002*a*; Larson et al. 2013). We cored red spruce at the site in 2024.

Number 3 Pond: This old-growth, nearly pure eastern hemlock site is located in central Maine. Eastern hemlocks were cored in 2002 for paleoclimatology study (Cook 2002*b*).

Howland Research Forest: This long-term research site in central Maine is well known for ecological research in a red spruce-eastern hemlock forest. Red spruce and eastern hemlock cores were collected in 2016 to assess climate–growth relationships (Teets et al. 2018). In 2023 we cored additional trees to enhance the eastern hemlock chronology.

Kanoti Woodlot: This mature mixed-species woodlot is located in central Maine. Red spruce cores were collected in 2022, in part to investigate arborvitae leafminer (*Argyresthia* spp.) outbreaks (Fraver et al. 2024). A small number of eastern hemlock cores were also collected at that time; in 2024 we returned to the site to core additional eastern hemlocks.

Penobscot Experimental Forest: This long-term experimental forest is the site of U.S. Forest Service research in a spruce-fir-eastern hemlock forest. Red spruce and eastern hemlock cores were collected in 2009 to determine how drought and competition interact to influence forest growth (Gleason et al. 2017)

Pemetic Mountain: This red spruce-eastern hemlock site is located in Acadia National Park in coastal Maine. Eastern hemlock and red spruce cores were collected in 2021 as part of a larger study describing changes in coastal red spruce forests (Seirup 2024).

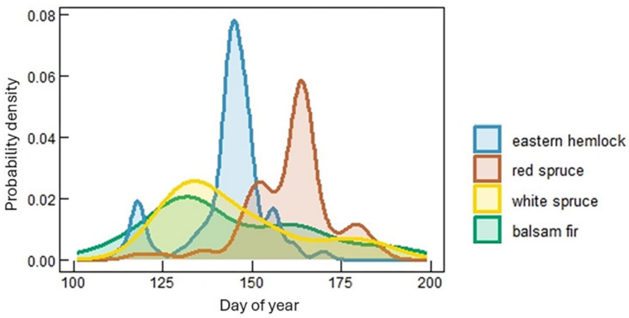
Dendrochronological analysis

Increment cores were dried and sanded to a fine polish following standard methods (Stokes and Smiley 1996). Ring widths were measured with a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Samples were cross-dated by species and site using the marker-year method (Yamaguchi 1991) with statistical verification by COFECHA (Holmes 1983). All tree-ring series were standardized to remove size-related growth trends. The red spruce series from the Big Reed Forest Preserve was standardized using a 100-year cubic spline with a 50% frequency response, to be consistent with Fraver et al. (2007). The remaining tree-ring series were standardized with the Friedman super smoother (default settings) using the "dplR" package (Bunn 2008) in R (R Core Team 2023).

We used an established record of budworm outbreaks in northern Maine (Fraver et al. 2007) to guide our analyses. That study, conducted via host-nonhost analysis, identified budworm outbreaks as distinct 4–6-year growth reductions initiating in 1709, 1762, 1808, 1914, and 1976. With these dates in mind, we visually identified similar radial growth reductions in the standardized red spruce site chronologies as probable budworm defoliation events at each site. An outbreak was thus identified in the primary visual assessment as a 4–6-year reduction in radial growth beginning on or shortly after established budworm outbreak periods. After identifying an outbreak in the red spruce chronology, the eastern hemlock chronology for that site was then assessed visually for a similar growth reduction.

To support results from our visual assessment, we used the "dfoliatR" R package (v0.3.0, Guiterman et al. 2020) to define outbreaks based on the percent of defoliated trees at a given site. Defining outbreaks in the dfoliatR package typically includes a host–nonhost analysis, which reduces the potentially confounding effects of a synchronous climate response in the tree-ring record. Although we did not have access to nonhost series at our sites, insect outbreaks have been successfully reconstructed without comparison to a nonhost chronology (Paritsis et al. 2009; Fraver et al. 2024), and the dfoliatR package includes options for identifying host species defoliation events in the absence of a nonhost chronology. We used the known outbreak history at our Big Reed site to calibrate the dfoliatR parameters (see Speer et al. 2001). By using parameters that best match known outbreaks, we could then evaluate potential outbreaks at other sites. We thus defined a budworm defoliation event as having ring-width indices (the result of standardization) 1.28 standard deviations below the mean index value and reductions lasting at least 4 years. We defined a stand-level outbreak as a defoliation event reducing growth in at least 50% of trees in the stand, with the peak of defoliation beginning on or shortly after documented budworm outbreaks. These analyses were conducted only on por-

Fig. 2. Probability density estimates for first budbreak dates of eastern hemlock and other budworm host species in northern New England (Vermont, New Hampshire, Maine). Overlapping budbreak dates with preferred hosts (balsam fir and white spruce) may partially explain eastern hemlock's suitability as an alternate host for eastern spruce budworm.



tions of the tree-ring series with adequate sample depth (subsample signal strength > 0.85).

To determine whether growth reductions may have resulted from drought stress, we used a side-by-side graphical comparison to assess the relationship between our tree-ring chronologies and the Palmer drought severity index (PDSI). Instrumental PDSI values (1895–2024) were obtained from the NOAA National Centers for Environmental Information (2023); earlier values were obtained from North American Drought Atlas (NADA; Cook and Krusic 2004). We note that several tree-ring datasets used in our analyses were likely used in the NADA regional drought reconstructions. However, to the best of our knowledge, NADA is the only source of reconstructed PDSI for this region and remains the most appropriate source of pre-instrumental PDSI values.

Results

Budbreak phenology assessment

Probability density functions derived from phenometric observations for balsam fir, white spruce, eastern hemlock, and red spruce showed eastern hemlock in closer phenological synchrony with white spruce and balsam fir than with red spruce (Fig. 2). Balsam fir budbreak peak probability begins around day of year (DOY) 130 (early May), with white spruce peaking shortly thereafter at DOY 135. Eastern hemlock budbreak peaks about ten days later, on DOY 145 (late May). Peak probability for red spruce budbreak occurs 35 days after balsam fir, at approximately DOY 165 (early June).

Dendrochronological analysis

The nine study sites represented a wide range of stand characteristics (Table 1). Basal areas ranged from 32 to 55 m^2 ha^{-1}, and tree densities from 432 to 1271 trees ha^{-1}. Both eastern hemlock and red spruce relative basal area varied widely by site, from 6%–75% (eastern hemlock) and 4%–68% (red spruce). Both species cross-dated well, with inter-series correlations > 0.45 (Table 1). Chronology temporal extent (subsample signal strength > 0.85) varied by site and species; chronologies were truncated at year 1700, if necessary, for both visual assessment and dfoliatR analysis.

A visual assessment of the red spruce and eastern hemlock chronologies revealed substantial variability in the number and severity of outbreaks among sites (Fig. 3); in fact, two sites (PF and PM) showed no evidence of budworm outbreaks. Nevertheless, eastern hemlock often showed growth reductions coincident with and similar in magnitude to those of red spruce during previously identified budworm outbreaks. During outbreak periods previously identified by Fraver et al. (2007) (shown as vertical grey bars in Fig. 3) in which red spruce showed the budworm signal in our chronologies (i.e., substantial growth reductions beginning ca. 1762 at BR; 1808 at BR; 1914 at BR, BB, HF, KW, 1976 at BR, BB), eastern hemlock showed the budworm signal in all but two of those periods (1976 at BR, BB). In addition, our eastern hemlock chronologies showed growth reductions beginning ca. 1808 and 1914 at two sites (SL, N3) that did not include red spruce chronologies and ca. 1808 at a third site (MK) where the red spruce chronology did not extend back to that period (Fig. 3). None of the outbreaks coincided with periods of drought represented by growing season (June–August) Palmer Drought Severity Index values (Fig. 3).

The dfoliatR analysis identified outbreaks separately by species and by site (Figs 3 and 4). Outbreak evidence based on dfoliatR (>50% of trees showed reduced growth) was weaker than that of the visual assessments of the chronologies. For example, dfoliatR identified outbreak evidence in both species ca. 1762, 1808, 1914 at BR and ca. 1914 at HF, but showed evidence in red spruce but not eastern hemlock ca. 1914 at BB and ca. 1976 at BR and BB (Fig. 3). In addition, dfoliatR results identified eastern hemlock outbreak evidence beginning ca. 1914 at one site (SL) that did not include a red spruce chronology and ca. 1808 at one site (MK) where the red spruce chronology did not extend back to that period (Fig. 3). At sites where an outbreak was identified in both species, the first outbreak year and year of maximum defoliation were similar, but eastern hemlock defoliation often preceded and attained maximum defoliation before red spruce.

Discussion

Eastern hemlock's overlapping budbreak period with highly preferred host species (balsam fir and white spruce) may partially explain eastern hemlock's suitability as an alternate host species for budworm. Differences in peak budbreak between eastern hemlock and balsam fir, as they relate to budworm phenology, likely drive differences in defoliation severity between the host species, although these differences may disappear during severe outbreaks (Hennigar et al. 2008). Eastern hemlock budbreak appears to peak about 2 weeks earlier than that of red spruce, which might suggest eastern hemlock as a more suitable host. However, foliar nutrient quality and shoot development, in addition to budbreak timing, likely also influence eastern hemlock's suitability as a host species (Nealis and Régnière 2004). For example, red spruce and black spruce have similar phenological patterns, but red spruce foliage quality is superior to that of black spruce for budworm, making red spruce a more sus-

Fig. 3. Growing season Palmer Drought Severity Index (PDSI, top panel) followed by standardized red spruce (brown) and eastern hemlock (blue) chronologies for each of nine sites. Vertical shaded bars indicate outbreaks previously identified by Fraver et al. (2007). Upward-pointing arrows indicate budworm outbreaks from visual assessment, while downward-pointing arrows indicate strong evidence for budworm outbreaks from dfoliatR analyses (see text). Arrow color indicates where outbreak evidence appears in both species (gray), eastern hemlock only (blue), or red spruce only (brown). Dashed line in the top panel (at year 1895) indicates where data source changes from instrumental to reconstructed PDSI values (see text). Sites arranged from north (top) to south (bottom). See Table 1 for site codes and Fig. 1 for site locations.

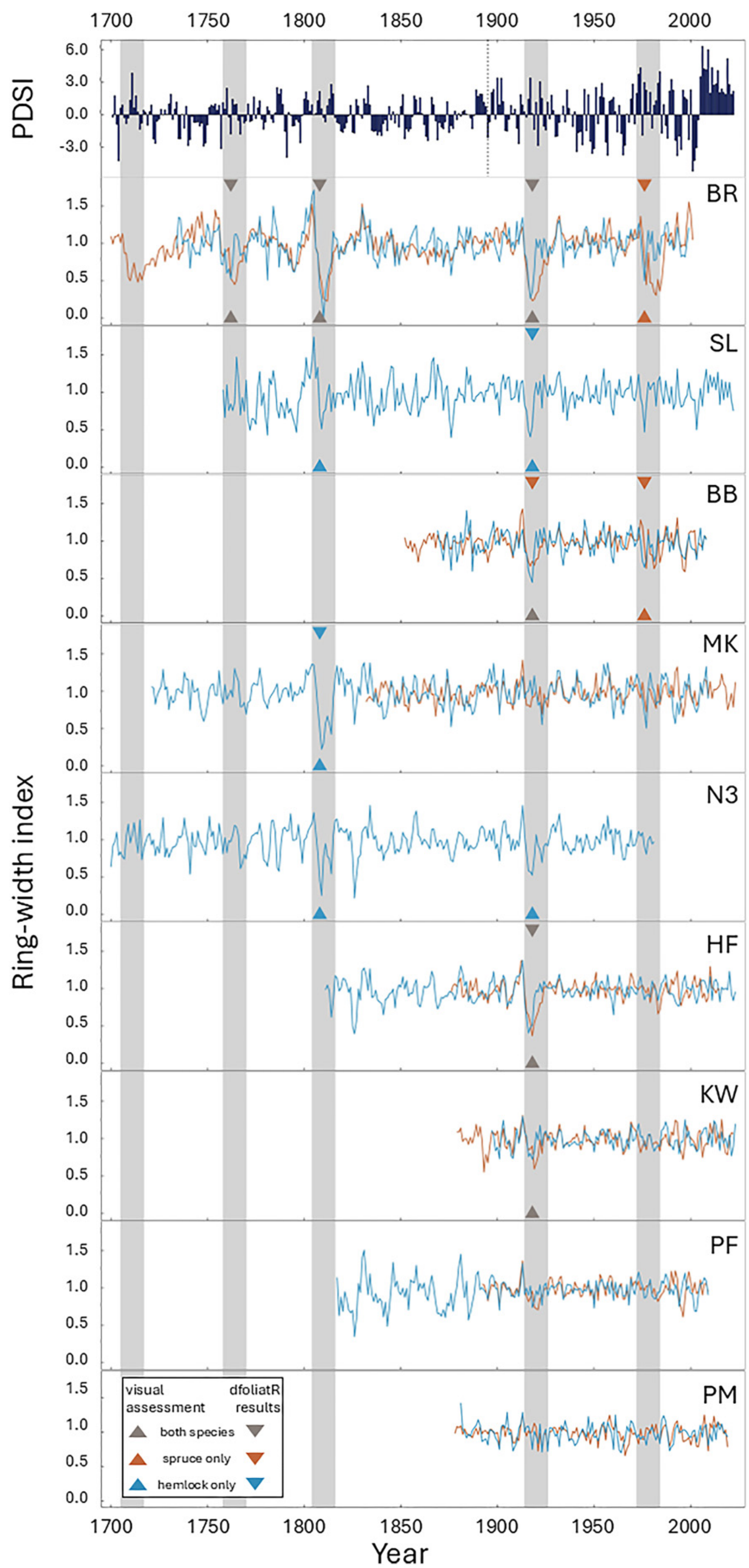
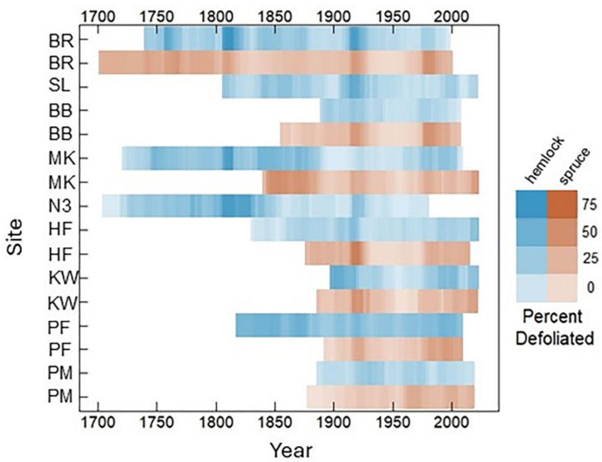


Fig. 4. Estimated percent of trees defoliated over time by site and species, based on dfoliatR results. Vertical axis labels distinguish chronologies by a two-letter site code (see Table 1). Chronologies are trimmed to subsample signal strength > 0.85 and sample depth > 10. While budworm outbreak evidence varied among sites, outbreak synchrony was seen across species and sites most clearly in the 1914 outbreak. Sites arranged from north (top) to south (bottom).



ceptible host (Irland et al. 1988). Research on eastern hemlock foliage palatability could further explain budworm host preferences.

Our primary objective was to determine whether eastern hemlock tree-ring series show substantial growth reductions concomitant with those of red spruce, which would confirm earlier reports (e.g., Godman and Lancaster 1990; Irland et al. 1988) of eastern hemlock as an alternate budworm host. We observed substantial radial growth reductions in eastern hemlock standardized tree-ring chronologies concurrent with documented budworm outbreaks and independent of drought across Maine, suggesting that eastern hemlock was defoliated during these outbreaks. Importantly, for most outbreak periods in which both red spruce and eastern hemlock had adequate sample depth, growth reductions seen in red spruce chronologies aligned with reductions in eastern hemlock chronologies. Similarly, for sites lacking outbreak evidence in the red spruce chronology (Penobscot Forest, Pemetic Mountain), no growth reductions were apparent in the eastern hemlock chronology.

Outbreak analyses based on dfoliatR generally supported the visual evidence in the standardized chronologies. However, evidence from dfoliatR (based on criteria applied to individual trees) appeared to be weaker than that of the standardized chronology (composite of all trees), perhaps due to the lack of a nonhost species for use in dfoliatR or that a standardized chronology reduces tree-level variation. For example, the response to climate evident in a standardized chronology is much stronger when compared to evidence from individual trees (Carrer 2011).

Outbreak evidence in both hemlock and red spruce showed substantial spatial and temporal variability across the nine sites. This spatial variability is well-reported in the spruce budworm literature (e.g., Zhao et al. 2014) and remains somewhat poorly understood (e.g., Navaro et al. 2018). Budworm defoliation and host mortality rates can vary even within sites with high proportions of preferred hosts such as balsam fir (i.e., Baskerville and MacLean1979). At both of our sites lacking outbreak evidence in red spruce and eastern hemlock chronologies (Penobscot Forest and Pemetic Mountain), evidence of spruce budworm outbreaks is documented in nearby stands (Irland et al. 1988; Kenefic and Seymour 2000). Additionally, aerial insecticide spraying programs in Maine during the 1950s–1980s (Irland et al. 1988) may have weakened the budworm signal during the 1976 outbreak. Spray maps obtained from the Maine Forest Service indicate that spraying may have occurred at the three northerly sites and at Howland Forest between 1975 and 1982, although map resolution is insufficient to determine if our particular study sites were sprayed. Regarding temporal variability, recent forest health reports from Wisconsin describe sudden and severe eastern hemlock defoliation by budworm in 2023, but found no defoliation in 2024 (Wisconsin Department of Natural Resources 2023, 2024).

Without a nonhost analysis, climate-related growth reductions could be interpreted as insect outbreaks. Both eastern hemlock and red spruce growth rates are positively correlated with cool, moist summers, and negatively correlated with high summer temperatures (Teets et al. 2018). The outbreak periods detected in our study do not coincide with substantial summer droughts (assessed with PDSI), suggesting that climate is an unlikely explanation for these periods of reduced radial growth.

Eastern hemlock radial growth reductions did not appear to lag behind those of red spruce at any site, which was somewhat surprising given the consensus (e.g., Godman and Lancaster 1990; MacLean and Clark 2021) that eastern hemlock defoliation occurs only after preferred fir and spruce species have been defoliated. Further research on the relationship between defoliation (timing and severity) and radial growth sensitivity in eastern hemlock and other budworm host species may provide clarity.

Other insects are known to damage eastern hemlock in Maine; however, the timing of documented budworm outbreaks does not coincide with the eastern hemlock growth reductions reported here. These insects include spongy moth, hemlock looper, and the ongoing infestation of hemlock woolly adelgid (HWA). During spongy moth outbreaks in the early 1950s and the 1980s, eastern hemlocks in Maine were defoliated after deciduous hosts were preferentially targeted (Souto and Shields 2000). Total defoliation from spongy moth feeding led to eastern hemlock mortality rates of 74% at some sites. The 1989–1993 hemlock looper outbreak is the only such outbreak known to occur in Maine (Trial and Devine 1994). The affected area exceeded 200 000 ha throughout the state; however, severity was extremely variable among locations. Compounding stressors, including recent harvests or multiple insect infestations, increased eastern hemlock mortality at sites across New England during the looper outbreak (Souto and Shields 2000). Both spongy moth and hemlock looper outbreaks have been linked to radial growth reductions in eastern hemlock in southern Maine (DeMaio 2008).

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While these defoliation events could reduce radial growth in eastern hemlock at our study sites, their dates do not align with those of budworm outbreaks, suggesting they have not confounded our interpretation of results. HWA was first discovered in Maine forests in 2003 and continues to spread throughout the state (Maine Forest Service 2025). Because no known HWA outbreaks had yet to occur at our sites at time of sampling, the growth reductions evident in our chronologies cannot be attributed to HWA-induced decline.

Management implications of our findings rely in part on defoliation severity of eastern hemlock relative to that of other preferred and non-preferred hosts, and how that may be influenced by stand structure and composition. Previous reports note a relationship between the presence of balsam fir and eastern hemlock defoliation during budworm outbreaks (Godman and Lancaster 1990; MacLean and Clark 2021), but specifics are lacking. In addition, likelihood of eastern hemlock growth reduction and mortality at given levels of budworm infestation, or during coincident infestation by budworm and other damaging insects, such as eastern hemlock woolly adelgid, merit investigation in light of the latter's northward expansion (Maine Forest Service 2025). Nevertheless, increased recognition of potential budworm impacts on eastern hemlock health and productivity will be useful to managers in planning for and silviculturally responding to budworm outbreaks, for example through pre-salvage or composition control. Diversifying species mixture by increasing hardwoods composition (i.e., mixedwood management) has been suggested as a means to reduce budworm susceptibility and vulnerability of spruce species and balsam fir due to dispersal losses and increased parasitism (MacLean and Clark 2021). These factors would likely similarly reduce budworm effects on eastern hemlock in mixedwood stands and thus merit further investigation.

Conclusion

To the best of our knowledge, ours is the first study to quantify spruce budworm outbreaks in eastern hemlock, providing evidence for its role as an alternate host. As above, eastern hemlock is currently threatened by a variety of insect pests, the most serious being hemlock wooly adelgid (Orwig et al. 2012), which is causing widespread host mortality throughout the eastern U.S. (Ellison et al. 2018). Understanding how budworm could further threaten eastern hemlock is critical for managing eastern hemlock in face of these potentially compounding threats as budworm outbreaks continue to develop and spread throughout Maine and eastern Canada.

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Competing interests

The authors declare there are no competing interests.

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