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Note

Dendrochronological reconstruction of arborvitae leafminer (*Argyresthia* spp.) outbreaks on northern white-cedar (*Thuja occidentalis*) in Maine, USA

Shawn Fraver[a], **Colby Bosely-Smith**[a], **Camilla Seirup**[b], **Christopher H. Guiterman**[c,d], **Thomas Schmeelk**[e], **Aaron Teets**[f,g], **Ruth Van Kampen**[a], **and Laura S. Kenefic**[h]

[a]School of Forest Resources, University of Maine, Orono, ME 04469, USA; [b]Northeast Temperate Network, U.S. National Park Service, Bar Harbor, ME 04609, USA; [c]Cooperative Institute for Research in Environmental Sciences, University of Colorado, Boulder, CO 80309, USA; [d]NOAA's National Centers for Environmental Information, Boulder, CO 80309, USA; [e]Maine Forest Service, Department of Agriculture Conservation and Forestry, Augusta, ME 04333, USA; [f]Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ 86001, USA ; [g]U.S.D.A. Forest Service, Pacific Northwest Research Station, Olympia, WA 98512, USA; [h]U.S.D.A. Forest Service, Northern Research Station, Bradley, ME 04411, USA

Corresponding author: **Shawn Fraver** (email: shawn.fraver@maine.edu)

Abstract

Although northern white-cedar (*Thuja occidentalis*; henceforth cedar) is thought to have few insect pests, arborvitae leafminers (primarily *Argyresthia thuiella*) have been known to cause leaf necrosis. Yet, historical evidence for leafminer outbreaks is limited. We combined leafminer larval surveys conducted between 1950 and 1992 with tree-ring analyses from eight cedar stands to reconstruct a history of leafminer outbreaks in Maine, USA. Our tree-ring data show distinctive 2- to 3-year growth reductions that we attribute to leafminers. Several such growth reductions correspond to peak leafminer larval abundances, providing evidence that the reductions are reliable indicators of leafminer activity. Outbreak severity within a site was unrelated to cedar abundance. Outbreak periods thus identified (beginning ca. 1919, 1937, 1950, 1962, mid-1970s, but not at all sites) suggest that leafminer damage may have been more prevalent (albeit patchy) than previously thought. This historical information is relevant given current outbreaks in Maine and elsewhere.

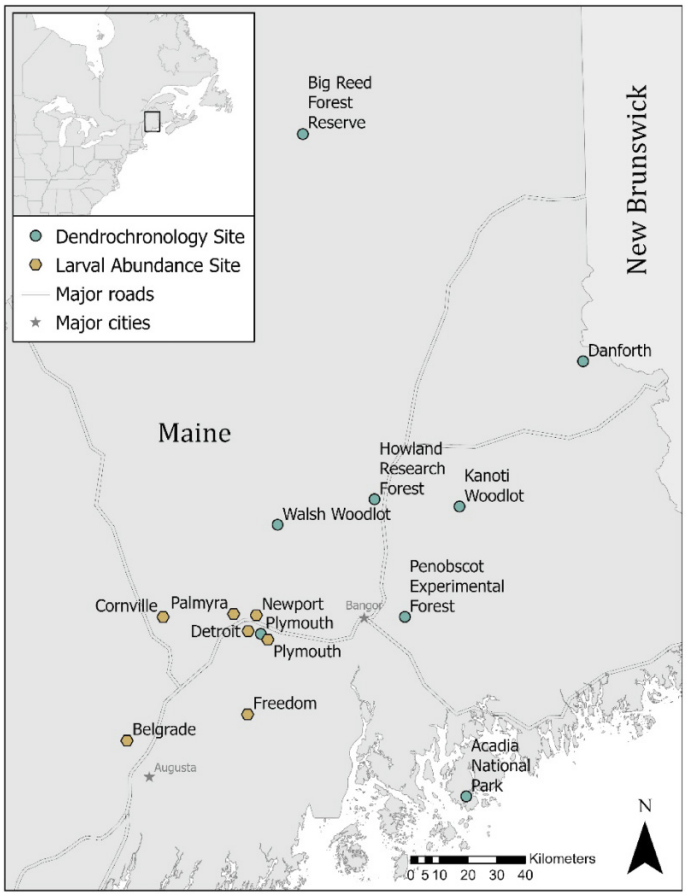
Key words: arborvitae, *Argyresthia thuiella*, eastern white cedar, dfoliatR, dendroecology, host-non-host analysis, insect defoliation

Introduction

Northern white-cedar (*Thuja occidentalis*; henceforth cedar) has substantial ecological and economic importance in northeastern North America. Unlike the other conifers common in the region, cedar is thought to have very few insect pests. The Silvics of North America states that the species is "relatively free from serious insect injury" (Johnston 1990). Nevertheless, leafminers (Lepidopterans generally referred to as the arborvitae leafminers, first described by Packard (1871)) have been reported to cause leaf necrosis leading to branch and occasionally tree death, as the larvae burrow into and feed on the cedar leaf scales (Brower 1952). A leafminer outbreak in northeastern North America ca. 1950 prompted a review of the insects involved (Silver 1957) and motivated a leafminer larval survey program conducted by the Maine Forest Service. More recently, the Minnesota (USA) Department of Natural Resources reports an outbreak affecting cedar across more than 4000 ha in 2017 (Minnesota Department of Natural Resources 2018, 2019). Yet, historical evidence for arborvitae leafminer outbreaks remains poorly documented and restricted to scant field observations and surveys, despite mention of cedar damage in forest health reports and handbooks from New England, the US lake states, and the Canadian provinces of Ontario, Quebec, New Brunswick, and Prince Edward Island (e.g., Rose et al. 2000).

In a recent silvicultural experiment conducted at the Penobscot Experimental Forest, Maine, USA, we collected radial cross-sections (i.e., "cookies") from the upper surface of cut cedar stumps, following silvicultural treatments, for dendrochronological analyses. In doing so, we noticed four distinct 2- to 3-year periods of dramatically reduced growth occurring between the 1930s and 1970s. This finding led us to explore the Maine Forest Service (MFS) archives for documented evidence of insect defoliators affecting cedar. Finding such evidence, in the form of MFS entomology staff's field surveys describing the native arborvitae leafminer (primarily *Argyresthia thuiella*), we in turn obtained dendrochronological data from seven additional sites in central and eastern Maine, USA. Our objective was to document the prevalence of past arborvitae leafminer outbreaks on eight sites in Maine, USA,

Fig. 1. Location of seven sites repeatedly surveyed for leafminer larval abundance by the Maine Forest Service's entomology staff, as well as our eight dendrochronology study sites. The map was created using ArcGIS Pro version 3.1.2 and assembled from the following data sources provided by Esri: US state boundaries, US major cities (U.S. Census Bureau, Esri), US major highways (TomTom, Esri), Canadian boundary (Garmin International Inc., Esri).



using dendrochronological approaches. This work is timely, given the nascent arborvitae leafminer outbreak in Maine (A. Bergdahl (personal communication, 2022)) and recent outbreaks in Minnesota (Minnesota Department of Natural Resources 2018, 2019).

Methods

Maine Forest Service's leafminer larval surveys

The MFS entomology staff began field surveys of leafminer larval abundance in 1950, following reports of widespread cedar needle necrosis across south-central Maine. These records were collected somewhat sporadically for 5 years at ca. 50 locations. By 1962, their annual field surveys had targeted seven locations in south-central Maine for repeated monitoring; these surveys continued through 1992 (Fig. 1). Between 1971 and 1975, the MFS also recorded leafminer species, recognizing four species: *Argyresthia thuiella*, *Argyrest hia freyella*, *Argyresthia aureoargentella*, and *Recurvaria thujaella* (now *Coleotechnites thujaella*), with *A. thuiella* being by far the most prevalent, representing 87% of samples. During these surveys, the average number of larvae per twig was recorded, after sampling 100 twigs. The nature of these data precludes rigorous statistical tests; however, they provide corroborating evidence for temporal patterns seen in reduced radial growth of cedar from nearby sites.

Dendrochronology study sites and field sampling

Forest inventory and tree-ring data used in this study were compiled from various studies and study sites in central and eastern Maine, USA (Fig. 1). The studies were largely unrelated, except that they included dendrochronological samples of cedar and red spruce (*Picea rubens*), the latter of which was intended to serve as the leafminer non-host for analyses (see below). As such, sampling methods differed among studies; however, the studies conveniently provided a wide range of site conditions and locations. Despite the differences in study purpose and design, all increment cores were collected at breast height (1.37 m) from trees ≥10 cm diameter at breast height. One core (or cookie, see below) was collected from each sampled tree. The number of trees sampled varied by site, ranging from 20 to 210, for a total of 434 trees (i.e., 434 tree-ring series). Descriptions of each site follow; further details are provided in Table 1.

Penobscot Experimental Forest (PEF) and Danforth study sites

Both sites form part of an active, operational-scale study of irregular shelterwood harvests applied to lowland cedar stands. Harvests were conducted in February 2019 (Penobscot Experimental Forest [PEF]) and February 2020 (Danforth). Following harvest, cookies were cut from cedar and red spruce stumps throughout the stands in June 2019 (PEF) and June 2020 (Danforth), initially to determine stand age structures. At both sites, 0.08 ha (1/5th acre) circular plots were used to characterize the stands (9 plots at the PEF, 4 at Danforth).

Howland Research Forest

This long-term research site includes a 3 ha fully mapped plot. In September 2015, we cored 10% of all plot trees (selected in a stratified random manner), including cedar and red spruce, to evaluate climate–growth relationships (Teets et al. 2018).

Big Reed Forest Reserve

This 2000 ha old-growth site supports several forest types, including lowland cedar. In 2001, we extracted increment cores from all trees on six 0.15 ha lowland cedar-dominated plots for the purpose of reconstructing past disturbances (Fraver et al. 2009, 2020).

Table 1. Site codes, stand basal areas, tree densities, relative basal area of cedar (%), number of cedar tree-ring series, and the cedar tree-ring inter-series correlations (Int.Corr.) for each of the eight dendrochronology sites in Maine, USA. Sites arranged by the strongest evidence of leafminer outbreaks (top row) to the weakest or absent evidence (bottom row).

Site	Code	Basal Area m^2 ha^{-1}	Density trees ha^{-1}	Cedar (%)	No. of Cedar	Int.Corr
Penobscot Experimental Forest	PEF	51.1	1321	81	49	0.545
Howland Research Forest	HRF	40.6	1055	10	33	0.520
Kanoti woodlot	KWL	51.1	1087	15	34	0.626
Plymouth forest	PLY	38.7	1284	52	32	0.605
Danforth study site	DAN	46.3	1084	80	20	0.466
Walsh woodlot	WWL	65.3	1494	87	33	0.624
Big Reed Forest Reserve	BRR	44.3	591	71	210	0.526
Acadia National Park	ANP	43.9	1210	50	23	0.389

Acadia National Park

The Northeast Temperate Network of the U.S. National Park Service maintains 176 vegetation monitoring plots within Acadia National Park (Tierney et al. 2022). Thirteen of these plots lie within lowland cedar stands. A small number of cedar cores were collected immediately off-plot at each of these stands. In addition, red spruce cores were similarly collected off-plot from scattered lowland locations within the park. Cores were collected between 2012 and 2018.

Plymouth forest

This nearly pure lowland cedar stand was selected for this study because of its proximity to a cluster of Maine State Forest Service's leafminer monitoring sites (see below). In May 2022, cedar trees were cored within the stand; red spruce were cored in the area surrounding the stand. We established one 0.08 ha (1/5th acre) inventory plot to characterize the cedar stand.

Kanoti woodlot

This mixed-species conifer stand was sampled for a group project in a graduate-level dendrochronology course at the University of Maine. In September 2022, we cored cedar and red spruce trees selected to span a range of diameters. We established one 0.08 ha (1/5th acre) inventory plot to characterize the stand.

Walsh woodlot

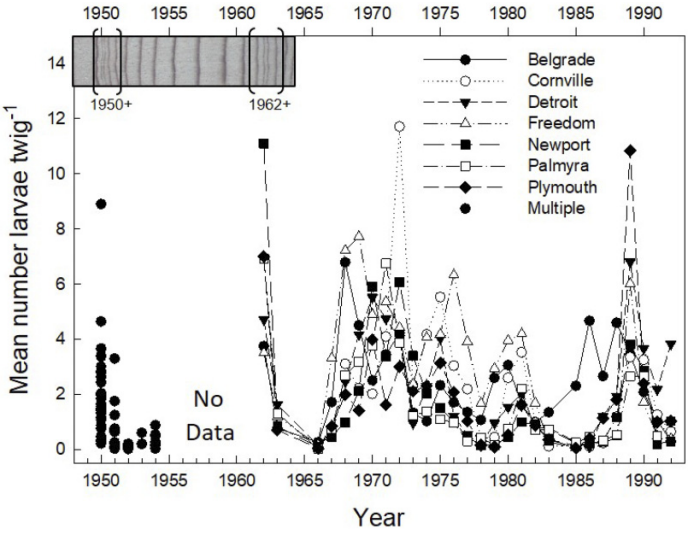
This nearly pure lowland cedar stand was selected to expand the spatial extent in a region suspected of having leafminer outbreaks, based on preliminary dendrochronology results from the sites listed above. In May 2023, cedar and red spruce trees were cored within the stand. We established one 0.08 ha (1/5th acre) inventory plot to characterize the stand.

Dendrochronological analysis

Increment cores and cookies were air-dried before being affixed to wooden mounts (cores) or plywood supports (cookies, when necessary to avoid breakage). Samples were sanded to a fine polish using standard methods (Stokes and Smiley 1996). Ring widths were measured on a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Cross-dating (by species, within a site) was conducted using the marker-year method of Yamaguchi (1991), with statistical verification by COFECHA (Holmes 1983). Marker years included those with narrow bands of latewood or unusual widths. Tree-ring series were standardized to remove size-related growth trends within the "DplR" R package, using the Freidman super smoother (Bunn et al. 2023, version 1.7.5).

Our analysis intended to compare growth patterns from the insect host species (cedar) to those of the non-host (red spruce); significant growth reductions evident in cedar but not red spruce would suggest host-specific insect defoliation. Red spruce was chosen as the non-host because it was the only species co-occurring with cedar on multiple sites. However, red spruce did not function well as a non-host because it experienced two growth reductions concomitant with those of cedar: an unexplained growth reduction in 1952 and a spruce budworm (*Choristoneura fumiferana* (Clem.)) defoliation beginning in the mid-1970s (Fraver et al. 2007). Red spruce did not show a growth reduction at any site during the 1937 leafminer outbreak (see below). Because its use as a non-host produced spurious results, we conducted our analysis without a non-host species, following several other studies that successfully identified insect defoliations without the use of non-host species (Paritsis et al. 2009; Tremblay et al. 2011). We used the "dfoliatR" (version 0.3.0) package in R (Guiterman et al. 2020), which includes options for identifying host-tree defoliation without reliance on a non-host to develop a growth suppression index. Based on the growth response of cedar during the documented 1950 leafminer outbreak (see above), we define an outbreak as having indices 1.28 standard deviations below the mean index and reductions lasting at least 2 years. We identified stand-level leafminer outbreaks as periods in which at least 50% of trees experienced growth reduc-

Fig. 2. Summary of Maine Forest Service's surveys of arborvitae leafminer larvae (primarily *Argyresthia thuiella*) in central Maine, USA. Sampling in the early 1950s was conducted sporadically on ca. 50 sites. In 1962, seven sites were selected for repeated annual sampling, which continued through 1992. Insert photograph shows a cedar core exhibiting typical 2- to 3-year radial growth reductions (bracketed) beginning ca. 1950 and 1962.



tions and attributed the timing of outbreaks to the first year of these periods.

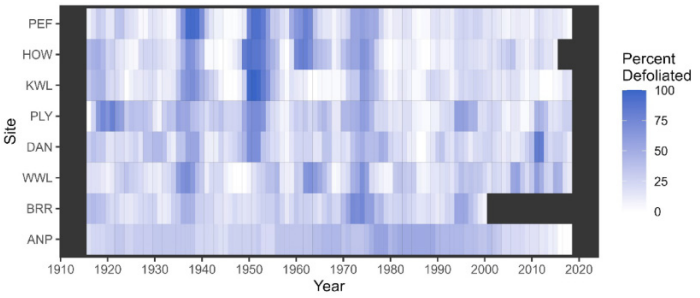
Results

The MFS larval surveys showed a peak in leafminer larval abundance in 1950, the first year of their recorded surveys, followed by a decline in abundance through 1954 (Fig. 2), at which time a hiatus in surveys began. Surveys resumed in 1962, showing additional peaks in larval abundance at that time on the seven sites selected for repeated annual surveys (Fig. 2). Surveys conducted on these sites from the late 1960s through the early 1980s showed somewhat sporadic and moderately high larval counts. Many of these sites show a strong, synchronized peak in larval abundance in 1989 (Fig. 2).

The dendrochronology study sites represent a large range of basal areas (38.7–65.3 m^2 ha^{-1}) and tree densities (591–1494 trees ha^{-1}; Table 1), the result of differing past disturbance, and species composition. Importantly, sites also represent a large range of cedar relative abundance. For example, when expressed in terms of cedar relative basal area, sites ranged from 10% cedar (Howland Research Forest) to 87% cedar (Walsh Woodlot; Table 1), allowing us to assess the extent to which cedar abundance may influence outbreak histories.

Dendrochronological crossdating of the cedar trees proved quite strong, with inter-series correlations >0.450 at all but one site (Table 1). Acadia National Park had the lowest inter-series correlation (0.389), likely because samples were collected from scattered locations within the park, unlike the remaining sites where samples came from the same stand or stands relatively close to each other. Chronology statistics from the dplR package showed that each site met the commonly used standards of signal strength and expressed population signal (Bunn et al. 2023; Wigley et al. 1984) back to at least 1915, which we used as the cut-off for inferring leafminer outbreak activity.

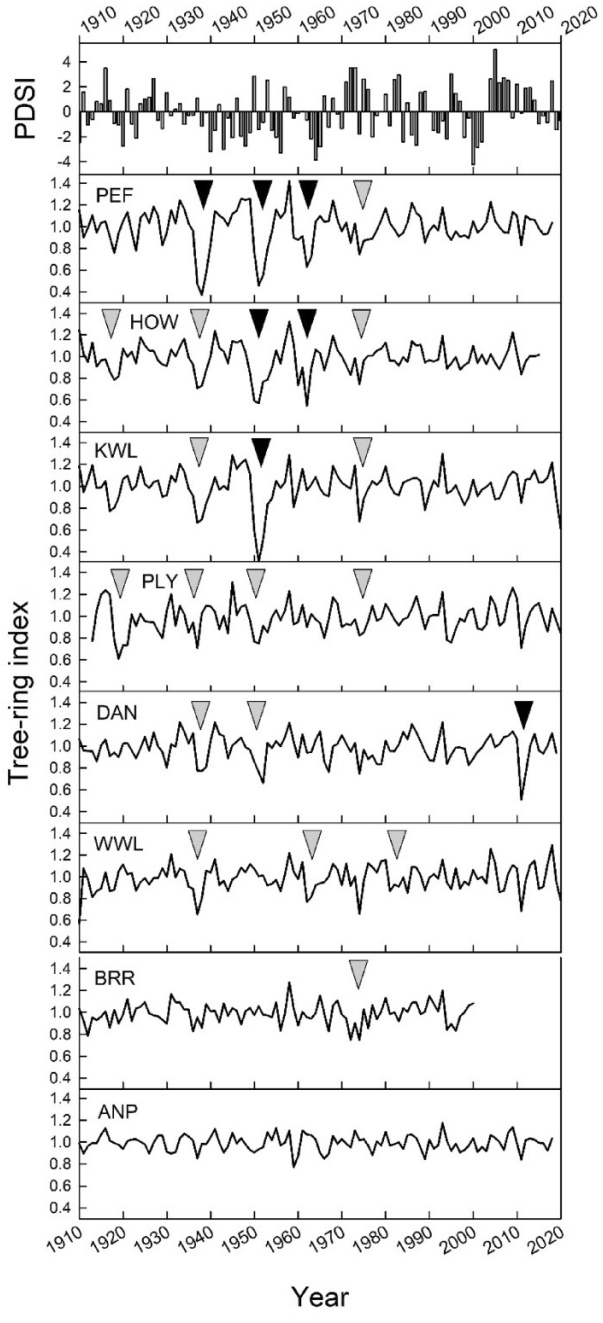
Fig. 3. Percent of trees for which defoliation was inferred (via thresholds set in the *dfoliatR* package in R, see text) over time, by site. Sites arranged by strongest evidence of leafminer outbreaks (top row) to weakest or absent evidence (bottom row). See Table 1 for site codes and Fig. 1 for locations.



Visual evidence of leafminer defoliation on individual trees was inferred from 2- to 3-year growth reductions seen on the prepared wood samples (Fig. 2 inset). These events were largely synchronous among trees at each site (Fig. 3), leading us to infer outbreak levels of the insects during distinct periods of time (Fig. 4). However, the timing and magnitude of outbreaks varied considerably among sites, with some sites showing strong evidence of four outbreaks (Penobscot Experimental Forest, Howland Research Forest), while others showed little or no evidence (Big Reed Forest Reserve, Acadia National Park) (Figs. 3 and 4).

The dendrochronology results point to outbreak periods beginning ca. 1919, 1937, 1950, 1962, and mid-1970s on multiple sites (Figs. 3 and 4). The two earlier outbreaks are generally corroborated by the Maine Annual Forest Commissioner's Reports (e.g., Violette et al. 1930) mentioning the leafminer as "abundant" or "very abundant" in the 1920s and 1930s (although locations are not provided): two of our dendrochronology sites show growth reductions beginning ca. 1919, and six sites show reductions beginning ca. 1937 (Figs. 3 and 4). The ca. 1950 outbreak seen as dramatic growth reductions on five of our dendrochronology sites was documented in 1949 in Maine (Forest Commissioner's Reports) and in 1947 in New Brunswick, Canada (Silver 1957). Further evidence for this outbreak is seen as a 1950 peak in the MFS larval surveys (Fig. 2). The 1962 outbreak seen in at least three of our dendrochronology sites corresponds to high larval abundances recorded in that same year (Fig. 2). The minor-to-moderate growth reductions in the mid-1970s in five of our dendrochronology sites (Fig. 4) roughly correspond to moderate larval abundances recorded from that time period (Fig. 2). The peak in MFS larval surveys in 1989, particularly evident at Plymouth (Fig. 2), did not appear as cedar growth reduc-

Fig. 4. Growing season Palmer Drought Severity Index (PDSI, top panel) followed by standardized cedar chronologies showing growth reductions associated with leafminer outbreaks at eight study sites. Black arrows indicate strong evidence of outbreak (>75% trees meeting criteria) and grey arrows indicate moderate evidence (50%–74%). Sites arranged by the strongest evidence of leafminer outbreaks (top) to the weakest or absent evidence (bottom). See Table 1 for site codes and Fig. 1 for locations.



tions at any of our dendrochronology sites, including the site near Plymouth. Finally, these outbreaks did not coincide with periods of insufficient (drought) or excessive moisture, based on annual or growing season (June–August) Palmer Drought Severity Index (PDSI) values from central Maine (NOAA National Centers for Environmental Information 2023, Fig. 4).

Discussion

Our tree-ring series show distinctive 2- to 3-year growth reductions in cedar trees, which we attribute to leaf damage caused by leafminers. Several of these growth reductions correspond to peak leafminer larval abundances recorded in the MFS entomology staff's surveys, providing evidence that the reductions are reliable indicators of leafminer outbreaks. Taken together, the dendrochronology results and the MFS larval surveys point to outbreak periods beginning ca. 1919, 1937, 1950, 1962, and mid-1970s on multiple sites. Although these results suggest that leafminer defoliation may have been more prevalent than previously thought, they also highlight spatial patchiness within the region, as even the most widespread outbreaks do not appear at all sites (Figs. 3 and 4).

Both data sources also suggest that leafminer outbreaks were short-lived. Peaks in larval abundance often appeared as 1-year spikes, while reduced radial growth spanned 2–3 years. These periods of reduced growth showed rapid recovery to pre-outbreak growth rates. In no case did our dendrochronological analysis detect locally absent rings during these outbreaks; in contrast, locally absent rings are quite common during spruce budworm (*C. fumiferana*) outbreaks in *P. rubens*, which span 6–8 years (Fraver et al. 2007). Although we have no information on cedar mortality, these short-duration outbreaks, coupled with rapid recovery, suggest that mortality may have been uncommon during outbreaks.

Growth reductions in our dendrochronology sites from central and eastern Maine and the MFS larval surveys show some degree of synchrony among sites within a data source, as well as between data sources, particularly for the 1950s and 1960s. However, the tree-ring chronologies from our sites beyond central interior Maine (i.e., Acadia National Park, Big Reed Forest Reserve) showed little or no evidence of the outbreaks. The limited number of sites, from both data sources, precludes any assessment of the true spatial extent of outbreaks. As above, both data sources indicated that outbreak intensity (larval abundance) and severity (growth reductions) were spatially patchy, even at fine scales. For example, the MFS larval surveys show that even sites within 10 km of each other differed markedly in larval abundance. One possible explanation for this patchiness and occasional lack of synchrony could be the observation that outbreaks usually involve more than one leafminer species (Silver 1957); species may behave differently in response to environmental cues.

Outbreak severity within a site did not appear to be related to cedar abundance. For example, the Howland site showed some of the strongest evidence of past outbreaks (evidence of five outbreaks) yet had the lowest relative basal area of cedar, at 10%. Similarly, the Kanoti Woodlot had evidence of at least three outbreaks, yet had relative cedar basal area of only 15%.

Any reconstruction of past insect outbreaks necessarily includes uncertainties, recognizing that factors other than insect defoliation may have caused growth reductions (Speer at al. 2001). For example, short-term growth reductions in cedar

can result from both insufficient (Housset et al. 2015) and excessive moisture (Yamamoto and Kozlowski 1987). However, a comparison of our purported outbreaks to growing-season PDSI values revealed that outbreaks did not coincide with periods of insufficient (drought) or excessive moisture.

To the best of our knowledge, ours is the first study to reconstruct the history of arborvitae leafminer outbreaks using dendrochronology techniques. Our findings raise additional questions regarding the spatial extent and causes for the episodic outbreaks; however, speculating on these issues is beyond the scope of this study. Our purpose here was to simply document the outbreaks to raise awareness, particularly in light of the current outbreak in Maine (A. Bergdahl (personal communication)) and recently elsewhere (Minnesota Department of Natural Resources 2018, 2019). These recent outbreaks add to existing concerns regarding cedar: (1) cedar stands often display a regeneration bottleneck, where abundant cedar seedlings do not reach the sapling stage, for reasons that remain unclear (Larouche et al. 2011; Allogio et al. 2021); (2) deer browsing greatly limits cedar regeneration in some parts of its range (Villemaire-Côté et al. 2022); and (3) climate change may create conditions inhospitable to cedar regeneration and growth in some parts of its range, potentially increasing mortality risk in trees stressed by other agents (Janowiak et al. 2018). The extent to which the current leafminer outbreak may contribute to these threats remains to be seen, and taken together these threats suggest the need for continued monitoring.

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Data are available upon request from the first author.

Author information

Author ORCIDs

Shawn Fraver https://orcid.org/0000-0003-1614-9072
Camilla Seirup https://orcid.org/0000-0002-1004-3456
Laura S. Kenefic https://orcid.org/0000-0001-5060-963X

Author contributions

Conceptualization: SF, LK
Data curation: SF, CB-S, CS, TS, AT, RVK, LK
Formal analysis: SF, CB-S, CS, CG
Investigation: SF, CB-S, LK
Methodology: SF, CB-S, CG
Supervision: SF, LK
Writing – original draft: SF
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Competing interests

The authors declare there are no competing interests.

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