

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

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20 **Abstract:** Although northern white-cedar (*Thuja occidentalis*; henceforth cedar) is thought to
21 have few insect pests, arborvitae leafminers (primarily *Argyresthia thuiella*) have been known to
22 cause leaf necrosis. Yet historical evidence for leafminer outbreaks is limited. We combined
23 leafminer larval surveys conducted between 1950 and 1992 with tree-ring analyses from eight
24 cedar stands to reconstruct a history of leafminer outbreaks in Maine, USA. Our tree-ring data
25 show distinctive two- to three-year growth reductions that we attribute to leafminers. Several
26 such growth reductions correspond to peak leafminer larval abundances, providing evidence that
27 the reductions are reliable indicators of leafminer activity. Outbreak severity within a site was
28 unrelated to cedar abundance. Outbreak periods thus identified (beginning ca. 1919, 1937, 1950,
29 1962, mid-1970s, but not at all sites) suggest that leafminer damage may have been more
30 prevalent (albeit patchy) than previously thought. This historical information is relevant given
31 current outbreaks in Maine and elsewhere.

32
33 *Keywords:* Arborvitae, *Argyresthia thuiella*, eastern white cedar, dfoliatR, dendroecology, host-
34 non-host analysis, insect defoliation

35 Introduction

36 Northern white-cedar (*Thuja occidentalis*; henceforth cedar) has substantial ecological
37 and economic importance in northeastern North America. Unlike the other conifers common in
38 the region, cedar is thought to have very few insect pests. The *Silvics of North America* states
39 that the species is “relatively free from serious insect injury” (Johnston 1990). Nevertheless,
40 leafminers (Lepidopterans generally referred to as the arborvitae leafminers, first described by
41 Packard [1871]) have been reported to cause leaf necrosis leading to branch and occasionally tree
42 death, as the larvae burrow into and feed on the cedar leaf scales (Brower 1952). A leafminer
43 outbreak in northeastern North America ca. 1950 prompted a review of the insects involved
44 (Silver 1957) and motivated a leafminer larval survey program conducted by the Maine Forest
45 Service. More recently, the Minnesota (USA) Department of Natural Resources report an
46 outbreak affecting cedar across more than 4,000 ha in 2017 (MNDNR 2018, 2019). Yet
47 historical evidence for arborvitae leafminer outbreaks remains poorly documented and restricted
48 to scant field observations and surveys, despite mention of cedar damage in forest health reports
49 and handbooks from New England, the US Lake States, and the Canadian provinces of Ontario,
50 Quebec, New Brunswick, and Prince Edward Island (e.g., Rose et al. 2000).

51 In a recent silvicultural experiment conducted at the Penobscot Experimental Forest,
52 Maine, USA, we collected radial cross-sections (i.e., ‘cookies’) from the upper surface of cut
53 cedar stumps, following silvicultural treatments, for dendrochronological analyses. In doing so
54 we noticed four distinct two- to three-year periods of dramatically reduced growth occurring
55 between the 1930s and 1970s. This finding led us to explore the Maine Forest Service (MFS)
56 archives for documented evidence of insect defoliators affecting cedar. Finding such evidence, in
57 the form of MFS entomology staff’s field surveys describing the native arborvitae leafminer

58 (primarily *Argyresthia thuiella*), we in turn obtained dendrochronological data from seven
59 additional sites in central and eastern Maine, USA. Our objective was to document the
60 prevalence of past arborvitae leafminer outbreaks on eight sites in Maine, USA, using
61 dendrochronological approaches. This work is timely, given the nascent arborvitae leafminer
62 outbreak in Maine (Aaron Bergdahl, *personal communication*) and recent outbreaks in
63 Minnesota (MNDNR 2018, 2019).

65 **Methods**

66 ***Maine Forest Service's Leafminer Larval Surveys***

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

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81 ***Dendrochronology Study Sites and Field Sampling***

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

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

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

102 *Big Reed Forest Reserve:* This 2000-ha old-growth site supports several forest types,
103 including lowland cedar. In 2001, we extracted increment cores from all trees on six 0.15-ha

104 lowland cedar-dominated plots for the purpose of reconstructing past disturbances (Fraver et al.
105 2009; Fraver et al. 2020).

106 *Acadia National Park:* The Northeast Temperate Network of the U.S. National Park
107 Service maintains 176 vegetation monitoring plots within Acadia National Park (Tierney et al.
108 2022). Thirteen of these plots lie within lowland cedar stands. A small number of cedar cores
109 were collected immediately off-plot at each of these stands. In addition, red spruce cores were
110 similarly collected off-plot from scattered lowland locations within the Park. Cores were
111 collected between 2012 and 2018.

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

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

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

126

127 *Dendrochronological Analysis*

128 Increment cores and cookies were air-dried before being affixed to wooden mounts
129 (cores) or plywood supports (cookies, when necessary to avoid breakage). Samples were sanded
130 to a fine polish using standard methods (Stokes and Smiley 1996). Ring widths were measured
131 on a Velmex sliding-stage stereomicroscope to the nearest 0.01 mm. Cross-dating (by species,
132 within a site) was conducted using the marker-year method of Yamaguchi (1991), with statistical
133 verification by COFECHA (Holmes 1983). Marker years included those with narrow bands of
134 latewood or unusual widths. Tree-ring series were standardized to remove size-related growth
135 trends within the 'Dplr' R package, using the Friedman super smoother (Bunn et al. 2019,
136 version 1.7.0).

137 Our analysis intended to compare growth patterns from the insect host species (cedar) to
138 those of the non-host (red spruce); significant growth reductions evident in cedar but not red
139 spruce would suggest host-specific insect defoliation. Red spruce was chosen as the non-host
140 because it was the only species co-occurring with cedar on multiple sites. However, red spruce
141 did not function well as a non-host, because it experienced two growth reductions concomitant
142 with those of cedar: an unexplained growth reduction in 1952 and a spruce budworm
143 (*Choristoneura fumiferana* (Clem.)) defoliation beginning in the mid-1970s (Fraver et al. 2007).
144 Red spruce did not show a growth reduction at any site during the 1937 leafminer outbreak (see
145 below). Because its use as a non-host produced spurious results, we conducted our analysis
146 without a non-host species, following several other studies that successfully identified insect
147 defoliations without the use of non-host species (Paritsis et al. 2009, Tremblay et al. 2011). We
148 used the 'dfoliatR' (version 0.3.0) package in R (Guiterman et al. 2020), which includes options
149 for identifying host-tree defoliation without reliance on a non-host to develop a growth

150 suppression index. Based on the growth response of cedar during the documented 1950 leafminer
151 outbreak (see above), we define an outbreak as having indices 1.28 standard deviations below the
152 mean index and reductions lasting at least two years. We identified stand-level leafminer
153 outbreaks as periods in which at least 50% of trees experienced growth reductions, and attributed
154 the timing of outbreaks to the first year of these periods.

155

156 **Results**

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

164 The dendrochronology study sites represent a large range of basal areas (38.7 to 65.3 m²
165 ha⁻¹) and tree densities (591 to 1494 trees ha⁻¹; Table 1), the result of differing past disturbance
166 and species composition. Importantly, sites also represent a large range of cedar relative
167 abundance. For example, when expressed in terms of cedar relative basal area, sites ranged from
168 10% cedar (Howland Research Forest) to 87% cedar (Walsh Woodlot; Table 1), allowing us to
169 assess the extent to which cedar abundance may influence outbreak histories.

170 Dendrochronological crossdating of the cedar trees proved quite strong, with inter-series
171 correlations >0.450 at all but one site (Table 1). Acadia National Park had the lowest inter-series
172 correlation (0.389), likely because samples were collected from scattered locations within the

173 Park, unlike the remaining sites where samples came from the same stand or stands relatively
174 close to each other. Chronology statistics from the dplR package showed that each site met the
175 commonly used standards of signal strength and expressed population signal (Bunn et al. 2019;
176 Wigley et al. 1985) back to at least 1915, which we used as the cut-off for inferring leafminer
177 outbreak activity.

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

185 The dendrochronology results point to outbreak periods beginning ca. 1919, 1937, 1950,
186 1962, and mid-1970s on multiple sites (Figures 3 and 4). The two earlier outbreaks are generally
187 corroborated by the Maine Annual Forest Commissioner's Reports (e.g., Violette 1930)
188 mentioning the leafminer as 'abundant' or 'very abundant' in the 1920s and 1930s (although
189 locations are not provided): two of our dendrochronology sites show growth reductions
190 beginning ca. 1919, and six sites show reductions beginning ca. 1937 (Figures 3 and 4). The ca.
191 1950 outbreak seen as dramatic growth reductions on five of our dendrochronology sites was
192 documented in 1949 in Maine (Forest Commissioner's Reports) and in 1947 in New Brunswick,
193 Canada (Silver 1957). Further evidence for this outbreak is seen as a 1950 peak in the MFS
194 larval surveys (Figure 2). The 1962 outbreak seen in at least three of our dendrochronology sites
195 corresponds to high larval abundances recorded in that same year (Figure 2). The minor to

196 moderate growth reductions in the mid-1970s in five of our dendrochronology sites (Figure 4)
197 roughly correspond to moderate larval abundances recorded from that time period (Figure 2).
198 The peak in MFS larval surveys in 1989, particularly evident at Plymouth (Figure 2), did not
199 appear as cedar growth reductions at any of our dendrochronology sites, including the site near
200 Plymouth. Finally, these outbreaks did not coincide with periods of insufficient (drought) or
201 excessive moisture, based on annual or growing season (June-August) Palmer Drought Severity
202 Index (PDSI) values from central Maine (NOAA 2023, Figure 4).

203

204 **Discussion**

205 Our tree-ring series show distinctive two- to three-year growth reductions in cedar trees, which
206 we attribute to leaf damage caused by leafminers. Several of these growth reductions correspond
207 to peak leafminer larval abundances recorded in the MFS entomology staff's surveys, providing
208 evidence that the reductions are reliable indicators of leafminer outbreaks. Taken together, the
209 dendrochronology results and the MFS larval surveys point to outbreak periods beginning ca.
210 1919, 1937, 1950, 1962, and mid-1970s on multiple sites. Although these results suggest that
211 leafminer defoliation may have been more prevalent than previously thought, they also highlight
212 spatial patchiness within the region, as even the most widespread outbreaks do not appear at all
213 sites (Figures 3 and 4).

214 Both data sources also suggest that leafminer outbreaks were short-lived. Peaks in larval
215 abundance often appeared as a one-year spikes, while reduced radial growth spanned two to
216 three years. These periods of reduced growth showed rapid recovery to pre-outbreak growth
217 rates. In no case did our dendrochronological analysis detect locally absent rings during these
218 outbreaks; in contrast, locally absent rings are quite common during spruce budworm

219 (*Choristoneura fumiferana*) outbreaks in *P. rubens*, which span six to eight years (Fraver et al.
220 2007). Although we have no information on cedar mortality, these short-duration outbreaks,
221 coupled with rapid recovery, suggest that mortality may have been uncommon during outbreaks.

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

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

238 Any reconstruction of past insect outbreaks necessarily includes uncertainties,
239 recognizing that factors other than insect defoliation may have caused growth reductions (Speer
240 et al. 2001). For example, short-term growth reductions in cedar can result from both insufficient
241 (Housset et al. 2015) and excessive moisture (Yamamoto and Kozlowski 1987). However, a

242 comparison of our purported outbreaks to growing-season PDSI values revealed that outbreaks
243 did not coincide with periods of insufficient (drought) or excessive moisture.

244 To the best of our knowledge, ours is the first study to reconstruct the history of
245 arborvitae leafminer outbreaks using dendrochronology techniques. Our findings raise additional
246 questions regarding the spatial extent and causes for the episodic outbreaks; however,
247 speculating on these issues is beyond the scope of this paper. Our purpose here was to simply
248 document the outbreaks in order to raise awareness, particularly in light of the current outbreak
249 in Maine (Aaron Bergdahl, *personal communication*) and recently elsewhere (MNDNR 2018,
250 2019). These recent outbreaks add to existing concerns regarding cedar: (1) cedar stands often
251 display a regeneration bottleneck, where abundant cedar seedlings do not reach the sapling stage,
252 for reasons that remain unclear (Larouche et al. 2011, Allogio et al. 2021); (2) deer browsing
253 greatly limits cedar regeneration in some parts of its range (Villemaire-Côté 2022); and (3)
254 climate change may create conditions inhospitable to cedar regeneration and growth in some
255 parts of its range, potentially increasing mortality risk in trees stressed by other agents (Janowiak
256 et al. 2018). The extent to which the current leafminer outbreak may contribute to these threats
257 remains to be seen, and taken together these threats suggest the need for continued monitoring.

258

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275

276 **Author Information**

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278 **Author contributions**

279 Conceptualization: SF, LK

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287 **Competing interests**

288 The authors declare there are no competing interests.

289

290 Data are available upon request from the first author

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376 **Figure Captions**

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

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

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

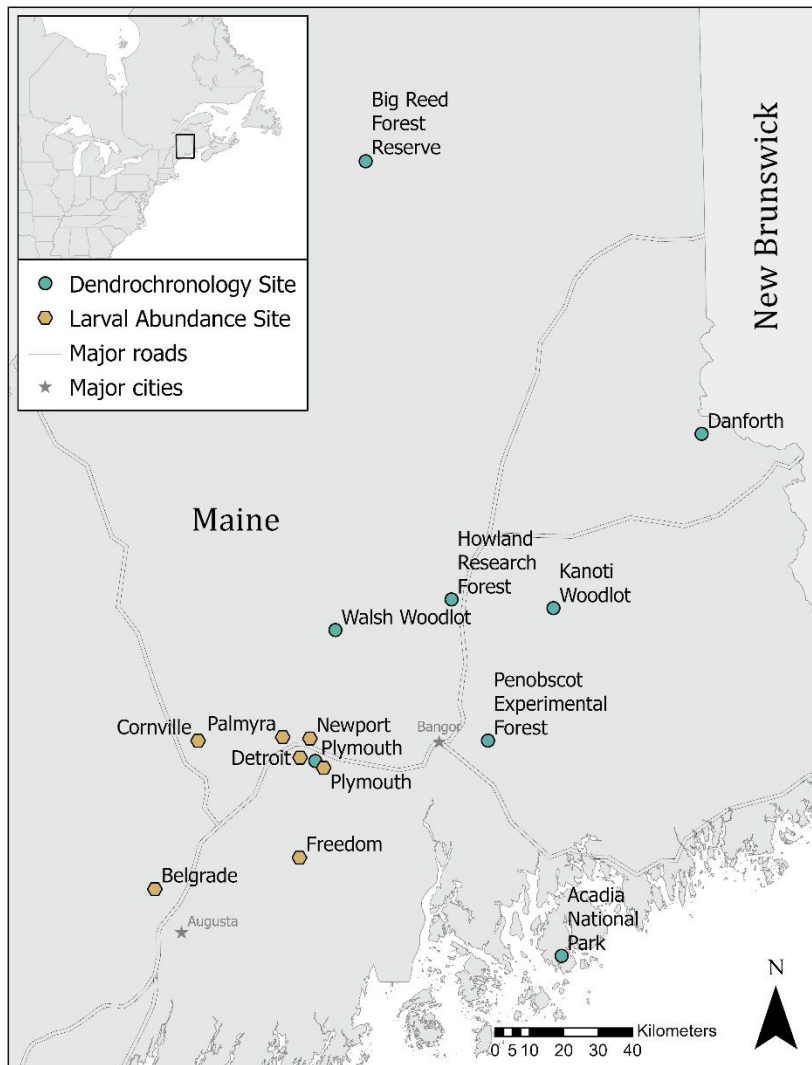
392 **Fig. 4.** Growing season Palmer Drought Severity Index (PDSI, top panel) followed by
393 standardized cedar chronologies showing growth reductions associated with leafminer outbreaks
394 at eight study sites. Black arrows indicate strong evidence of outbreak (>75% trees meeting
395 criteria), grey arrows indicate moderate evidence (50-74%). Sites arranged by strongest evidence
396 of leafminer outbreaks (top row) to weakest or absent evidence (bottom row). See Table 1 for
397 site codes and Figure 1 for locations. [ONE COLUMN WIDTH]

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

402

Site	Code	Basal Area	Density	% Cedar	No. Cedar	Int.Corr
		m ² ha ⁻¹	trees ha ⁻¹			
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

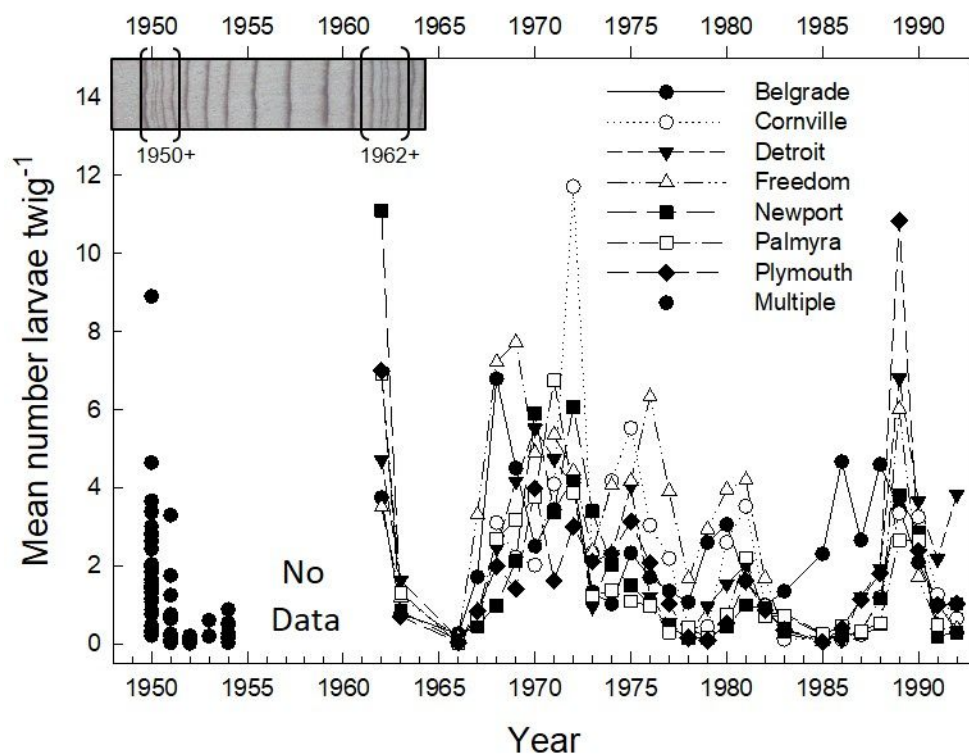
403



404

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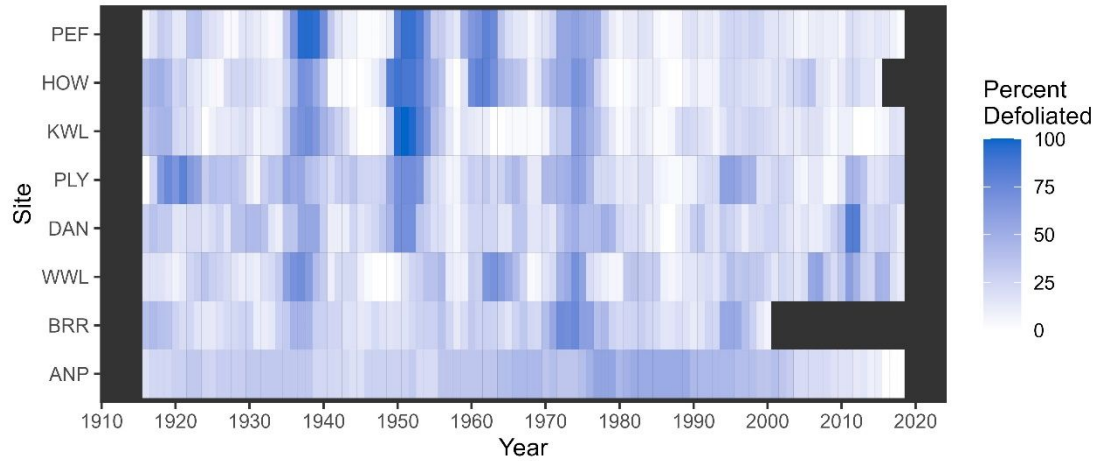
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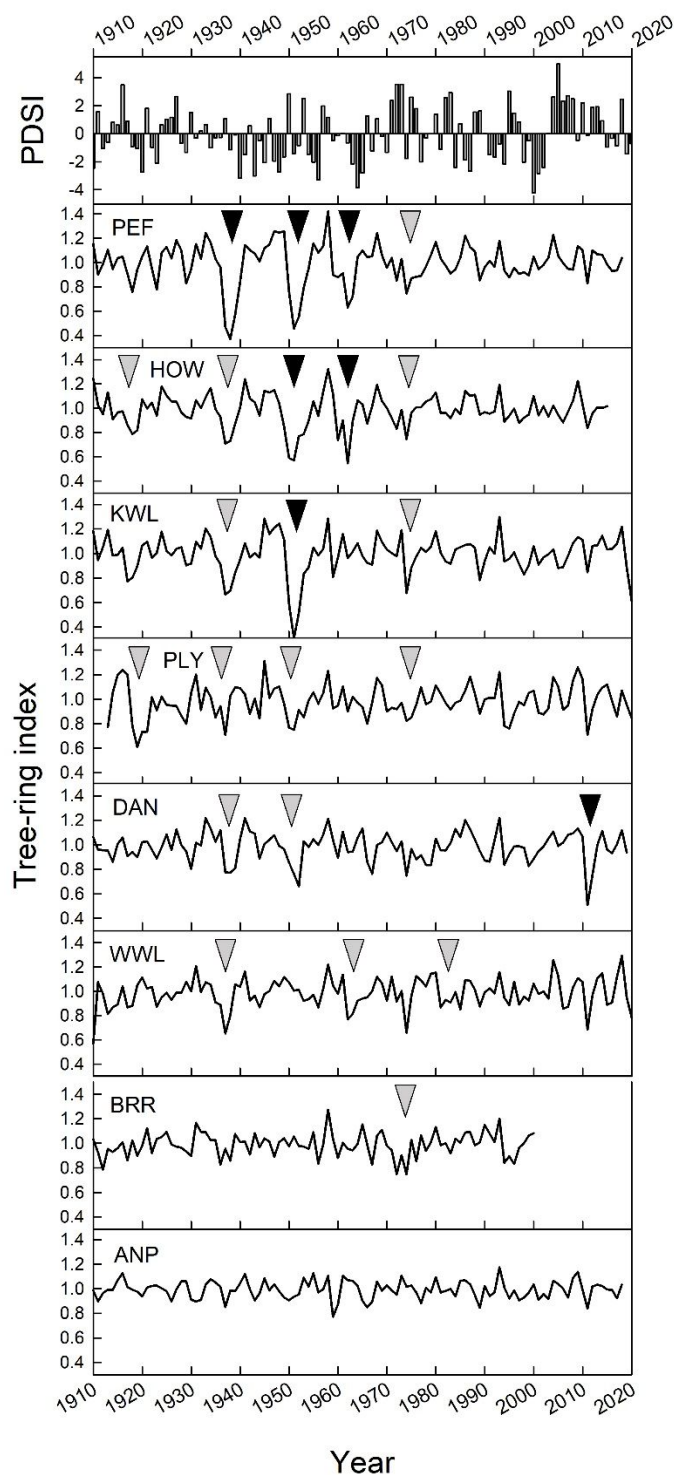
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