ABSTRACT

WOFFORD, CASEY KATHLEEN. Learning From Multiple Disturbances in Eastern and Carolina Hemlock Ecosystems in the Southern Appalachian Mountains. (Under the direction of Dr. Robert M. Jetton and Dr. Kelly L.F. Oten).

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is a foundation species throughout the Appalachian Mountains, where it regulates forest structure, hydrology, and habitat. Carolina hemlock (*Tsuga caroliniana* Engelm.), though far more restricted in range, is an ecologically significant endemic conifer that provides food, cover, and nesting habitat for wildlife in the southern Appalachians. Both species are imperiled by the invasive hemlock woolly adelgid (*Adelges tsugae* Annand, HWA), which has caused widespread decline and mortality since its introduction in the 20th century. The loss of these taxa would initiate cascading ecological changes and erode conifer diversity, yet uncertainty remains regarding the effectiveness of management interventions and the long-term demographic consequences of infestation. This thesis addresses these gaps through two complementary approaches: experimental evaluation of thinning and biological control in eastern hemlock, and dendroecological reconstruction of growth and disturbance histories in Carolina hemlock.

To test whether operational thinning can buffer eastern hemlocks against decline, we monitored crown and branch health, seasonal soil moisture, and counts of *Laricobius* spp. larvae, specialist predators introduced for HWA biological control over three years at two mixed-hemlock stands subjected to partial canopy reduction. At Sandy Mush, NC, both tree and branch level metrics showed strong year-by-treatment interactions, with thinned plots generally maintaining better crown condition, lower adelgid densities, and greater new growth than controls, particularly in 2024. At Mount Rogers, VA, responses were driven mainly by year rather than treatment, with improvements in crown density and new growth through 2025, but

minimal evidence of thinning effects. Soil moisture varied seasonally as expected and was higher at Sandy Mush, where overstory removal was more pronounced. Concurrently, *Laricobius* larvae increased at both sites and did not differ between thinned and unthinned sites, indicating successful predator establishment and potential compatibility between silvicultural and biological control. These findings suggest that structural interventions can help maintain photosynthetic capacity and growth potential under HWA pressure, although benefits were modest in the short term and likely contingent on site-specific conditions.

To assess the broader demographic and physiological consequences of HWA for Carolina hemlock, we reconstructed establishment dates, disturbance histories, and radial growth trends across four populations in the core of the species range. Recruitment was concentrated between 1920 and 1990, with little establishment after 2000. Growth release analyses revealed cyclical disturbance–recovery dynamics, with strong release events in the 1970s and 1990s, reflecting both natural and anthropogenic influences. However, this disturbance cycle was disrupted following the arrival of HWA. Within a decade of infestation, radial growth declined sharply, often by more than 50%, and suppression magnitudes exceeded those of past disturbance events. These declines were sustained, indicating long-term physiological stress and limited capacity for recovery under continued pest pressure. Together, the absence of new establishment and prolonged growth suppression demonstrate that HWA is fundamentally altering the disturbance dynamics and regeneration capacity of Carolina hemlock populations.

By integrating experimental management trials in eastern hemlock with historical reconstructions in Carolina hemlock, this work highlights both the potential and limits of intervention in the face of invasive-driven tree decline. Silvicultural thinning and biological control can temporarily sustain tree health and growth, but demographic bottlenecks and persistent suppression in Carolina hemlock point to deeper vulnerabilities that management alone may not resolve. Conservation strategies must therefore combine stand-level treatments with broader efforts, including chemical protection, classical biological control, and conservation plantings in genetically important stands. More broadly, this research illustrates how silvicultural, ecological, and dendrochronological approaches can be integrated to evaluate both short-term management outcomes and long-term population trajectories, providing a framework for conserving conifers under accelerating global change.

Learning from Multiple Disturbances in Eastern and Carolina Hemlock Ecosystems in the Southern Appalachian Mountains

by
Casey Kathleen Wofford

A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Master of Science

FORESTRY

Raleigh, North Carolina
2025

APPROVED BY:

Robert M. Jetton Committee Co-Chair	Dr. Kelly L.F. Oten Committee Co-Chair
Dr. Jodi A. Forrester	Dr. Albert E. Mayfield III

DEDICATION

I dedicate this thesis to anyone who thought they weren't enough and anyone who has found themselves thinking they would be better off leaving this plane of existence, but especially my husband, without whom I would not be here today.

BIOGRAPHY

Casey Wofford was born on June 18, 1993, in Brunswick County, North Carolina. Casey grew up with a love of the outdoors and a grand sense of adventure. Since transferring to NC State as an undergraduate student in Fall 2020, Casey has flourished within the College of Natural Resources with the help of many mentors. Casey graduated from NC State University in May 2023 with a Bachelor of Science in Forest Management and minor degrees in Biological Sciences and Entomology. Casey decided to pursue a Master of Science in Forestry and Entomology because of her love of forest health and a desire to continue learning everything she could about forestry at NC State. Casey is continuing to pursue her passion for forestry with the North Carolina Forest Service as the Longleaf Program Coordinator.

ACKNOWLEDGMENTS

This project took a tremendous amount of effort from not only me, but also many of my mentors, peers, friends, and family. Many thanks to my committee, Drs. Robert Jetton, Kelly Oten, Jodi Forrester, and Bud Mayfield. Thank you to Jonathan McCall and Christopher Shaw for welcoming and allowing our research to be conducted at Sandy Mush Game Lands and Jefferson National Forest. Special thanks to Tara Keyser, Marcus Wind, and Elle Gossman for collecting all of the data I used for my Carolina hemlock chapter. I truly could not have collected and completed all of my data without the help of Lauren Gonzalez, Abby Ratcilff, Anderson Wofford, Andy Whittier, Bryan Mudder, Ben Girgenti, Kyle Cavender, Liam Loftis, Thomas Hatling, Kristin Hilborn, Jon Kressuck, Delaney Serpan, Courtney Johnson, Pamela Zader, Dominic Manz, Cameron Carter, Luke McCormick, Archer Jones, Isabel Cranford, Adam Miller, Serenity Stueve, Emily Klein, Melodie Walter, Ana Cubas Baez, Jack Schulte, Morgan Schulte, Mac Boland, and Amber Payne. Many others also helped along the way in a plethora of ways that I also want to acknowledge, including Margot Wallston and Olivia Hall with The Hemlock Restoration Initiative, Dr. Nathan Havill with the USDA Forest Service's Northern Research Station, and Gwen Weaver for helping me gather 20+ 5-gallon buckets from local businesses.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: Impacts of Canopy Thinning on Soil Moisture, Eastern Hemlock Crown and Branch Conditions, Hemlock Woolly Adelgid Infestations, and Associated Predator Communities

Abstract

Eastern hemlock (*Tsuga canadensis* (L.) Carr.) is a foundation species throughout the Appalachian Mountains and into southeastern Canada, where it shapes forest composition and provides vital ecosystem services. These include regulating streamflow and temperature for aquatic species, providing evergreen shelter for wildlife during winter, and improving downstream water quality by reducing nutrient runoff. This ecological role is increasingly threatened by the invasive hemlock woolly adelgid (*Adelges tsugae* Annand), which has caused extensive decline and mortality in infested stands. If left unmanaged, the loss of eastern hemlock would trigger cascading ecological changes across its range. Previous research has demonstrated that individual hemlocks benefit from increased sunlight exposure after release from surrounding competition, exhibiting improved growth and crown health. However, less is known about whether these benefits scale to the stand level under operational thinning treatments. To address this gap, we established permanent 0.08 ha plots at two mixed-hemlock stands in North Carolina and Virginia slated to receive partial canopy thinning to increase light availability to targeted hemlocks. Over three years, we monitored crown and branch health metrics, alongside seasonal assessments of *Laricobius* larvae, specialist predators introduced for adelgid biological control. In 2024, we monitored soil moisture seasonally. Tree health responses to thinning were modest in the short term, with trends toward higher terminal shoot growth and reduced adelgid counts in treated plots. Soil moisture tended to be higher in thinned treatments relative to control treatments, potentially contributing to improved growing conditions. Initial results indicate

increasing *Laricobius* larval abundance at both sites, suggesting successful predator establishment. Continued monitoring will determine whether these trends persist or intensify with additional growing seasons. By integrating long-term tree health data with predator population dynamics, this study provides stand-level insights into the potential of combining silvicultural and biological control strategies to conserve eastern hemlock in the face of persistent adelgid pressure.

Introduction

Eastern hemlock (*Tsuga canadensis* (L.) Carrière) is a foundation species, significantly shaping ecosystems in which it is found. Eastern hemlock ranges from northern Alabama, U.S.A., north through the Appalachian Mountain range to New Brunswick and Nova Scotia, Canada, and westward to Minnesota, U.S.A. Growing from sea level to 732 meters in elevation, this species is commonly found growing in moist, but well-drained, acidic soils (Godman and Lancaster 1990). While scattered throughout mixed pine-hardwood forests in its southern extent, eastern hemlock can be a dominant canopy species in much of its northern extent. Especially dominant in riparian areas, eastern hemlock has great ecological significance directly and indirectly through site microclimate, community composition, productivity, nutrient cycling, and light availability (Martin and Gobel 2013). Although eastern hemlock no longer has commercial value in the southern part of its range, it plays a critical ecological role as a foundation species, providing year-round shade that moderates stream temperatures, creating unique understory habitats, and supporting diverse plant and animal communities throughout its range (Godman and Lancaster 1990).

The hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) is a devastating, invasive pest of eastern and Carolina (*Tsuga caroliniana* Engelmann) hemlocks in eastern North America.

Native to eastern Asia and the Pacific Northwest of North America, HWA is believed to have been introduced to the eastern United States in the early 1900s via infested Japanese hemlock (*T. sieboldii* Carrière) nursery stock (Havill et al. 2006; 2016; Radville et al. 2011). Following its introduction, HWA spread rapidly throughout the range of its hosts. The insect now infests more than half of the native range of eastern hemlock and the entire range of Carolina hemlock, with established populations reported as far north as Nova Scotia and Ontario, Canada (Ellison et al. 2018).

Hemlock woolly adelgid disperses through both natural and human-mediated pathways. Short-distance spread occurs when mobile first-instar "crawlers" are carried by wind currents, while long-distance movement can result from phoresy on birds or mammals. Long-distance dispersal can also be facilitated by human activity, particularly through the transport of infested nursery stock, logs, or other wood products across regions (McClure 1990; Evans and Gregoire 2007; Russo et al. 2019). These combined pathways contribute to the rapid and often discontinuous range expansion in the invaded range.

In eastern North America, where HWA's primary sexual host in its Asian range, tiger-tail spruce (*Picea torano* (Koch) Köhne), is absent, HWA reproduces exclusively via parthenogenesis. It produces two asexual generations annually: *sistens* (overwintering) and *progrediens* (spring) (McClure 1989; Havill et al. 2016). The crawler disperses to needle bases and inserts its stylet into xylem ray parenchyma cells, then envelops itself in its characteristic waxy wool, which serves as an ovisac (McClure 1990). The *sistens* generation hatches in early summer, enters aestival dormancy during summer months, and resumes feeding in the fall and through the winter, producing eggs late winter to early spring. The resulting *progrediens* generation matures rapidly and lays eggs within their woolly ovisacs by early summer (McClure

1989). Females may lay up to 300 eggs, and peak feeding activity coincides with new hemlock growth (McClure 1989). In its native Asian range, some *progrediens* nymphs develop into winged sexual forms (*sexuparae*) that migrate to spruce, enabling sexual reproduction; this cycle is absent in western and eastern North American populations, which remain strictly clonal (Havill et al. 2016).

Hemlock woolly adelgid feeding leads to severe defoliation, canopy thinning, and tree mortality within four to ten years of infestation (Ellison et al. 2018). Genetic analyses reveal that all eastern U.S. populations of the adelgid descend from a single maternal lineage (clonal haplotype) introduced from Japan (Havill et al. 2016), underscoring the invasion's genetic bottleneck. The spread and impact of HWA have dramatically altered hemlock forest ecosystems, with implications for biodiversity, succession, and hydrological processes (Ellison et al. 2018).

Over the last several decades, a robust integrated pest management (IPM) strategy has been developed to mitigate HWA's impact on eastern and Carolina hemlock forests. Chemical controls, particularly the systemic neonicotinoids imidacloprid and dinotefuran, are effective in reducing HWA populations and protecting infested trees for two to seven years (Cowles et al., 2006). Classical biological control efforts have introduced predatory beetles, such as *Laricobius nigrinus* Fender, from HWA's native range in Asia and the Pacific Northwest, to establish long-term natural enemies within affected ecosystems (Mayfield et al., 2020). Hybridization and genetic approaches, including selective breeding of naturally resistant individuals and conserving genetic diversity, also show promise for future restoration (Jetton et al. 2009; McCarty and Addesso 2019; Potter et al. 2010). More recently, silvicultural practices such as stand thinning have demonstrated potential to reduce tree stress and improve crown vigor, enhancing hemlock resilience to HWA infestation (Mayfield et al. 2023). Despite these multifaceted efforts, HWA continues to spread across the range of both hemlock species, causing widespread canopy decline and mortality.

Laricobius nigrinus, a specialist predator of HWA, is native to the Pacific Northwest of North America, where it coevolved with western hemlock (*T. heterophylla* (Raf.) Sarg.) and its associated HWA populations. Since 2003, *L. nigrinus* has been widely released in the eastern United States as part of classical biological control efforts against HWA (Mausel et al., 2010). Its life cycle is closely synchronized with the pest's overwintering (*sistens*) generation: adults emerge in autumn and feed on developing HWA nymphs through winter, before ovipositing in early spring when HWA egg masses are abundant. Larvae consume eggs and early instars before completing development and dropping to the forest floor to pupate in the soil in late spring (Lamb et al. 2006; Jubb et al. 2021). During this same period, HWA aestivates at the base of hemlock needles in a dormant state, resuming development in the fall. This subterranean pupation stage is a critical, and sometimes overlooked, phase in its life cycle, as soil conditions influence survival and subsequent adult emergence. Because *L. nigrinus* is univoltine and undergoes a prolonged aestival diapause, its activity ends before the *progrediens* generation of HWA develops, limiting its predation to a single adelgid generation per year (Zilahi-Balogh et al. 2003). Nonetheless, its seasonal synchrony with the most damaging generation of HWA and its successful establishment at many release sites make *L. nigrinus* a key component of IPM programs (Zilahi-Balogh et al. 2003). Monitoring efforts, including those assessing soil-dwelling pupae, are essential to evaluate long-term population persistence and biological control efficacy.

Silvicultural practices offer a complementary strategy to chemical and biological control by improving tree vigor and resilience. Research has shown that both eastern hemlock and HWA can survive in increased sunlight (Brantley et al. 2017; Mayfield et al. 2023). However, hemlocks in favorable environments, characterized by sufficient soil moisture (Ford and Vose 2007) and reduced competition for light and resources through canopy release (Brantley et al. 2017; Mayfield et al. 2023), can compensate for increased HWA feeding, maintaining or even improving growth. Garden and seedling trials show elevated light reduces adelgid densities and enhances carbon gain and growth (Brantley et al. 2017), and field studies confirm that creating small canopy gaps boosts hemlock shoot growth and crown health, even under active infestation (Mayfield et al. 2023). These findings suggest that stand-level thinning may offer benefits like chemical treatments, while also creating canopy conditions favorable for biological control agents such as *Laricobius* species. Stand-level silvicultural approaches remain understudied, particularly in operational forestry contexts. Implementing these treatments in commercially managed stands can reveal how eastern hemlocks respond when both interspecific and intraspecific competition are altered, information critical to developing large-scale, sustainable management strategies.

The goal of this study was to evaluate stand-level thinning as a silvicultural tool for improving the crown health of HWA-infested eastern hemlock. Specifically, we aimed to determine whether reducing overstory competition could enhance tree vigor and resilience under ongoing HWA pressure. Our objectives were to: (1) quantify the effects of stand-level thinning on eastern hemlock crown health, diameter growth, and soil moisture content in mixed-species stands, building on previous single-tree release studies, and (2) assess *Laricobius* species population trends to determine whether predator abundance is sustained, increasing, or decreasing over time. We hypothesized that increased sunlight from canopy thinning would improve hemlock growth and crown condition, while populations of *Laricobius* species would remain stable or increase over time.

Methods

Study Sites and Stand Thinning

This study was conducted in two southern Appalachian mixed conifer-hardwood stands containing a substantial component of over-, mid- and understory eastern hemlock (Figure 1.1). One site was in Sandy Mush Game Land in Buncombe County, NC (35.705135°N, 82.669729°W) and is managed by the North Carolina Wildlife Resources Commission. The second site was in Mount Rogers National Recreation Area in Wythe County, VA (36.778692°N, 80.988772°W) and is managed by the USDA Forest Service. Both sites received overstory thinning in 2023. The harvest goal at both sites was to remove merchantable overstory species, mainly eastern white pine (*Pinus strobus* L.) and white oak (*Quercus alba* L.), while leaving all over-, mid-, and understory hemlocks intact.

In Fall 2022, one year pre-treatment, 0.08 ha (one-fifth acre) fixed-radius plots were established inside (thin) and outside (control) planned harvest boundaries at both sites using pseudo-random sampling: plot locations were selected to approximate random distribution while ensuring adequate coverage of site variability (sensu Iles, 2003), with an eastern hemlock tagged as the plot center. Sandy Mush contained 19 plots [12 treatment (within thinned area) and 7 control (within uncut forest)] and Mount Rogers contained 21 plots (13 treatment, 8 control), totaling 40 plots. All trees ≥ 5 cm diameter at breast height (DBH) were measured, and every eastern hemlock was tagged. A subset of eight permanently tagged hemlocks was designated for detailed crown health assessments in all but four plots, which contained fewer than this minimum, across both sites. Species identity and DBH were recorded pre- and post-harvest, and all dead or bark- and bole-damaged hemlocks were noted during post-harvest inventory. Harvests occurred over multiple months in the Spring and Summer of 2023.

Pre-thinning stand characteristics were quantified from DBH and species of all trees ≥ 5 cm DBH across all plots (Table 1.1). Dominant live stems at Sandy Mush, listed in order from most to least prevalent, include eastern white pine, yellow-poplar (*Liriodendron tulipifera* L.), eastern hemlock, Virginia pine (*Pinus virginiana* Mill.), and hickory (*Carya* spp.). The site at Mount Rogers was dominated by eastern white pine, eastern hemlock, red maple (*Acer rubrum* L.), white oak, and scarlet oak (*Quercus coccinea* Muenchh.). Eastern white pine accounted for the highest percentage of relative live basal area at both sites, representing 25.6% at Sandy Mush and 45.4% at Mount Rogers.

Thinning treatments substantially reduced total stand basal area at both Sandy Mush and Mount Rogers, while leaving eastern hemlock largely intact (Figure 1.2). At Sandy Mush, controls averaged approximately 37 m^2/ha, whereas thinned plots decreased from approximately 40 m^2/ha to 10 m^2/ha between 2023 (pre-treatment) and 2024 (post-treatment). At Mount Rogers, control plots remained stable at approximately 49 m^2/ha, while thinned plots declined from approximately 49 m^2/ha to 26 m^2/ha over the same period. Eastern hemlock basal area showed little change, with controls at Sandy Mush near approximately 9 m^2/ha with thinned plots declining slightly form approximately 6 to 5 m^2/ha, and controls at Mount Rogers maintaining approximately 6-7 m^2/ha and thinned plots 4-5 m^2/ha. These reductions confirm that thinning prescriptions effectively reduced overall stand density while retaining overstory eastern hemlock, the target species of interest.

Post-harvest assessments aimed to: (1) quantitatively characterize thinning treatments and (2) quantify species-specific basal area and stem density removed and retained. Within each plot, DBH was measured for all trees ≥ 5 cm DBH using a logger's tape. Basal area ($m^2\ ha^{-1}$) was computed from DBH measurements using standard geometric formulas, with all calculations performed in R (R Core Team, 2025) employing base functions. To capture species-specific responses, basal area was calculated separately for eastern hemlock and for all non-hemlock species, both pre- and post-harvest. These metrics provided the basis for comparing thinning outcomes, such as the relative retention of hemlock basal area versus the reduction in associated species.

Tree Health, Laricobius, and Soil Moisture Data Collection

Crown and branch health assessments were conducted on a subset of up to eight tagged eastern hemlocks per plot in the winter before and after harvest. Crown health was assessed following USDA Forest Service Forest Inventory and Analysis (FIA) protocols using standardized crown rating cards (Schomaker et al. 2007). For each tree, live crown ratio, crown density, foliage transparency, and crown dieback were visually estimated to the nearest 5% using photographic reference guides after observer calibration. Live crown ratio was defined as the proportion of total tree height occupied by live foliage; crown density as the proportion of crown volume filled with branches, foliage, and reproductive structures; foliage transparency as the proportion of visible sky within the crown outline; and crown dieback as recent branch mortality progressing from the tips inward.

Branch-level condition was assessed by collecting HWA-infested branches from up to four cardinal directions when accessible using pole pruners. Following Mayfield et al. (2023), the first 30 cm of the terminal branch was examined to record the number of dead tips, number of new shoots on the first ten shoots, HWA index [ovisac counts (up to 100 per branch)], and the length of the terminal new shoot.

From the same subset of target trees, two randomly selected 30 cm branch cuttings per target tree were collected in late winter and brought back to observe *Laricobius* larval drop. Organized by plot, branches were stuck into cellophane-wrapped, water-soaked floral foam blocks. In the first year of collection, branches were placed in Lari-Leuco containers, a novel collection arena (Mayfield et al. 2021; Figure S1.1). In the following years, we used 5-gallon buckets following Gonzalez (2025). Containers were inspected every one to two days for *Laricobius* larvae, which were collected from the base of the buckets after dropping from branch clippings in search of pupation sites. Each plot-level container was monitored for a four-week period following setup. Larvae were collected and stored in 70% EtOH vials by site, plot, and date. A total of 21 *Laricobius* larvae from 2024 sampling, selected to represent both canopy treatments and plots at each site, were preserved in 95% EtOH and sent to the USDA Forest Service Northern Research Station Laboratory in Hamden, CT, for molecular determination of species (Davis et al. 2011).

Soil moisture readings were recorded seasonally (winter, spring, summer, and fall 2024) in all plots using an Aquaterr TEMP-350 Digital Soil Moisture and Temperature Meter (Aquaterr Instruments, Long Beach, CA). Five moisture readings were collected along a North-South transect at 11-meter intervals, then averaged by season. Each reading was collected by inserting the probe 13 cm into the ground and recording the percentage of soil saturation.

Data Analysis

All data analyses were conducted in SAS version 9.4 (SAS Institute Inc., 2018), with graphical outputs generated in R version 4.5.0 (R. Core Team, 2025). Mixed-model analysis of variance (ANOVA) was used to evaluate the main effects of year, canopy treatment, and their interaction (year × canopy treatment) on all measured variables, including foliar transparency, crown density, live crown ratio, DBH, HWA index, new growth, dead tips, terminal shoot length, and *Laricobius* counts. Mixed-model analysis of variance (ANOVA) was also used to evaluate the effects of treatment, season, location, and their interactions on volumetric soil moisture content. Sites were analyzed separately, with plot included as a random effect in all models. F-tests for fixed effects were considered significant at $P < 0.05$, and mean separations were performed using the Tukey–Kramer HSD procedure.

Results

At Sandy Mush, eastern hemlock health responses were strongly influenced by interannual variation, with most metrics also showing a significant year by treatment interaction (Figure 1.3A–C; Table 1.3). Foliar transparency varied significantly by year, with the lowest values pre-treatment, the highest values 1 year post-treatment, and intermediate values two years post-treatment (Figure 1.3A). Crown density also increased significantly by year ($p < 0.0001$), steadily rising annually from 2023 to 2025 (Figure 1.3B). Live crown ratio, by contrast, was influenced by the interaction of year and treatment ($p = 0.0004$). While all trees declined from 2023 to 2025, thinned plots consistently retained significantly higher ratios than control plots until 2025, when the treatments no longer differed (Figure 1.3C).

Branch-level responses at Sandy Mush reflected both year and treatment influences (Figure 1.3D-G; Table 1.3). Hemlock woolly adelgid infestation was influenced by year ($p < 0.0001$) with a strong interaction of year with treatment ($p < 0.0001$), peaking in 2024 with higher counts on control plots (per 10 cm branch) compared to thinned plots, before declining sharply in 2025 (Figure 1.3D). New growth exhibited significant year ($p < 0.0001$), treatment ($p = 0.0023$), and interaction of year with treatment effects ($p < 0.0001$), with thinned plots showing both higher overall growth in 2024 and a slower decline in 2025 relative to control plots (Figure

1.3E). The proportion of dead tips was not influenced by year or treatment alone but showed a modest interaction of year with treatment ($p = 0.0246$), with control plots declining more rapidly after 2023 before both thinned and control plots leveled out in 2025 (Figure 1.3F). Finally, terminal twig length was influenced by both year ($p < 0.0001$) and the interaction of year with treatment ($p = 0.0221$), peaking in both treatments during 2024 before control plots returned to 2023 levels and thinned plots stabilized in 2025 (Figure 1.3G).

At Mount Rogers, tree-level metrics showed strong year effects (Figure 1.4A–C; Table 1.3). Foliar transparency varied significantly by year ($p <0.0001$), increasing in 2024 post-treatment before declining in 2025 (Figure 1.4A). Crown density was likewise influenced by year ($p <0.0001$), remaining stable in 2023 and 2024, then significantly increasing in 2025 (Figure 1.4B). Live crown ratio was similarly influenced by year ($p <0.0001$), declining steadily from 2023 to 2025, but neither treatment effects nor the interaction of year with treatment were detected (Figure 1.4C).

Branch-level metrics at Mount Rogers (Figure 1.4D–G; Table 1.3) also reflected strong temporal dynamics with few interaction effects. Hemlock woolly adelgid counts varied significantly by year ($p <0.0001$), declining sharply from 2023 to 2024 before significantly rebounding in 2025 to levels comparable with 2023 (Figure 1.4D). New growth was influenced by year ($p <0.0001$), rising steadily from 2023 to 2025 (Figure 1.4E). The proportion of dead tips also showed a strong year effect ($p <0.0001$), declining significantly from 2023 to 2024, then remaining stable in 2025 (Figure 1.4F). Terminal leader length was influenced by both year ($p < 0.0001$) and exhibited a marginally significant year by treatment interaction ($p = 0.0078$), with both treatments significantly increasing from 2023 to 2024. While control plots declined significantly, thinned plots remained stable into 2025 (Figure 1.4G).

Overall, 2024 soil moisture content was higher at Sandy Mush (71.01% ± 17.21) compared to Mount Rogers (44.32% ± 17.02). Individual site analysis indicated that percent soil saturation at Sandy Mush was significantly affected by the main effect of season and by the interaction of canopy treatment with season (Table 1.4). While seasonal soil moisture was more variable in the control treatment relative to the thinned plots (Figure 1.5A), treatments differed significantly only in the spring, when percent soil saturation was nearly 10% lower in control plots compared to thinned plots. At Mount Rogers, percent soil saturation was significantly affected by the main effect of season only (Table 1.4), with the highest soil moisture levels occurring in the winter, followed by summer, and the lowest readings occurring during spring and fall (Figure 1.5B).

Patterns of *Laricobius* larval activity varied by site, year, and collection date (Figure 1.6). At Sandy Mush, we observed earlier and more pronounced activity, with captures beginning in mid-March and peaking sharply in late March 2023. In 2024, larvae were mostly collected between mid- and late March, while 2025 peaked in mid-March but at reduced abundance compared to 2023 and 2024. At Mount Rogers, larval captures were sparse in 2023, with only a few individuals dropping in early April. Activity increased modestly in 2024, concentrated between mid-March and early April. In 2025, Mount Rogers exhibited the most condensed and abundant larval activity period of the study, peaking in early April. Mixed-model ANOVA results (Table 1.5; Figure 1.7) indicated that at Sandy Mush, neither year, treatment, nor their interaction significantly influenced larval counts. Post-hoc comparisons confirmed no significant differences among years. At Mount Rogers, larval counts were significantly affected by year, but not treatment or their interaction. Post hoc tests showed 2025 counts were significantly higher than those of 2023 and 2024, whereas 2023 and 2024 did not differ. Our subset of larvae analyzed via DNA sequencing confirmed the presence of both *L. nigrinus* and the native *L. rubidus*. Across sites, *L. nigrinus* was more frequently detected than *L. rubidus*, with identical proportional representation between both sites (Figure 1.8).

Discussion

The outcomes of this study highlight the complex and site-specific nature of eastern hemlock responses to silvicultural thinning, HWA pressure, and biological control establishment. Rather than producing uniform results across locations, stand trajectories were shaped by interactions among basal area reduction, soil moisture regimes, crown and branch health, and *Laricobius* predator activity. These findings underscore that management prescriptions cannot be evaluated in isolation; their effectiveness is mediated by local site productivity, hydrological context, and the timing and intensity of adelgid pressure. By examining structural dynamics, physiological indicators, and predator establishment in tandem, this study provides insight into the mechanisms driving hemlock persistence under stress and informs adaptive approaches to integrated management.

By the end of the study period, crown and branch health responses revealed modest, yet ecologically meaningful, benefits of thinning at Sandy Mush. In 2025, trees showed greater live crown ratio and sustained new growth compared to controls, while live crown ratio, hwa index, new growth, dead tips, and terminal length had year-by-treatment interaction effects. These patterns suggest that canopy reduction buffered hemlocks against visible decline by maintaining photosynthetic foliage and branch vigor, even under persistent HWA pressure. Similar improvements in crown retention and branch growth following thinning or canopy modification have been reported in eastern hemlock and other conifer systems (Brantley et al. 2017, Mayfield et al. 2023), supporting the view that structural interventions can temporarily slow decline.

Collectively, these results indicate that thinning moderated HWA severity and maintained higher growth potential, while canopy-level responses were driven largely by interannual dynamics.

At Mount Rogers, however, crown density and transparency fluctuated, and live crown ratio steadily declined regardless of treatment, indicating more limited resilience under drier and more variable site conditions. Although branch-level responses showed some recovery in new growth and declining dead tips, these gains were insufficient to offset broader canopy deterioration. Because treatment effects were not significant at this site, this contrast highlights how local site productivity and moisture regimes mediate thinning effects, with management offering only short-term relief where stress conditions remain acute. Collectively, these findings align with long-term monitoring across southern Appalachians showing that modest rebounds in crown conditions can occur under HWA pressure, but sustained improvements typically require integrated management approaches that pair silvicultural interventions with adelgid suppression (Mayfield et al. 2023, Miniat et al. 2020).

Our study revealed marked differences in soil moisture dynamics between Sandy Mush and Mount Rogers, with the former maintaining consistently high percent saturation and the latter experiencing pronounced seasonal fluctuations. Soil moisture dynamics differed between sites and treatments in ways that reflect both stand structure and underlying soil properties. At both sites, season was the dominant driver of soil moisture variation, but at Sandy Mush, there was also a significant interaction of treatment by season, indicating that thinning moderated seasonal swings. At Sandy Mush, soil moisture in control plots fluctuated in a pattern similar to that observed at Mount Rogers, with rapid declines in late spring and summer, suggesting that intact stands exhibit similar seasonal water use dynamics across sites. In contrast, the thinned plots at Sandy Mush exhibited greater stability and higher overall soil moisture, consistent with the larger basal area reductions at the site compared to Mount Rogers. This pattern suggests that thinning reduced stand-level transpiration sufficiently to buffer against seasonal drying, an effect not as pronounced at Mount Rogers, where basal area reductions were smaller. Ford and Vose (2006) demonstrated that eastern hemlock maintains stable year-round transpiration, a trait that dampens seasonal fluctuations in soil water availability, and the loss of this canopy function following HWA infestation can elevate soil moisture, especially during dormant-season months, by reducing transpiration by up to 30%. Web Soil Survey data indicate that Sandy Mush soils are finer-textured clay loam soils, retaining more water than the coarse-textured, very-shaly silt loam soils at Mount Rogers (Soil Survey Staff, 2025). This likely contributes to the higher soil moisture observed at Sandy Mush, even under comparable seasonal conditions. These differences may also interact with precipitation inputs, as 2024 rainfall totals were above average, potentially amplifying site-level contrasts in water retention. Taken together, these results suggest that soil moisture responses in eastern hemlock systems are shaped by both management history and edaphic conditions, with thinning effects being more pronounced on finer-textured soils with greater water-holding capacity.

Soil moisture differences between sites help explain variation in crown condition. At Sandy Mush, consistently higher and more stable soil moisture coincided with increasing crown density and reduced foliar transparency, suggesting mesic conditions supported foliage retention despite adelgid pressure. In contrast, Mount Rogers soils showed stronger seasonal fluctuations and lower dormant-season moisture, patterns consistent with greater canopy thinning and transparency. Similar site-specific hydrologic controls on hemlock decline have been documented elsewhere (Brantley et al. 2017), underscoring the role of local moisture regimes in moderating HWA impacts.

Given these interacting factors, adaptive management that integrates pest suppression with ongoing long-term monitoring plots is essential for sustaining residual canopy and promoting recovery. One important component of integrated management is the establishment and persistence of biological control agents. The following section examines *Laricobius* larval collections at both sites as an indicator of predator establishment and long-term HWA suppression. Across sites and years, no consistent differences in larval abundance were observed between control and thinned treatments, suggesting that silvicultural thinning did not strongly influence *Laricobius* larval phenology or emergence timing. Instead, site-level dynamics and interannual variation played stronger roles in shaping predator activity.

At Sandy Mush, larval activity was characterized by consistent seasonal timing across years, with early spring peaks. However, overall abundance remained relatively stable at low densities, especially when compared to Mount Rogers. This likely reflects the relatively lower and more stable HWA populations observed at this site, as *Laricobius* activity is closely tied to adelgid availability (Figures 1.3–1.4). The absence of directional increases suggests that predator populations may have reached a local equilibrium, constrained by prey density as well as potential climatic and competitive factors. In contrast, Mount Rogers showed a clear trajectory of increasing larval detections over time, with the highest activity observed in the final year of sampling. This pattern corresponded with higher HWA densities at the site and mirrors findings from other release programs where *Laricobius* populations required several years to establish before reaching detectable, sustained levels (Mausel et al. 2010; Wiggins et al. 2016; Fischer et al. 2015). The strengthening signal at Mount Rogers suggests that predator populations are beginning to synchronize with adelgid lifecycles, which contributes to long-term suppression pressure.

Seasonal timing of *Laricobius* larval activity observed here, spanning late winter through spring, was broadly consistent with previous reports from southern Appalachian sites (Wiggins et al. 2016). Because emergence was monitored on field-collected branches held under constant laboratory conditions, these patterns may not perfectly mirror field phenology; however, similar branch-rearing approaches have been used in other studies and shown to capture relative timing differences among sites and years (e.g., Mausel et al. 2010; Wiggins et al. 2016). The earlier peaks observed at Sandy Mush compared to Mount Rogers are therefore likely meaningful and reflect elevational and climatic differences that shape both temperature regimes and HWA development. Such contrasts emphasize the importance of site-specific predator–prey synchrony: earlier emergence at lower elevations may coincide with initial HWA egg stages, while later peaks in higher, cooler habitats may extend feeding opportunities as egg laying continues. This variability underscores the need for predictive tools, such as degree-day models, to better align biological control strategies with local environmental conditions.

Genetic identifications further clarified predator community composition. Both *Laricobius nigrinus* (classical biological control) and *L. rubidus*, a native congener, were detected at both sites, with *L. nigrinus* occurring more frequently. The persistence of *L. nigrinus* several years after releases, alongside the continued presence of *L. rubidus*, supports previous findings that the introduced species can establish without displacing its native counterpart (Fischer et al. 2015). Unlike *L. nigrinus*, which specializes on adelgids, *L. rubidus* primarily feeds on pine bark adelgid (*Pineus strobi* Hartig) but is facultatively associated with HWA when available (Zilahi-Balogh et al. 2003; Mausel et al. 2010). Although *L. rubidus* is not considered an effective control agent on its own, its presence may augment overall predation pressure on HWA and reflects the dietary and habitat flexibility of the *Laricobius* guild. The retention of both taxa points to dietary and habitat flexibility, with potential implications for management. For instance, reducing eastern white pine dominance, the primary target of the thinning operations at both sites, may help focus *L. rubidus* on HWA prey, especially considering their dietary flexibility in field settings (Zilahi-Balogh et al. 2005), reinforcing the role of silviculture treatments in shaping predator communities.

Taken together, these findings suggest that while predator presence alone does not guarantee rapid canopy recovery, site-specific establishment trajectories, particularly the upward trend at Mount Rogers, indicate that *Laricobius* populations may contribute to HWA suppression over longer timescales. Moreover, maintaining taxonomic diversity within predator assemblages could enhance the stability and resilience of biological control in the southern Appalachians.

Conclusions and Management Implications

This study demonstrates that site-specific environmental conditions strongly mediate the health trajectories of eastern hemlock, the population dynamics of *Laricobius* predators, and the impacts of silvicultural thinning. At Sandy Mush, consistently high soil moisture and stable *Laricobius* abundance were paired with modest health declines, suggesting that mesic conditions may buffer against rapid deterioration even under sustained adelgid pressure. In contrast, Mount Rogers experienced more pronounced seasonal water deficits and a sharp increase in *Laricobius* larvae in 2025, yet tree health indicators still declined in several metrics—highlighting that predator abundance alone may not be sufficient to reverse crown loss without concurrent improvements in growing conditions.

While thinning effects were modest and often outweighed by year-to-year variation, evidence of improved early-season soil moisture and sustained leader growth in treated plots suggests that strategic canopy reduction may offer short-term benefits. However, the lack of a consistent treatment signal across sites underscores the need for context-specific application rather than a one-size-fits-all prescription.

Given the complexity of interactions among climate, site hydrology, pest pressure, and predator dynamics, future research should prioritize long-term monitoring that integrates microclimate, adelgid phenology, and predator–prey interactions. Such work will be essential for refining adaptive management strategies that maximize hemlock persistence. Ultimately, our findings reinforce that effective hemlock conservation will require site-tailored approaches that align biological control efforts with habitat conditions most conducive to tree recovery.

Tables

Table 1.1: Pre-harvest statistics for Sandy Mush and Mount Rogers, including live stems per ha, live basal area (m2/ha), relative live stems/ha (%), and relative live basal area (%) for every present woody species at each site. The top five dominant species are highlighted in light gray.

	Pre-harvest							
	Sandy Mush				Mount Rogers			
Species	Live stems/ha	Live BA (m2/ha)	Relative live stems/ha (%)	Relative live BA (%)	Live stems/ha	Live BA (m2/ha)	Relative live stems/ha (%)	Relative live BA (%)
ACRU	307.80	11.89	2.34	1.62	2879.88	74.8	20.23	9.65
AMAR	-	-	-	-	98.88	1.69	0.69	0.22
BELE	37.08	0.51	0.28	0.07	197.80	6.42	1.39	0.83
CACA	494.40	5.07	3.76	0.69	-	-	-	-
CARYA	1260.72	53.1	9.58	7.23	420.24	18.66	2.95	2.41
COFL	333.72	3.58	2.54	0.49	74.16	0.55	0.52	0.07
FRAM	37.08	2.79	0.28	0.38	-	-	-	-
ILOP	12.36	0.06	0.09	0.01	-	-	-	-
JUNI	12.36	2.10	0.09	0.29	-	-	-	-
LITU	1248.36	143.47	9.48	19.53	37.08	3.36	0.26	0.43
MAAC	135.96	4.51	1.03	0.61	-	-	-	-
MAFR	-	-	-	-	12.36	0.12	0.09	0.02
NYSY	173.04	4.71	1.31	0.64	791.04	12.35	5.56	1.59
OSVI	12.36	0.36	0.09	0.05	86.52	0.98	0.61	0.13
OXAR	271.92	8.00	2.07	1.09	-	-	-	-
PIST	2014.68	188.07	15.31	25.60	3881.04	352.26	27.26	45.42
PIVI	1050.60	69.59	7.98	9.47	37.08	2.13	0.26	0.27
PLOC	12.36	0.29	0.09	0.04	-	-	-	-
PRSE	234.84	10.27	1.78	1.40	-	-	-	-
QUAL	568.56	46.27	4.32	6.30	902.28	72.12	6.34	9.30
QUCO	309.00	30.33	2.35	4.13	543.84	70.39	3.82	9.08
QUFA	49.44	4.22	0.38	0.57	-	-	-	-
QUMO	-	-	-	-	556.2	37.66	3.91	4.86
RHMA	-	-	-	-	98.88	0.62	0.69	0.08
ROPS	98.88	7.33	0.75	1.00	12.36	0.26	0.09	0.03
SAAL	49.44	1.00	0.38	0.14	-	-	-	-
TIAM	98.88	6.28	0.75	0.85	-	-	-	-
TSCAN	4338.36	130.87	32.96	17.81	3609.12	121.13	25.35	15.62

Table 1.2: Mean diameter at breast height (DBH; cm) ± standard error (SE) of only eastern hemlocks at Sandy Mush and Mount Rogers, summarized by silvicultural treatment and year.

		Sandy Mush	Mount Rogers
Control	**2023**	22.55 (±1.58)	20.29 (±1.62)
	2024	23.11 (±1.56)	20.49 (±1.61)
	2025	23.90 (±1.6)	20.32 (±1.62)
Thin	**2023**	17.66 (±1.17)	19.06 (±1.21)
	2024	18.69 (±1.22)	19.99 (±1.40)
	2025	18.48 (±1.15)	19.79 (±1.36)

Table 1.3: Results of two-way analysis of variance (ANOVA) testing the effects of year, treatment (trt), and their interactions at Sandy Mush and Mount Rogers. Significant values (P < 0.05) are shown in bold.

		Sandy Mush			Mount Rogers		
		df	F	P	df	F	P
Metric	**Effect**						
Foliar transparency (%)	**year**	2, 418	52.18	**<0.0001**	2, 431	50.34	**<0.0001**
	trt	1, 418	0.86	0.3533	1, 431	0.05	0.8254
	year*trt	2, 418	0.83	0.4373	2, 431	1.59	0.2048
Crown density (%)	**year**	2, 418	18.95	**<0.0001**	2, 431	174.99	**<0.0001**
	trt	1, 418	1.19	0.2763	1, 431	3.39	0.0663
	year*trt	2, 418	2.17	0.1156	2, 431	0.9	0.408
Live crown ratio (%)	**year**	2, 418	140.18	**<0.0001**	2, 431	33.74	**<0.0001**
	trt	1, 418	6.39	**0.0118**	1, 431	1.63	0.2021
	year*trt	2, 418	8.02	**0.0004**	2, 431	2.06	0.1292
HWA index	**year**	2, 378	20.19	**<0.0001**	2, 381	59.74	**<0.0001**
	trt	1, 378	0.46	0.4981	1, 381	1.85	0.1749
	year*trt	2, 378	33.73	**<0.0001**	2, 381	1.92	0.1483
New growth (%)	**year**	2, 369	32.49	**<0.0001**	2, 380	212.13	**<0.0001**
	trt	1, 369	9.44	**0.0023**	1, 380	0.11	0.7393
	year*trt	2, 369	18.19	**<0.0001**	2, 380	0.98	0.3761
Dead tips (%)	**year**	2, 378	0.5	0.6046	2, 380	15.3	**<0.0001**
	trt	1, 378	0.75	0.3869	1, 380	0.1	0.7554
	year*trt	2, 378	3.74	**0.0246**	2, 380	0.42	0.6606
Twig length (cm)	**year**	2, 368	11.75	**<0.0001**	2, 373	72.51	**<0.0001**
	trt	1, 368	2.37	0.1249	1, 373	0.65	0.4191
	year*trt	2, 368	3.86	**0.0221**	2, 373	4.91	**0.0078**

Table 1.4: Results of mixed-model analysis of variance (ANOVA) testing the effects of treatment, season, location, and their interactions on volumetric soil saturation (%) at Sandy Mush and Mount Rogers. Sites were analyzed individually, and plot was included as a random effect. Significant P-values (< 0.05) are shown in bold.

		Sandy Mush			Mount Rogers		
		df	F	P	df	F	P
Soil Moisture (%)	**treatment**	1, 318	0.2	0.6545	1, 361	1.38	0.2408
	season	3, 318	11.53	**<0.0001**	3, 361	19.21	**<0.001**
	location	4, 318	0.48	0.7492	4, 361	1.89	0.1118
	treatment*season	3, 318	3.6	**0.0139**	3, 361	0.51	0.6771
	treatment*location	4, 318	0.52	0.7176	4, 361	0.62	0.6454
	season*location	12, 318	1.22	0.2695	12, 361	1	0.4471
	treatment*season*location	12, 318	0.88	0.5641	12, 361	0.88	0.5692

Table 1.5: Results of mixed-model analysis of variance (ANOVA) testing the effects of year, treatment, and their interaction (year × treatment) on *Laricobius* species counts at Sandy Mush and Mount Rogers. Sites were analyzed individually and plot was included as a random effect. Significant P-values (< 0.05) are shown in bold.

		Sandy Mush			Mount Rogers		
		df	**F**	**P**	**df**	**F**	**P**
Laricobius	**year**	2, 34	0.0612	0.9407	2, 38	27.5889	**<0.0001**
	treatment	1, 17	1.1255	0.3036	1, 19	0.608	0.4452
	year*treatment	2, 34	0.9535	0.3954	2, 38	0.6736	0.5158

Figures

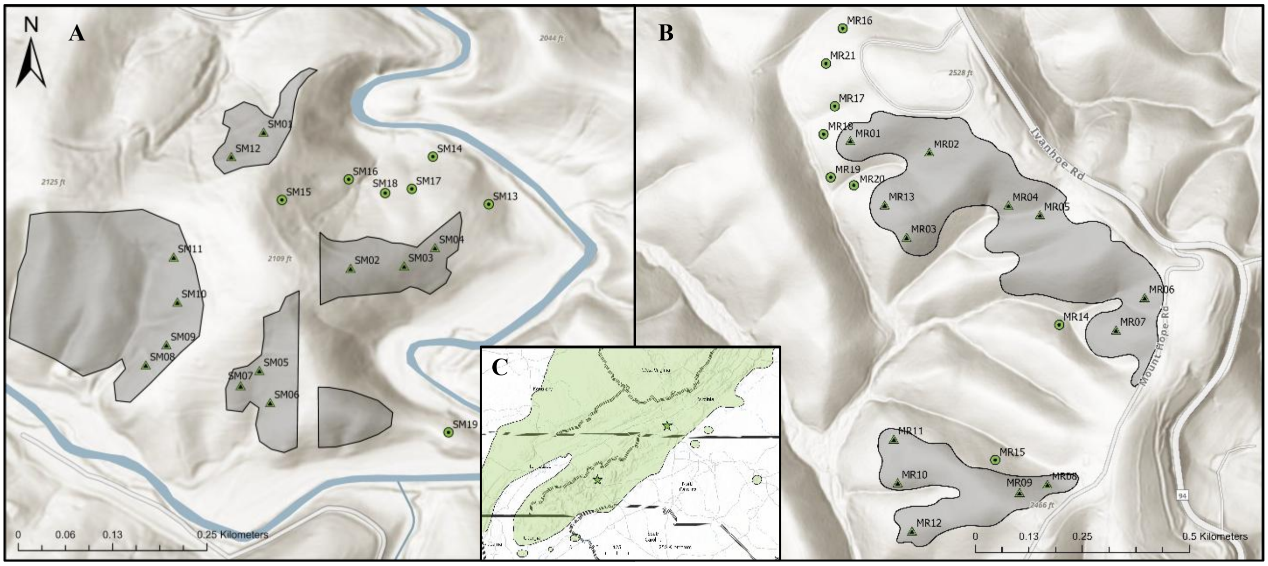

Figure 1.1: Location of the two harvest sites at (A) Sandy Mush Game Lands in North Carolina and (B) Mount Rogers Recreation Area in Virginia. Control plots are represented by a green-filled circle, found outside of the shaded thinned boundaries. Thinned plots are represented by a green-filled triangle, found within the shaded thinned boundaries. The inset map (C) shows the southern Appalachian extent of eastern hemlock’s range with green-filled stars indicating the location of sites A and B.

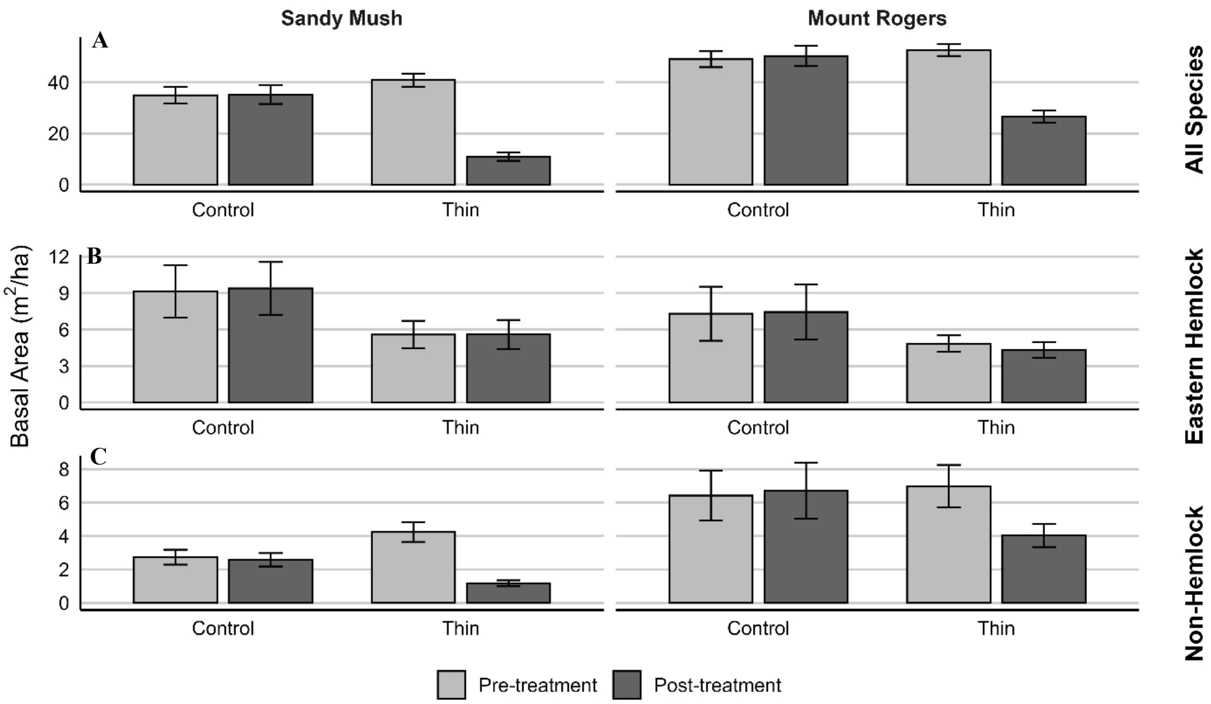

Figure 1.2: Mean basal area (m²/ha) in control and thinned plots at Sandy Mush and Mount Rogers for all species (A), eastern hemlock (B), and non-hemlock (C) pre- (2023) and post- (2024) treatment. Basal area changes show the effects of overstory species removal. Bars represent means ± 1 SE.

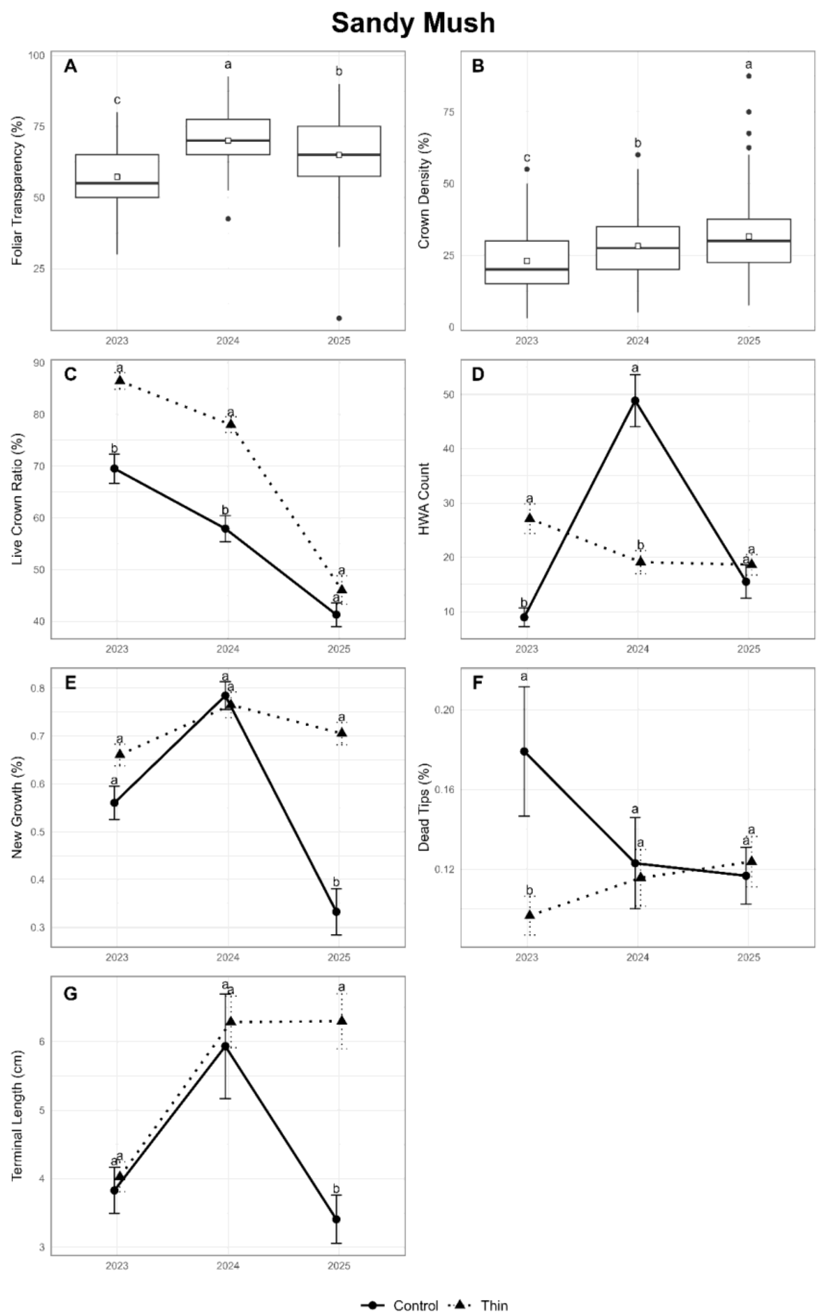

Figure 1.3: Tree-level (A–C) and branch-level (D–G) health metrics for control (solid lines) and thinned (dashed lines) eastern hemlocks at Sandy Mush, NC, 2023–2025. Boxplots display medians, interquartile ranges, ranges, and means (□). Tree-level metrics include foliar transparency (A), crown density (B), and live crown ratio (C). Branch-level metrics include HWA count (D), new growth (E), dead tips (F), and terminal leader length (G). Points indicate means ± SE. Different lowercase letters denote significant differences among years within treatments ($P < 0.05$).

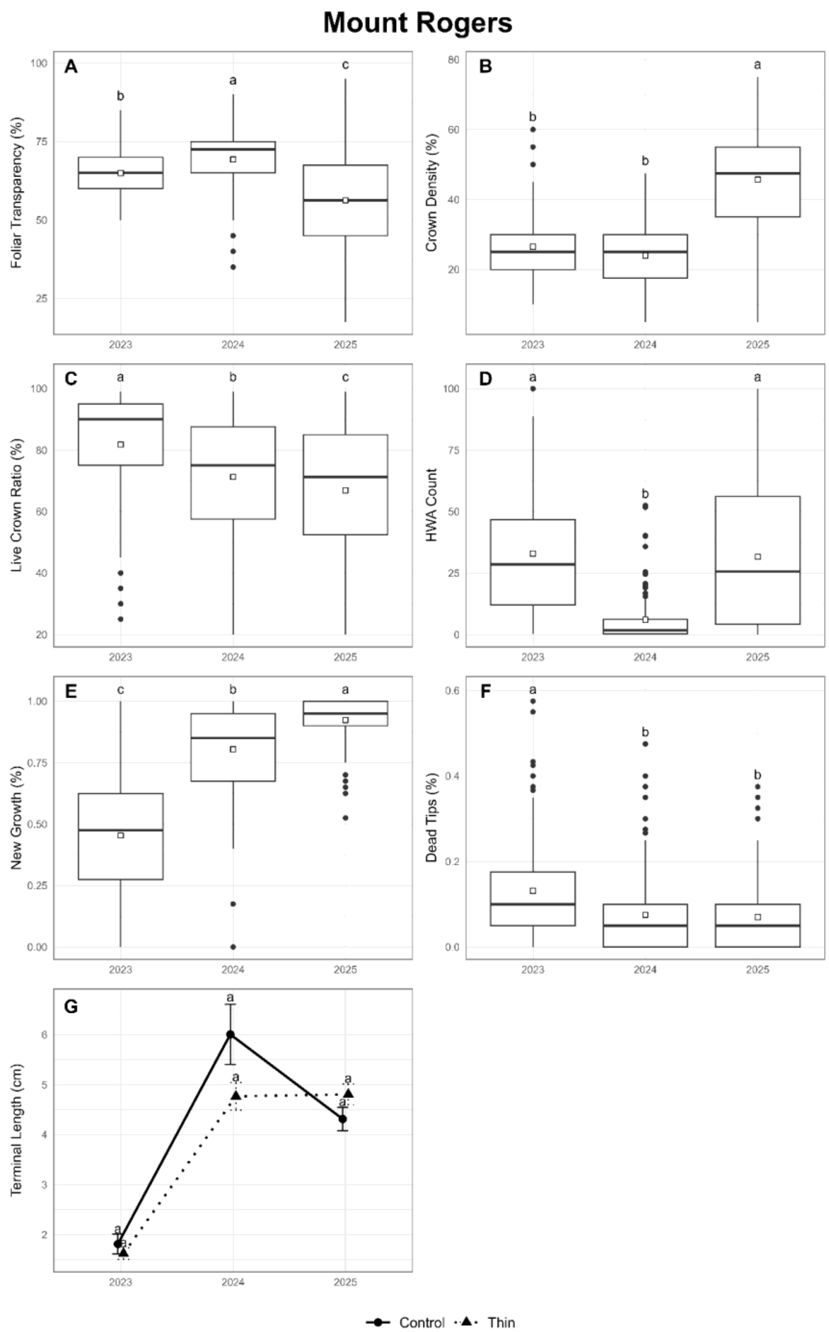

Figure 1.4: Tree-level (A–C) and branch-level (D–G) health metrics for control (solid lines) and thinned (dashed lines) eastern hemlocks at Mount Rogers, VA, 2023–2025. Boxplots display medians, interquartile ranges, ranges, and means (□). Tree-level metrics include foliar transparency (A), crown density (B), and live crown ratio (C). Branch-level metrics include HWA count (D), new growth (E), dead tips (F), and terminal leader length (G). Points indicate means ± SE. Different lowercase letters denote significant differences among years within treatments ($P < 0.05$).

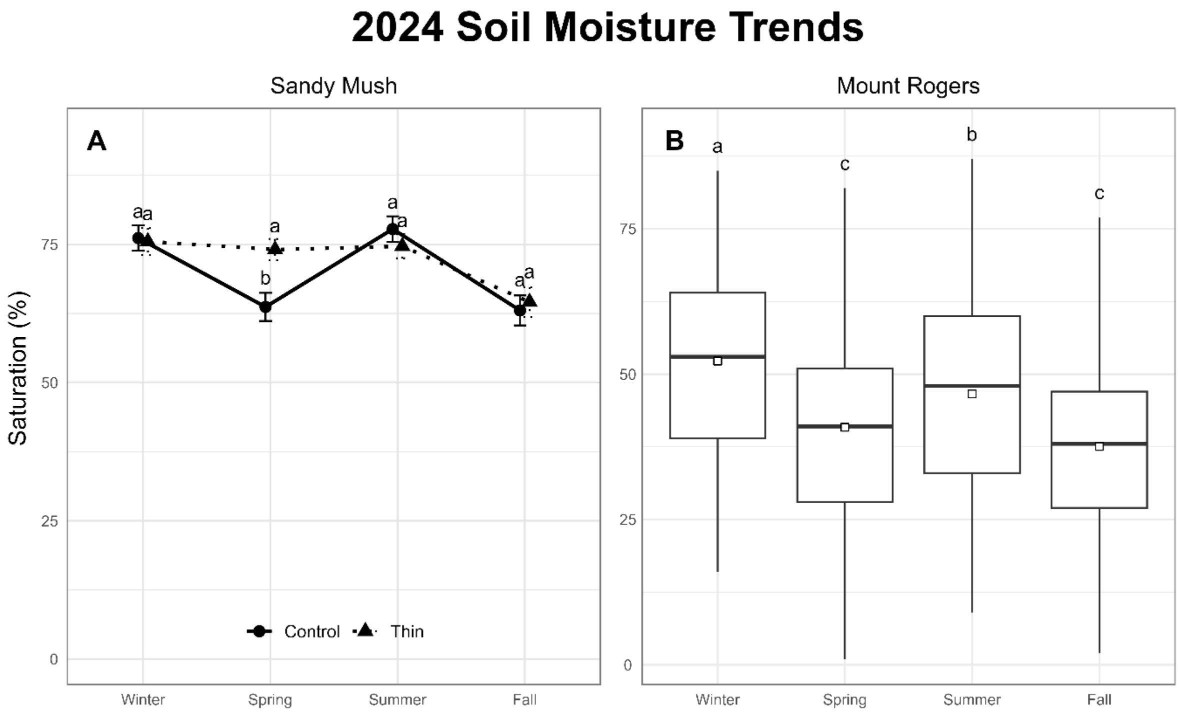

Figure 1.5: (A) Mean percent soil moisture saturation (±SE) at Sandy Mush showing the interaction of season and canopy treatment. (B) Boxplots showing the response of soil moisture saturation to season at Mount Rogers. Different lowercase letters denote significant differences among seasons within site and treatment ($p < 0.05$).

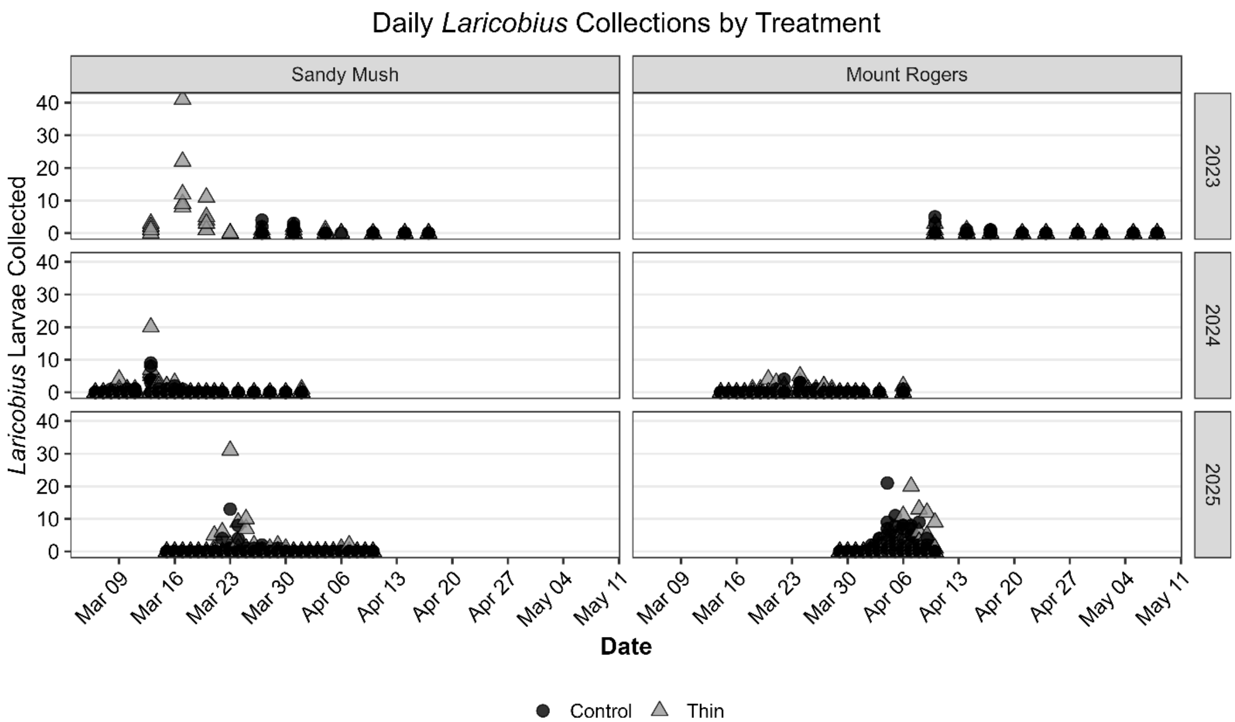

Figure 1.6: Daily *Laricobius* larvae collections by site and treatment across three years (2023–2025). Data are shown for Sandy Mush and Mount Rogers under control and thin treatments. Symbols indicate treatments: control (●) and thin (△).

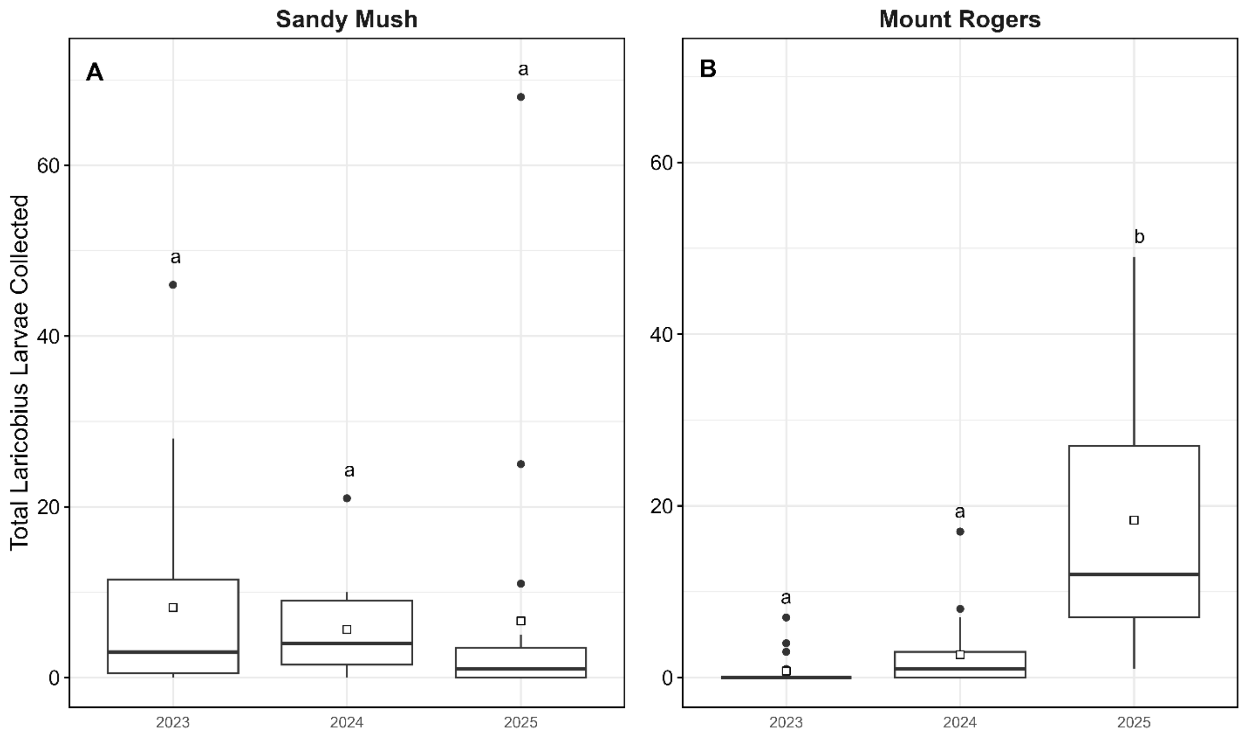

Figure 1.7: Mean (± SE) *Laricobius* larvae counts per plot across three study years (2023–2025) at Sandy Mush (left) and Mount Rogers (right). Boxplots show median, interquartile range, range, and mean (□). Different letters above boxplots indicate significant differences among years within each site based on post hoc comparisons ($p < 0.05$).

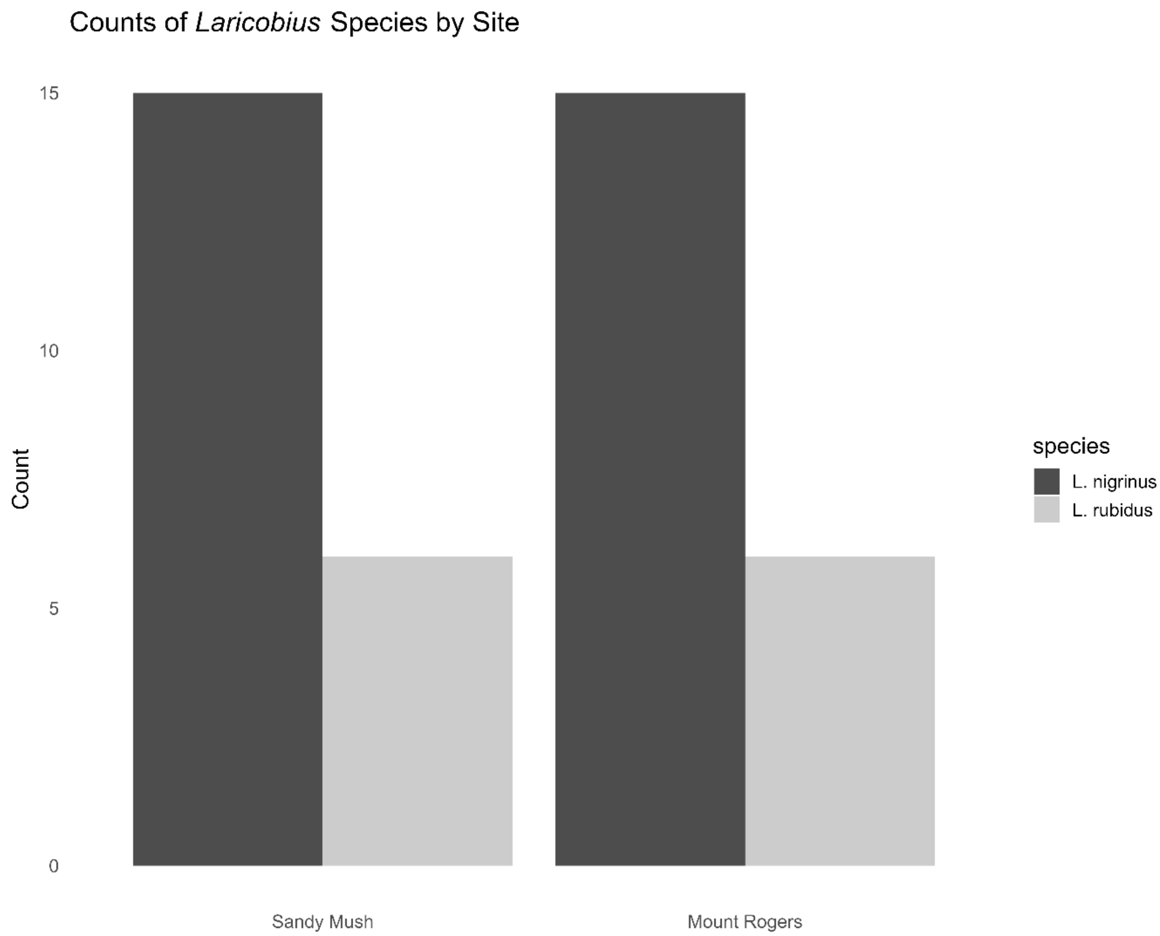

Figure 1.8: Distribution of *Laricobius* species collected as larvae from Sandy Mush and Mount Rogers in 2025. DNA analysis conducted by the USDA Forest Service, Northern Research Station (Nathan Havill) identified individuals as L. nigrinus or L. rubidus. Counts represent the total number of larvae identified per species at each site.

References

Aquaterr Instruments. TEMP-350 digital soil moisture and temperature meter [Equipment]. Long Beach, CA. https://www.aquaterr.com/temp-350

Brantley, S. T., Mayfield, A. E., Jetton, R. M., Miniat, C. F., Zietlow, D. R., Brown, C. L., & Rhea, J. R. (2017). Elevated light levels reduce hemlock woolly adelgid infestation and improve carbon balance of infested eastern hemlock seedlings. *Forest Ecology and Management*, *385*, 150–160. https://doi.org/10.1016/j.foreco.2016.11.028

Chagnon, C., Dumont, S., Morin-Bernard, A., Jactel, H., Achim, A., & Moreau, G. (2025). Potential of thinning to increase forest resilience and resistance to drought, pest, windstorm and fire: A meta-analysis. *Forest Ecology and Management*, *590*, 122788. https://doi.org/10.1016/j.foreco.2025.122788

Cowles, R. S., Montgomery, M. E., & Cheah, C. A. S. J. (2006). Activity and residues of imidacloprid applied to soil and tree trunks to control hemlock woolly adelgid (Hemiptera: Adelgidae) in forests. *Journal of Economic Entomology*, *99*(4), 1258–1267. https://doi.org/10.1603/0022-0493-99.4.1258

Davis, D. D., Fromm, M. S., & Davis, M. D. (2007). Impact of the Hemlock Woolly Adelgid on Radial Growth of Eastern Hemlock in Pennsylvania. *Proceedings of the 15th Central Hardwood Forest Conference*. Central Hardwood Forest Conference, Knoxville, TN.

del Campo, A. D., Otsuki, K., Serengil, Y., Blanco, J. A., Yousefpour, R., & Wei, X. (2022). A global synthesis on the effects of thinning on hydrological processes: Implications for forest management. *Forest Ecology and Management*, *519*, 120324. https://doi.org/10.1016/j.foreco.2022.120324

Dharmadi, S. N., Elliott, K. J., & Miniat, C. F. (2019). Lack of forest tree seedling recruitment and enhanced tree and shrub growth characterizes post-*Tsuga canadensis* mortality forests in the southern Appalachians. *Forest Ecology and Management*, *440*, 122–130. https://doi.org/10.1016/j.foreco.2019.03.024

Ellison, A. M., Orwig, D. A., Fitzpatrick, M. C., & Preisser, E. L. (2018). The Past, Present, and Future of the Hemlock Woolly Adelgid (Adelges tsugae) and Its Ecological Interactions with Eastern Hemlock (Tsuga canadensis) Forests. *Insects*, *9*(4), 172. https://doi.org/10.3390/insects9040172

Evans, A. M., & Gregoire, T. G. (2007). A geographically variable model of hemlock woolly adelgid spread. *Biological Invasions*, *9*(4), 369–382. https://doi.org/10.1007/s10530-006-9039-z

Fajvan, Mary Ann. (2008). The role of silvicultural thinning in eastern forests threatened by hemlock woolly adelgid (*Adelges tsugae*). In: Deal, R.L., tech. ed. Integrated restoration of forested ecosystems to achieve multiresource benefits: proceedings of the 2007 national silviculture workshop; 2007 May 7-10; Ketchikan, AK. Gen. Tech. Rep. PNW-733. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 247-256.

Fischer, M. J., Havill, N. P., Brewster, C. C., Davis, G. A., Salom, S. M., & Kok, L. T. (2015). Field assessment of hybridization between *Laricobius nigrinus* and *L. rubidus*, predators of Adelgidae. *Biological Control*, *82*, 1–6. https://doi.org/10.1016/j.biocontrol.2014.12.002

Ford, C. R., Elliott, K. J., Clinton, B. D., Kloeppel, B. D., & Vose, J. M. (2010). Forest dynamics following eastern hemlock mortality in the southern Appalachians. *Oikos*, *121*(4), 523–536. https://doi.org/10.1111/j.1600-0706.2011.19622.x

Ford, C. R., & Vose, J. M. (2006). Eastern hemlock transpiration: Patterns, controls, and implications for its decline in southern Appalachian forests. *In: Second Interagency Conference on Research in the Watersheds, May 16-18, 2006. 7 p.* https://research.fs.usda.gov/treesearch/28998

Godman, R. M., & Lancaster, K. (1990). Tsuga canadensis (L.) Carr. Eastern Hemlock. In *Silvics of North Aerica: 1. Conifers.* (R.M. Burns and B.H. Honkala, pp. 604–612). USDA Forest Service.

Gossman, S. (2023). *Carolina Hemlock Community Structure and Vitality* [Master's Thesis, NC State University]. https://www.lib.ncsu.edu/resolver/1840.20/41461

Gouger, R. J. (1971). Control of Adelges tsugae on hemlock in Pennsylvania. *Scientific Tree Topics*, *3*(1), 1–9.

Hart, J. L., & Kupfer, J. A. (2011). Sapling richness and composition in canopy gaps of a southern Appalachian mixed Quercus forest1. *The Journal of the Torrey Botanical Society*, *138*(2), 207–219. https://doi.org/10.3159/TORREFY-D-11-00006.1

Havill, N. P., Montgomery, M. E., & Foottit, R. (2008). Molecular ecology of hemlock woolly adelgid, its hosts, and its natural enemies. *In: Onken, Brad; Reardon, Richard, Comps. Fourth Symposium on Hemlock Woolly Adelgid in the Eastern United States; 2008 February 12-14; Hartford, CT. FHTET 2008-01. Morgantown, WV: U.S. Forest Service, Forest Health Technology Enterprise Team: 147-148.*, 147–148.

Havill, N. P., Montgomery, M. E., Yu, G., Shiyake, S., & Caccone, A. (2006). Mitochondrial DNA from Hemlock Woolly Adelgid (Hemiptera: Adelgidae) Suggests Cryptic Speciation and Pinpoints the Source of the Introduction to Eastern North America. *Annals of the Entomological Society of America*, *99*(2), 195–203. https://doi.org/10.1603/0013-8746(2006)099[0195:MDFHWA]2.0.CO;2

Havill, N. P., Shiyake, S., Lamb Galloway, A., Foottit, R. G., Yu, G., Paradis, A., Elkinton, J., Montgomery, M. E., Sano, M., & Caccone, A. (2016). Ancient and modern colonization of North America by hemlock woolly adelgid, Adelges tsugae (Hemiptera: Adelgidae), an invasive insect from East Asia. *Molecular Ecology*, *25*(9), 2065–2080. https://doi.org/10.1111/mec.13589

Jetton, R. M., Hastings, F. L., & Hain, F. P. (2009). Arthropod Diversity Associated with Old and Secondary Growth Eastern Hemlock (tsuga Canadensis) in the Great Smoky Mountains National Park. *Journal of the North Carolina Academy of Science*, *125*(2), 70–77.

Jubb, C. S., McAvoy, T. J., Stanley, K. E., Heminger, A. R., & Salom, S. M. (2021). Establishment of the predator *Laricobius nigrinus*, introduced as a biological control agent for hemlock woolly adelgid in Virginia, USA. http://hdl.handle.net/10919/107073

Krapfl, K. (2010). Impacts of Hemlock Woolly Adelgid on Tsuga Canadensis Forest Communities in Great Smoky Mountains National Park, USA. [Master's Thesis, Southern Illinois University]. https://opensiuc.lib.siu.edu/theses/175

Limbu, S., Keena, M. A., & Whitmore, M. C. (2018). Hemlock Woolly Adelgid (Hemiptera: Adelgidae): A Non-Native Pest of Hemlocks in Eastern North America. *Journal of Integrated Pest Management*, *9*(1), 27. https://doi.org/10.1093/jipm/pmy018

Martin, K. L., & Goebel, P. C. (2013). The foundation species influence of eastern hemlock (Tsuga canadensis) on biodiversity and ecosystem function on the Unglaciated Allegheny Plateau. *Forest Ecology and Management*, *289*, 143–152. https://doi.org/10.1016/j.foreco.2012.10.040

Mausel, D. L., Salom, S. M., Kok, L. T., & Davis, G. A. (2010). Establishment of the Hemlock Woolly Adelgid Predator, *Laricobius nigrinus* (Coleoptera: Derodontidae), in the Eastern United States. *Environmental Entomology*, *39*(2), 440–448. https://doi.org/10.1603/EN09088

Mayfield, A.E., III; S.M. Salom; K. Sumpter; T. McAvoy; N.F. Schneeberger; R. Rhea. (2020). Integrating chemical and biological control of the hemlock woolly adelgid: a resource manager's guide. FHAAST-2018-04. USDA Forest Service, Forest Health Assessment and Applied Sciences Team, Morgantown, West Virginia.

Mayfield, A., Dietschler, N., & Whitmore, M. C. (2021). The Lari-Leuco container: A novel collection arena for separating insects ascending or descending from a plant foliage sample. *Journal of Economic Entomology*, *114*, 2400–2405. https://doi.org/10.1093/jee/toab181

Mayfield, A. E., Jetton, R. M., Mudder, B. T., Whittier, W. A., Keyser, T. L., & Rhea, J. R. (2023). Silvicultural canopy gaps improve health and growth of eastern hemlocks infested with Adelges tsugae in the southern Appalachian Mountains. *Forest Ecology and Management*, *546*(Journal Article), 121374. https://doi.org/10.1016/j.foreco.2023.121374

McCarty, E., & Addesso, K. M. (2019). Hemlock Woolly Adelgid (Hemiptera: Adelgidae) Management in Forest, Landscape, and Nursery Production. *Journal of Insect Science*, *19*(2), iez031. https://doi.org/10.1093/jisesa/iez031

McClure, M. S. (1989). Evidence of a Polymorphic Life Cycle in the Hemlock Woolly Adelgid, *Adelges tsugae* (Homoptera: Adelgidae). https://doi.org/dx.doi.org/10.1093/aesa/82.1.50

McClure, M. S. (1990). Role of wind, birds, deer, and humans in the dispersal of hemlock woolly adelgid (Homoptera: Adelgidae). *Environmental Entomology*, *19*, 36–43.

Miniat, C. F., Zietlow, D. R., Brantley, S. T., Brown, C. L., Mayfield, A. E., Jetton, R. M., Rhea, J. R., & Arnold, P. (2020). Physiological responses of eastern hemlock (Tsuga canadensis) to light, adelgid infestation, and biological control: Implications for hemlock restoration. *Forest Ecology and Management*, *460*. https://doi.org/doi.org/10.1016/j.foreco.2020.117903

Potter, K., & Crane, B. S. (2010). Forest Tree Genetic Risk Assessment System: A Tool for Conservation Decision Making in Changing Times. *User Guide*, *Version 1*.

Potter, K. M., Escanferla, M. E., Jetton, R. M., Man, G., & Crane, B. S. (2019). Prioritizing the conservation needs of United States tree species: Evaluating vulnerability to forest insect and disease threats. *Global Ecology and Conservation*, *18*, e00622. https://doi.org/10.1016/j.gecco.2019.e00622

Radville, L., Chaves, A., & Preisser, E. L. (2011). Variation in plant defense against invasive herbivores: Evidence for a hypersensitive response in eastern hemlocks (*Tsuga canadensis*). *Journal of Chemical Ecology*, *37*(6), 592–597. https://doi.org/10.1007/s10886-011-9962-z

Russo, N. J., Elphick, C. S., Havill, N. P., & Tingley, M. W. (2019). Spring bird migration as a dispersal mechanism for the hemlock woolly adelgid. *Biological Invasions*, *21*(5), 1585–1599. https://doi.org/10.1007/s10530-019-01918-w

Schomaker, M. E., Zarnoch, S. J., Bechtold, W. A., Latelle, D. J., Burkman, W. G., & Cox, S. M. (2007). Crown-condition classification: A guide to data collection and analysis (No. SRS-GTR-102; p. SRS-GTR-102). *U.S. Department of Agriculture, Forest Service, Southern Research Station*. https://doi.org/10.2737/SRS-GTR-102

Tomback, D. F., & Achuff, P. (2010). Blister rust and western forest biodiversity: Ecology, values and outlook for white pines. *Forest Pathology*. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1439-0329.2010.00655.x

Vose, J. M., & Swank, W. T. (1994). Effects of long-term drought on the hydrology and growth of a white pine plantation in the southern Appalachians. *Forest Ecology and Management*, *64*(1), 25–39. https://doi.org/10.1016/0378-1127(94)90124-4

Wiggins, G. J., Grant, J. F., Rhea, J. R., Hakeem, A., & Lambdin, P. L. (2016). A Field-Based Method to Estimate Densities of *Laricobius nigrinus* (Coleoptera: Derodontidae), an Introduced Predator of Hemlock Woolly Adelgid (Hemiptera: Adelgidae). *Florida Entomologist*, *99*(4), 805–807. https://doi.org/10.1653/024.099.0442

Willig, J., Schwarz, J., Comeau, P., Hartmann, H., Kohnle, U., Espelta, J. M., Mäkinen, H., Ogaya, R., Peltoniemi, M., Penuelas, J., Roth, B., Ruiz-Peinado, R., Ruge, F., & Bauhus, J. (2025). No increased drought-related mortality after thinning: A meta-analysis. *Annals of Forest Science*, *82*(1), 6. https://doi.org/10.1186/s13595-025-01278-7

Young, D., Dillingham, C., & Zhang, J. (2012). *[PDF] HFQLG Soil Moisture Monitoring – Aug 2009 to Sep 2012*. https://nanopdf.com/download/hfqlg-soil-moisture-monitoring-aug-2009-to-sep-2012_pdf

Zilahi-Balogh, G. M. G., Kok, L. T., & Salom, S. M. (2003). A Predator Case History: *Laricobius* nigrinus, A Derodontid Beetle Introduced Against the Hemlock Woolly Adelgid. *Econd International Symposium on Biological Control of Arthropods*, *Host Range Testing of Laricobius nigrinus*, 651–664.

CHAPTER 2: Canopy Disturbance and Growth Dynamics of Carolina Hemlock Forests

Abstract

Carolina hemlock (*Tsuga caroliniana* Engelm.), a rare conifer endemic to the southern Appalachian Mountains, plays an important ecological role by providing nesting sites for birds, forage for wildlife, and critical winter shelter for animals. Since the early to mid-20th century, the non-native hemlock woolly adelgid (HWA; *Adelges tsugae* Annand) has threatened the persistence of both Carolina and eastern hemlocks (*T. canadensis* (L.) Carrière) throughout the Appalachians. To assess the long-term impacts of HWA within the context of historical growth patterns, we used dendroecological methods to reconstruct establishment dates, disturbance events, and radial growth trends for four Carolina hemlock populations in North Carolina and Tennessee. Establishment was concentrated between 1920 and 1990, after which recruitment sharply declined. No new establishment was detected after 2000 across all sites. Growth release analyses revealed a cyclical disturbance–recovery pattern, with major releases concentrated in the 1970s and 1990s and moderate releases more evenly distributed across decades. However, this disturbance cycle was disrupted following the arrival of HWA in each county. Within a decade of infestation, radial growth declined by more than 50% at some sites, and the magnitude of suppression often exceeded that observed following natural disturbance events. These declines were persistent, suggesting long-term physiological stress and limited recovery potential under continued pest pressure. The loss of recruitment, combined with sustained growth suppression, indicates that HWA is fundamentally altering the disturbance dynamics of Carolina hemlock populations. These findings underscore the urgency of conservation interventions before visible canopy decline, when treatment windows may already be closing. Site-specific strategies, such as targeted chemical protection, classical biological control, and conservation plantings in

genetically important stands, will be critical to preserving this species. By linking historical growth cycles to modern pest impacts, this study provides a framework for understanding and mitigating invasive-driven disturbance in rare conifer systems under a changing climate.

Introduction

Carolina hemlock (*Tsuga caroliniana* Engelm.) is a rare, endemic conifer restricted to isolated, mid-elevation rocky outcroppings on dry, upland sites within its limited southern Appalachian Mountain range(Fig. 2.1). The fragmented distribution of Carolina hemlock, spanning only about 465 km x 165 km (Fig. 2.1, inset), reflects its ecological specialization and heightened vulnerability to threats, such as climate shifts, fire suppression, and, most recently, the invasive hemlock woolly adelgid (HWA; *Adelges tsugae* Annand). Despite its patchy occurrence, Carolina hemlock plays an ecologically significant role in maintaining habitat structure, supporting unique understory communities, and providing food and shelter for wildlife within pure and mixed pine/hardwood stands (Farjon 1990; Rentch et al. 2000; Jetton 2008; Havill et al. 2016a). Based on Carolina hemlock's current disjunct distribution, it is theorized that Pleistocene glaciation is a leading cause of the range (Jetton 2008), with all remaining populations today found from Rabun County, Georgia, north to Rockbridge County, Virginia. Carolina hemlock's limited dispersal ability and genetic diversity further restrict its capacity to colonize new geographic locations, increasing its susceptibility to disturbance and ongoing environmental change (Humphrey 1989; Potter et al. 2017; Keyser et al. 2023; Gossman 2023; Whittier et al. 2025).

Microclimate conditions greatly restrict the occurrence of Carolina hemlock, with low summer precipitation limiting it to the north and high summer temperatures restricting it to the south (Jetton et al. 2008). Within the range, high spring and summer temperatures suppress radial growth, with older trees showing greater sensitivity to precipitation and drought (Austin et al. 2016). This indicates that changing environmental conditions will amplify the competitive disadvantage of the species, particularly relative to the hardwood competitors promoted by the reduction in fire frequency. Establishment events within isolated populations have been linked to the decline of the American chestnut [*Castanea dentata* (Marsh.) Borkh] due to chestnut blight, as well as by ice storms and wind damage (Rentch et al. 2000; Austin et al. 2016). Past descriptive efforts of Carolina hemlock communities have shown that even when the species is dominant in the overstory, it is nearly absent in the regeneration layer (Rentch et al. 2000). Instead, shade-tolerant species such as maple (*Acer* spp.) are more dominant in the understory and stand to replace Carolina hemlock as mortality occurs (Keyser et al. 2023). Understanding the disturbance and replacement patterns is important for designing management to maintain or conserve declining species and may be particularly critical for Carolina hemlock due to its rarity and vulnerability to introduced and invasive pests such as HWA.

Conservation efforts for other conifer species, such as shortleaf pine (*Pinus echinata* Mill.), longleaf pine (*Pinus palustris* Mill.), and red spruce (*Picea rubens* Sarg.), have sought to mitigate threats associated with commercial logging, altered fire regimes, climate change, and invasive pests. Common strategies include assisted migration, targeted restoration plantings, prescribed burning, and integrated pest management programs (Goode et al. 2021; Mitchell et al. 2006). Understanding the disturbance dynamics within these systems is critical for determining whether a species depends on periodic disturbances for regeneration and for identifying the spatial and temporal scales over which such disturbances are most beneficial (Hart & Kupfer 2011). Certain conifers, for example, exhibit enhanced recruitment following fire or windthrow events, whereas others decline in the absence of prolonged disturbance-free intervals (Mitchell et al. 2006; Hart & Kupfer 2011).

In contrast to natural disturbances, the impacts of invasive forest insects can be more abrupt and transformative. The disturbance generated by HWA, for instance, differs markedly from events such as fire or storm damage: rather than producing a patchy canopy structure that facilitates gradual regeneration, HWA infestation often causes rapid, widespread mortality, leading to substantial alterations in forest structure and microclimatic conditions (Ellison et al. 2005). Comparable cases, such as the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in lodgepole pine (*Pinus contorta* Dougl.) forests, show that novel pests can disrupt long-established disturbance–recovery cycles and trigger unanticipated ecological cascades (Holmes et al. 2008).

Within hemlock ecosystems, HWA infestations can fundamentally alter stand composition by causing mortality across all age classes. In eastern hemlock (*Tsuga canadensis* (L.) Carrière) stands, mortality rates have been reported up to 99% (Ellison et al. 2018; McAvoy 2025), and surviving trees can experience growth reductions of approximately 50% (Vogt et al. 2016). Such large-scale die-offs often initiate successional shifts toward hardwood dominance, replacing the dense hemlock overstories and understories that previously suppressed hardwood recruitment. Prior to HWA infestation, Carolina hemlock stands similarly exhibited strong establishment patterns and cyclical regeneration, with hemlocks occupying both canopy and understory positions and effectively outcompeting hardwoods (Austin et al. 2016). Despite its ecological importance, the restricted range of Carolina hemlock results in it being far less studied than eastern hemlock. A clearer understanding of its disturbance history and establishment dynamics is essential for predicting future compositional changes under mounting climatic and biotic stressors, particularly now that HWA has established residence throughout its entire range.

Our goal was to determine the establishment patterns and disturbance history of Carolina hemlock using dendrochronology across four populations in the southern Blue Ridge Mountains. We addressed this by focusing on two main objectives: (1) reconstruct the disturbance events and how these have influenced Carolina hemlock establishment and growth, and (2) document the occurrence of HWA outbreaks and whether these correspond to growth declines. We expected to find that periods of increased Carolina hemlock establishment correlated with the decline of American chestnut in the early 20th century (Elliot & Swank 2008). We hypothesized that Carolina hemlock would show marked growth declines coinciding with the period HWA was first reported in the surrounding counties. Additionally, by using dendroecological techniques, such as cross-referencing growth patterns with historical disturbance records, we aimed to describe the ecological history of these remnant Carolina hemlock populations and provide insights into their resilience and vulnerability under ongoing environmental pressures (Abrams et al. 1995; Fraver & White 2005a).

Methods

Study Area

The initial study and physical data collection were conducted in western North Carolina and eastern Tennessee within the Blue Ridge Mountains (Fig. 2.1). The sites were chosen based on their central location within the entire range of Carolina hemlock and were inventoried in 2018, as five distinct sites per Keyser et al. (2023). The vegetation structure and composition of these five sites are described further in Keyser et al. (2023); however, we consolidated all data from Iron Mountain Top and Iron Mountain Bottom into a single site, "Iron Mountain (IM)" based on proximity to each other and a lack of genetic diversity (Potter et al., 2017; Jetton et al., 2008). Therefore, we focused on four sites: Cliff Ridge (CR) and Iron Mountain (IM) in Tennessee, as well as Dobson's Knob (DK) and Lost Cove (LC) in North Carolina. Carolina hemlock was a major component at each site, with Importance Values (IV) ranging from 20 to 65%. The basal area of the sites ranged from 30-60m^2 ha^{-1}, and density (stems > 5 cm dbh) ranged from 1120 - 1615 stems ha^{-1}. We used the Hemlock Woolly Adelgid National Initiative database (downloaded from ArcGIS Online) to identify the date HWA was first noted as being present in the home county of each site between 2001 and 2006 (Table 1). Additional information regarding the overall tree health in these and other prominent Carolina hemlock sites was referenced from Gossman (2023) and Loftis (2025), including canopy density, health index, and soil characteristics.

Field Sampling and Data Collection

At four 0.05-ha fixed radius plots used for vegetation inventory (Keyser et al. 2023), two increment cores (n = 1,250) were taken at breast height (1.3 m) on opposing sides of the trunk from every tree (> 5 min dbh) within the 20 plots in an effort to maximize cross dating accuracy and capture within-tree growth variability. Increment cores were mounted and sanded to a fine polish using standard methods (Stokes and Smiley 1996). Most cores were scanned (Epson Perfection V39 Scanner; dpi = 1200) and ring widths were measured using CooRecorder software (Cybis Elektronik & Data AB; Maxwell & Larsson 2021). One core per tree was chosen for analysis based on ring visibility/accuracy and completeness of each core (lack of missing segments). When rings were difficult to discern, they were measured on a Velmex sliding-stage stereomicroscope (Velmex Inc., Bloomfield, NY) to the nearest 0.01 mm and recorded in Measure J2X software (Voorhis and Krusic 2006). Raw ring width data from both methods were combined in CDendro (Cybis Elektronik & Data AB) for uniform file types.

Data Analysis

All data and statistical analyses were conducted in R version 4.5.0. Tree-ring series were standardized for all species to remove size-related growth trends using the dplR package (Bunn et al. 2025). Standardization was performed using the Friedman smoothing spline with a frequency cutoff of 0.5 to retain interannual to decadal variability while minimizing age-related trends, and with negative slopes preserved to avoid artificially inflating late-life growth. The resulting indices were prewhitened to remove temporal autocorrelation and expressed as residual chronologies. The x-axis was truncated in 1880 to ensure uniform temporal coverage among sites and species. From these standardized series, we developed site-level biweight robust-mean chronologies to assess long-term growth patterns and responses to disturbance. To assess how climate variability has influenced Carolina hemlock growth, we compared annual Palmer Drought Severity Index (PDSI) values to mean tree-ring indices for our sites in North Carolina (Linville, WNG538) and Tennessee (Cliff Ridge, WXK47).

Establishment dates and chronologies

All tree-ring series in each plot were classified into four species groups: Carolina hemlock, oaks (*Quercus* spp.), pines (*Pinus* spp.), and all other hardwoods. Estimated establishment dates for each species were determined by site and decade using the TRADER package (Altman et al., 2014). Growth releases, defined as abrupt and sustained increases in radial growth, were identified to reconstruct site-specific disturbance histories. Sequential 10-year ring-width averages were analyzed, and the number of major (>50%) and moderate (25–49.9%) growth releases was tallied by decade following the Nowacki and Abrams method (Nowacki & Abrams 1997). Site-level ring-width chronologies were compiled with TRADER to visualize temporal growth trends across all plots, sites, and species groups.

Defoliation Analysis

Natural and biological disturbance events, including ring-width suppression, were evaluated using the dfoliatR package (Guiterman et al. 2020), allowing us to refine the estimated timing of initial HWA presence. The timing and severity of defoliation events were calculated using standardized individual-tree chronologies that were analyzed with the defoliate_trees() function, using the following parameters: duration_years = 3, max_reduction = -1.28, bridge_events = TRUE, and series_end_event = TRUE. To focus on host-specific disturbance signals, non-host chronologies were excluded from analysis (nonhost_chron = NULL). Following Fajvan and Wood (2010), defoliation events were defined as at least three consecutive years of declining ring widths, with particular attention to declines coinciding with HWA introduction (Figure 4). Outbreak severity ranged from NA (no recorded defoliation), Minor (light defoliation), Moderate (some defoliation), or Severe (intense defoliation). From the defoliate_trees() output, the outbreak() function was applied with a minimum threshold of 50% of trees defoliated, a minimum of three occurrences per series to qualify as an outbreak, and a minimum sample year of 1955 to maintain a series depth of ≥ ten cores across all sites. The resulting data were visualized using the plot_outbreak() function to display sample depth, Normalized Growth Suppression Index (NGSI), and the proportion of trees defoliated.

Results

Stand Dynamics and Establishment

Across sites, we found that most Carolina hemlocks were young, with median ages ranging from 45 years at Dobson’s Knob to 62 years at Lost Cove, and an average of about 52 years across all sites. Maximum hemlock ages, however, revealed the presence of scattered older growth: Lost Cove contained the oldest individual hemlock sampled at 221 years, followed by Iron Mountain at 190 years, while Cliff Ridge and Dobson’s Knob topped out at 119 years and

91 years, respectively. In every stand, the youngest cores were measured to be 10-12 years old, but only trees with DBHs greater than or equal to 5 cm were cored.

Cross-dating the hemlocks proved challenging because of the relatively young age of most trees. Standard cross-dating functions start with 50-year segment lengths overlapping by 25 years (Bunn 2008); however, many of our cores did not exceed 50 years. Inter-series correlations using multi-year segments were no higher than 0.377, 0.310, 0.273, and 0.298 for CR, DK, IM, and LC, respectively (Table 2.2), yet still allowed for quality assessment of the measurements.

Initial establishment pulses were site-specific but fell within a three-decade window from 1910-1940 (Table 2.1). Subsequent peaks in recruitment shifted throughout the century: Iron Mountain and Lost Cove peaked earlier in 1960 and 1950, respectively, whereas both Cliff Ridge and Dobson's Knob exhibited maximum establishment counts in 1970 (Table 2.1). The last discernible recruitment pulse at each site occurred by 1990 at Cliff Ridge and Iron Mountain or by 1980 at Dobson's Knob and Lost Cove. These peaks in recruitment at all sites preceded county-level detection of HWA by roughly 10 to 25 years (Fig. 2.2).

Major growth releases were uncommon and highly concentrated in a single decade at most sites. Only one-third of cores, on average, exhibited at least one major release (24-39%), and ≤8 % recorded two or more release events. The maximum individual core release frequency never exceeded four total cores. The decade of the highest major release activity was 1990 for Cliff Ridge and Dobson's Knob, 23 and 13 releases, respectively, but shifted two decades earlier in the 1970s at Iron Mountain and Lost Cove (Table 2.1). Total counts of major releases mirrored this pattern, ranging from 37 at Cliff Ridge to 67 at Iron Mountain.

Moderate releases were more prevalent than major releases. Roughly one quarter of stems per stand recorded at least one moderate release (21-28%), but repeat events were rare (less than 4%). Peak decades for moderate releases centered on the 1990s at three sites, except Lost Cove, which peaked in the 1970s. Iron Mountain and Lost Cove each accumulated 67 moderate releases, more than double the values recorded at Cliff Ridge and Dobson's Knob. Major releases are scarce, occurring in approximately one-third of the cores examined and tightly bunched in single decades; moderate releases are more common but still episodic.

Carolina hemlock populations are dominated by young trees with median ages of 45 to 62 years, which could imply stand-scale disturbances or land-use change early in the 20th century. Examples include a considerable number of canopy gaps following the fall of the American chestnut, severe weather and windstorms, or selective logging. Scattered older trees, between 119 and 221 years old, represent legacy trees that escaped those events and now serve as genetic refugia. Although the 2018 sampling targeted stems greater than 5 cm DBH, a field inventory confirmed a scarcity of saplings, underscoring limited regeneration (Keyser et al. 2023). Lost Cove, which harbors the oldest living individuals (221 years) and the deepest sample size (n = 205; Table 2.1), represents a critical genetic reservoir.

Population Trends

Carolina hemlock growth rates varied across the four study sites, with most exhibiting stable or increasing radial growth through much of the 20th century, followed by sharp declines beginning in the late 1990s to early 2000s (Fig. 2.3). At Cliff Ridge, growth increased steadily through the 20th century before declining markedly after 2005, coinciding with the arrival and spread of HWA. Similar trends were observed at Dobson's Knob and Iron Mountain, where growth peaked around 2000 before declining. Lost Cove, which had the largest sample depth (n = 205), showed a comparable downward trajectory, providing high confidence in the observed patterns.

Growth declines closely tracked the timing of HWA establishment across sites, suggesting a consistent radial growth response to infestation. To ensure comparability, a minimum sample depth of 10 cores per decade was applied, which standardized the record beginning in 1955. Although some decline years coincided with drought events identified by the Palmer Drought Severity Index (PDSI), moisture conditions generally improved while growth continued to decline, pointing to additional drivers. Site-level analyses revealed strong regional contrasts: in North Carolina, the ring-width index showed no relationship with PDSI ($R^2 <= 0.00$), indicating little sensitivity to interannual drought variability, whereas at the Tennessee site, growth was positively correlated with PDSI ($R^2 \approx 0.28$), with wider rings forming during wetter years. These results suggest that Carolina hemlock sensitivity to moisture availability varies regionally, with Tennessee populations more responsive to climate fluctuations than those in North Carolina.

Disturbance reconstructions further support these trends. Pre-2000, most sites exhibited moderate or minor release events, but post-2000, there was a disproportionate increase in severe defoliations, aligning with declines observed in the detrended growth chronologies (Fig. 2.4). The cyclical nature of suppression across geographically distinct sites underscores HWA infestation as the primary driver of recent declines in radial growth. The consistency of this pattern across elevations and site types highlights the species-wide susceptibility of Carolina hemlock to HWA-induced stress, potentially compounded by additional environmental stressors such as drought or site-specific resource limitations.

Discussion

Synchronous Establishment Pulses

All four sites share a prominent Carolina hemlock recruitment wave that falls within a three-decade window, followed by site-specific secondary pulses that seemingly dissipate by the

1980s. Two regional drivers plausibly created the required establishment windows: (1) canopy openings after mature American chestnut mortality in the 1930s and 1940s favored shade-tolerant hemlocks in the southern Appalachians (Butler et al. 2014), and (2) Depression-era bark harvesting for tanning and subsequent farm abandonment (Hepting 1964) generated fresh microsites on xeric ridges (Schwartz et al. 2020; Dupont et al. 2020; Tang et al. 2023). These episodic pulses reinforce concerns that Carolina hemlock successfully replaces canopy losses only when disturbance events create regeneration opportunities. By 2000, recruitment had virtually ceased at all sites. Woody understory surveys at these and other locations (Wind, 2021; Gossman, 2023) indicate that Carolina hemlock seedlings and saplings now compose only 3% of the total regeneration layer. Peaks in recruitment coincide with earlier findings that the development of Carolina hemlock forests was linked to American chestnut decline and other episodic disturbances (Rentch et al. 2000). Regeneration dynamics for Carolina hemlock remain poorly understood, particularly under natural conditions, though most studies report limited recruitment beneath closed canopies. Recent studies conducted at the same and additional Carolina hemlock sites found that abiotic factors, such as soil texture, soil pH, elevation, slope, and aspect, are the best indicators of HWA presence in Carolina hemlock stands (Keyser et al. 2023; Gossman 2023; Loftis 2025). By aging individuals and constructing establishment chronologies, these studies highlight gaps in regeneration, supporting concerns about long-term population sustainability. Our research suggests that recruitment is episodic and tied to disturbance events, which may provide insight into regeneration bottlenecks.

Growth Release Dynamics Reveal Past Disturbance Regimes

The disturbance chronologies reveal that decadal disturbance rates rarely exceed 40 percent and indicate variable disturbance rates through time and by site. Taken together, the chronologies depict episodic rather than chronic disturbance. Only one-third of cores recorded a major release, and those events cluster in single decades, in the 1970s at Iron Mountain and Lost Cove, and in the 1990s at Cliff Ridge and Dobson's Knob. This may indicate discrete canopy openings rather than gradual competitive thinning. Moderate releases were more common but equally episodic, consistent with previous studies documenting cyclical growth and disturbance patterns in hemlock-dominated stands (Black & Abrams 2004; Orwig & Foster 1998). The scarcity of repeat major releases and the species' modest bark thickness point to a disturbance-avoidance strategy rather than true fire adaptation (Jetton et al. 2008). Further, Gonzalez (in prep) found that, alongside eastern hemlock, Carolina hemlock can profit from moderate light increases, though opportunities for a sudden increase in diameter growth are rare and locally specific. Additional research comparing historical climate and weather events to find specific precipitation, temperature, and other climatic correlations could prove useful.

The impact of HWA on eastern hemlock has been well documented, but fewer long-term growth records exist of Carolina hemlock, especially using tree-ring data from multiple populations. Our analysis clearly shows a decline in radial growth after HWA infestation in some sites, even where trees remain alive. This supports anecdotal and observational reports of decline but adds robust, quantitative evidence from increment cores. Additionally, our study highlights site-specific variation in severity, implying that microsite conditions, climate buffering, or partial host resistance could mediate HWA impacts, which aligns with Gossman (2023) and Loftis (2025), who found that abiotic factors, such as soil texture, soil pH, elevation, slope, and aspect, are the best indicators of HWA presence in Carolina hemlock stands.

Post-1990s Growth Decline Correlations

Across all sites, after the county-level HWA introduction, there is a steep decline in RWI. County-level records place HWA arrival in the study region around 2001 (Dodd, n.d.). At every site, radial growth declined sharply 10 to 15 years after the first county-level HWA detection, mirroring lagged patterns documented for eastern hemlock (Orwig & Foster, 1998). Three consecutive years of decreasing ring width, a diagnostic threshold for HWA infestation in growth chronologies, occurring across our datasets during that interval, allow us to estimate infestation timing even more accurately, where direct field observations were lacking. Because this decline was synchronous across elevations and aspects, HWA emerges as the primary driver rather than site factors alone. This interpretation is further supported by climate-growth analyses. In North Carolina, tree-ring indices were not significantly correlated with PDSI, indicating that drought was not a primary limiting factor on growth. Conversely, in Tennessee, tree growth showed a significant positive relationship with PDSI, suggesting some sensitivity to moisture availability (Fig. 2.7). However, the timing and magnitude of the growth decline at both sites aligned closely with adelgid invasion rather than most climatic trends. Therefore, despite some site-level climatic influence, HWA pressure remains the dominant force driving the observed decline.

The disturbance history of Carolina hemlock stands reflects a legacy of both biotic and abiotic stressors, with episodic canopy release events serving as key indicators. Notably, across all study sites, there was a cluster of major growth releases in the early to mid-1990s, suggesting a widespread disturbance agent. The timing closely aligns with the passage of Hurricane Hugo in September 1989, A high-intensity storm that made landfall northeast of Charleston, SC, and moved through the western North Carolina Piedmont, over the Blue Ridge Mountains, and into Tennessee. A maximum wind gust of 81 mph was recorded in Hickory, NC, with sustained winds reaching up to 46 mph, along with flash flooding in the northern NC mountains (Fig. 5). While Hugo's eye tracked farther east, its outer bands produced strong gusts and heavy rainfall that spanned across the southern Appalachians, particularly impacting exposed ridges where Carolina hemlock is commonly found. The lag between storm impact and observed release reflects delayed canopy openings or gap expansion from storm-damaged trees. In addition to Hugo, other windstorms and ice events have historically shaped forest structure in the region, although none with as widespread a growth signal. These findings underscore how extreme weather events, potentially increasing under a warming climate, may amplify disturbance regimes in high-elevation hemlock habitats. In combination with pest outbreaks and drought variability, hurricanes and windthrow contribute to a multiscale disturbance mosaic that continues to shape the demographic and growth dynamics of Carolina hemlock.

Eastern and Carolina Hemlock Comparisons

Compared to eastern hemlock, Carolina hemlock's narrower niche and limited regeneration amplify HWA effects, underscoring why even modest adelgid pressure translates quickly into growth loss. The impact of HWA on eastern hemlock has been well documented, but fewer long-term growth records exist for Carolina hemlock, particularly those derived from tree-ring data across multiple populations. This study builds on earlier single-site investigations (e.g., Levy and Walker, 2014) and recent compositional surveys (Keyser et al., 2023) by offering one of the first multi-site dendrochronological reconstructions of Carolina hemlock growth decline in response to HWA. Like Ford and Vose (2007) and Orwig and Foster (1998), who reported a lag of several years between HWA detection and detectable growth suppression in eastern hemlock, we observed a consistent decline in radial growth relatively aligned with county-level data on HWA arrival. This synchronous decline across diverse sites, aspects, and elevations suggests that adelgid pressure, and not site condition alone, is the principal driver of recent growth reduction. Moreover, our data align with Davis et al. (2007), who found that trees exhibiting slower pre-infestation growth were more likely to suffer severe growth declines following HWA infestation. Likewise, our results, especially at sites like Cliff Ridge and Dobson's Knob with high release activity in the 1990s, suggest that pre-infestation growth conditions may exacerbate later vulnerability. Compared to eastern hemlock, Carolina hemlock's narrower ecological amplitude and limited natural regeneration further amplify the long-term consequences of even modest HWA infestations, lending quantitative support to concerns expressed previously (Keyser et al. 2023) about population persistence. Our findings not only corroborate observed trends in other hemlock species but also extend them by clarifying how site history and disturbance legacies can mediate Carolina hemlock's decline trajectory. Additionally, this study highlights the need to use an integrated pest management approach, where disturbance-based forest history with contemporary pest dynamics is used when assessing endemic species resilience. By documenting growth release patterns and establishment chronologies, we show that disturbance history plays a critical role in shaping both population structure and vulnerability to modern threats, such as HWA. This may be especially true in species with low recruitment potential and fragmented distributions, like we see in Carolina hemlock.

Conclusions and Management Implications

Our findings demonstrate that Carolina hemlock, a narrowly distributed and ecologically unique conifer, exhibits disturbance and growth-suppression patterns under HWA pressure comparable to those documented in eastern hemlock (Orwig et al. 2024). The consistent lag between adelgid colonization and measurable radial growth decline emphasizes the danger of relying on canopy condition as a primary management trigger. By the time visible defoliation becomes apparent, the optimal window for intervention measures such as insecticide application or predator releases may have already passed (Vose et al. 2012).

The variation we observed across sites suggests that conservation efforts should be carefully tailored: genetically unique stands such as Lost Cove are strong candidates for gene banking and targeted conservation plantings, while drought-prone ridges like Cliff Ridge and

Dobson’s Knob may benefit most from a combination of chemical and classical biological control. At the landscape scale, integrating management with historical disturbance regimes could help maintain regeneration niches critical to long-term persistence. Where feasible, establishing ecological buffer zones to reduce anthropogenic stress and maintain habitat connectivity (Wang et al. 2024) could further safeguard these relict populations, although such measures may be constrained by land-use realities.

Overall, this research strengthens the scientific understanding of Carolina hemlock by offering rare, site-level dendrochronological data for a grossly understudied southern Appalachian endemic. It provides evidence of long-term growth declines and regeneration limitations, while framing the species’ response in a broader context of climate change and disturbance ecology. These contributions help fill a notable gap in the literature and advance both ecological theory regarding disturbance and range-limited species and practical conservation.

Given Carolina hemlock’s fragmented range, low genetic diversity, and vulnerability to both biotic and abiotic stressors, the synchronized decline documented here underscores a broader conservation challenge of endemic conifers, such as Carolina hemlock, red spruce, or those with narrow niches are uniquely vulnerable where invasive insects and climate variability interact. Proactive, site-tailored interventions that integrate genetic conservation with disturbance-based silviculture will therefore be critical to sustaining Carolina hemlock, as well as the biodiversity it supports, in the decades to come.

Tables

Table 2.1: Mean live overstory (stems ≥ 5 cm DBH) density, basal area, and importance value (IV) of Carolina hemlock (data from Keyser et al. 2023). Age range and peak year of establishment estimated from tree cores. HWA County establishment gathered from Dodd (n.d.).

Overstory attribute	**Tennessee**		**North Carolina**	
	Cliff Ridge	**Iron Mountain**	**Dobson's Knob**	**Lost Cove**
Density (stems/ha)*	1395	1120 - 1500	1270	1615
Basal area (m^2/ha)*	30.2	55.4 - 59.7	32.1	40.0
*IV**	30	20 - 42	37	65
Location (lat, lon)	36.102737, -82.450137	36.3363285, -82.09235	35.797365, -81.983687	35.664759, -82.210334
Elevation range (m)	618 - 725	854 - 963	1091 - 1118	706 - 855
Age range	10-119	12-190	10-91	10-221
Peak establishment	1970	1960-1965	1970	1950
HWA County establishment	2004	2002	2001	2006

Table 2.2: Summary table of descriptive variables compared across the four sites. Core ages, establishment decades, year of initial county infestation, and summary statistics for Major and Moderate releases are included for all sites.

Variable		**Cliff Ridge**	**Dobson's Knob**	**Iron Mountain**	**Lost Cove**
Median age		45.5	45	56.5	62
Oldest CH core		119	91	190	221
Youngest CH core		10	10	12	10
1st establishment pulse		1940	1930	1930	1910
Peak establishment pulse		1970	1970	1960	1950
Last establishment pulse		1990	1980	1990	1980
HWA County establishment		2004	2001	2002	2006
Major Releases					
	% At least 1 release	35	39	30	24
	% At least 2 releases	2	8	2	4
	median # releases	0	0	0	0
	max # releases	2	4	3	3
	decade with most releases	1990	1990	1970	1970
	# releases in previous decade	23	13	16	16
	total releases	37	40	67	59
Moderate Release					
	% At least 1 release	21	26	24	28
	% At least 2 releases	2	1	1	4
	median # releases	0	0	0	0
	max # releases	3	3	2	3
	decade with most releases	1990	1990	1990	1970
	# releases in previous decade	11	7	26	21
	total releases	25	23	67	67
TOTAL releases		62	63	134	126

Table 2.3: Summary table of multiple iterations of series intercorrelations across all sites. Correlations were combined/ organized into multiple groups (i.e., all cores, cores with at least 1 year to pith, 4 different DBH groupings, and 3 age groupings).

		Site			
Series Intercorrelation		**Cliff Ridge**	**Dobson's Knob**	**Iron Mountain**	**Lost Cove**
All cores		0.254	0.270	0.235	0.259
Cores with pith present		0.136	0.222	0.242	0.261
Cores with at least 1 year to pith		0.208	0.208	0.284	0.259
DBH					
	< 10 cm	0.186	0.161	0.246	0.185
	> 10 cm	0.276	0.287	0.275	0.270
	< 12.5 cm	0.208	0.270	0.254	0.219
	> 12.5 cm	0.314	0.280	0.262	0.270
	< 15 cm	0.232	0.302	0.269	0.235
	> 15 cm	0.289	0.291	0.261	0.291
	< 20 cm	0.227	0.259	0.273	0.257
	> 20 cm	0.298	0.309	0.251	0.299
Age					
	< 50 years	0.226	0.310	0.249	0.245
	> 50 years	0.273	0.204	0.260	0.259
	< 60 years	0.222	0.291	0.259	0.269
	> 60 years	0.350	0.150	0.269	0.265
	< 70 years	0.233	0.276	0.273	0.260
	> 70 years	0.377	0.228	0.217	0.267

Figures

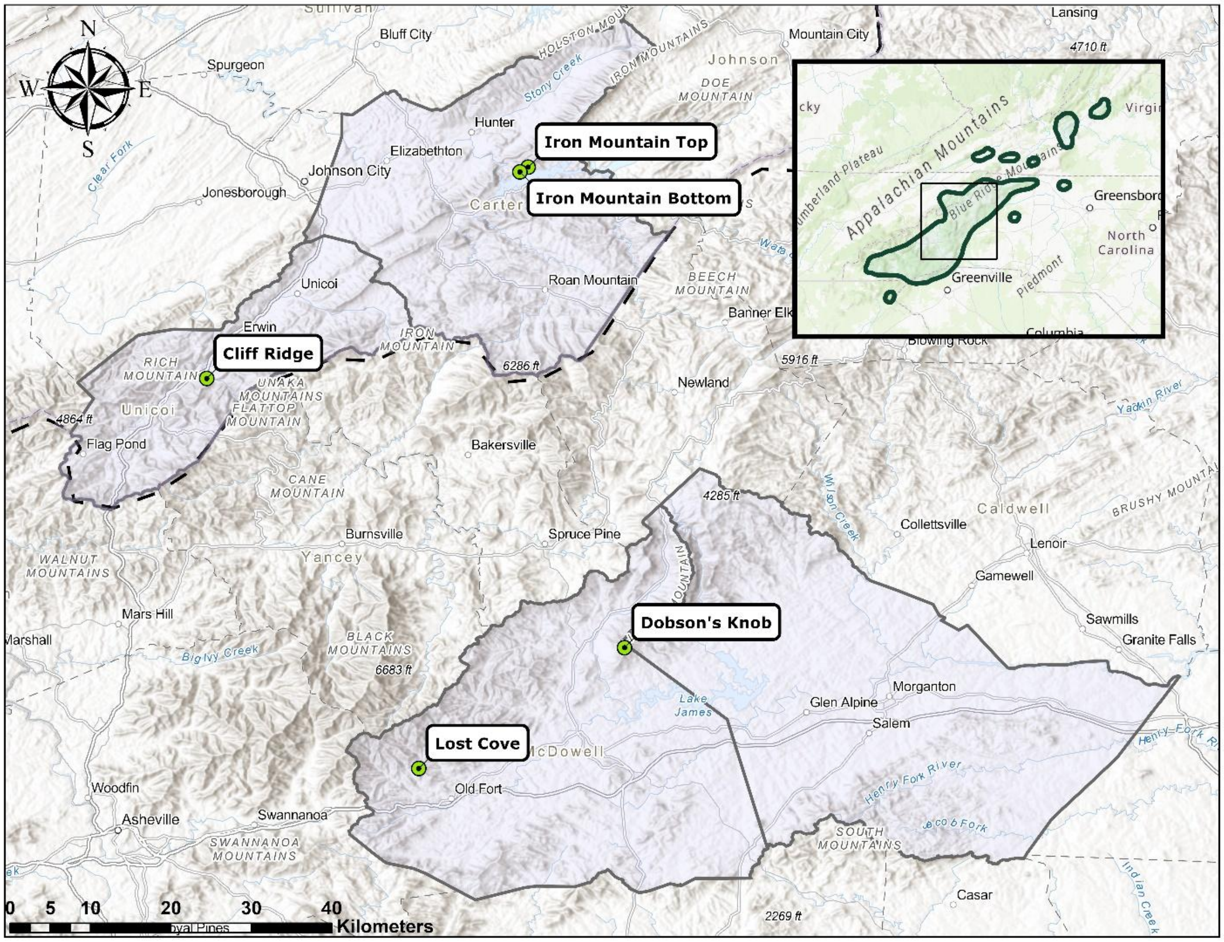

Figure 2.1: Location of the 4 populations and 5 Carolina hemlock sites and the county in which the site resides. Inset in upper right-hand corner depicts the range of Carolina hemlock with the box indicating the span of the larger map.

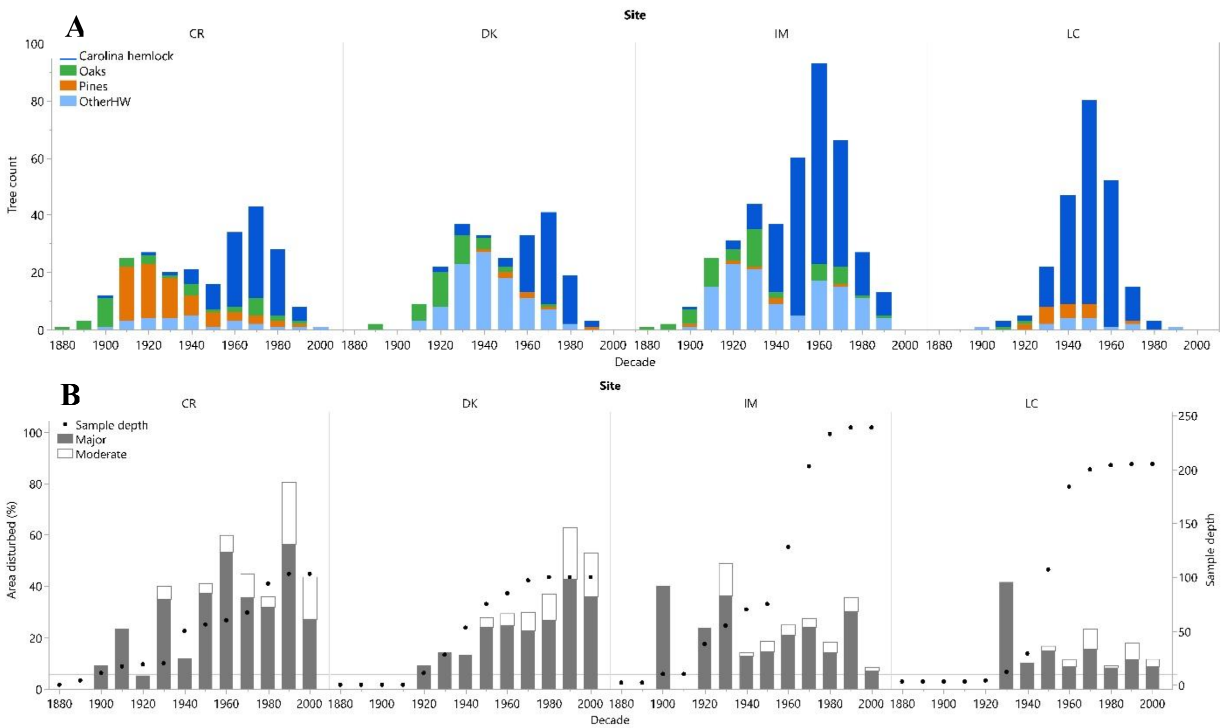

Figure 2.2: (A) Establishment ages for each species or group: Carolina hemlock, oaks, pines, and other hardwoods in relation to their establishment decade in each of the five sites, CR, DK, IMB, IMT and LC, where cores were gathered. *Chronologies were truncated to 1880 across all sites for a more uniform scale. (B) Disturbance chronologies of all species and groups across the five sites. Bars represent the percentage of trees disturbed each decade, split into major (gray) and moderate (white) releases at each of the five sites. Dots (•) represent the count of trees present each decade across the five sites, which were used to calculate the percentage of trees disturbed. The gray line above 0 indicates the minimum sample depth of 10 cores due to increased sampling variability.

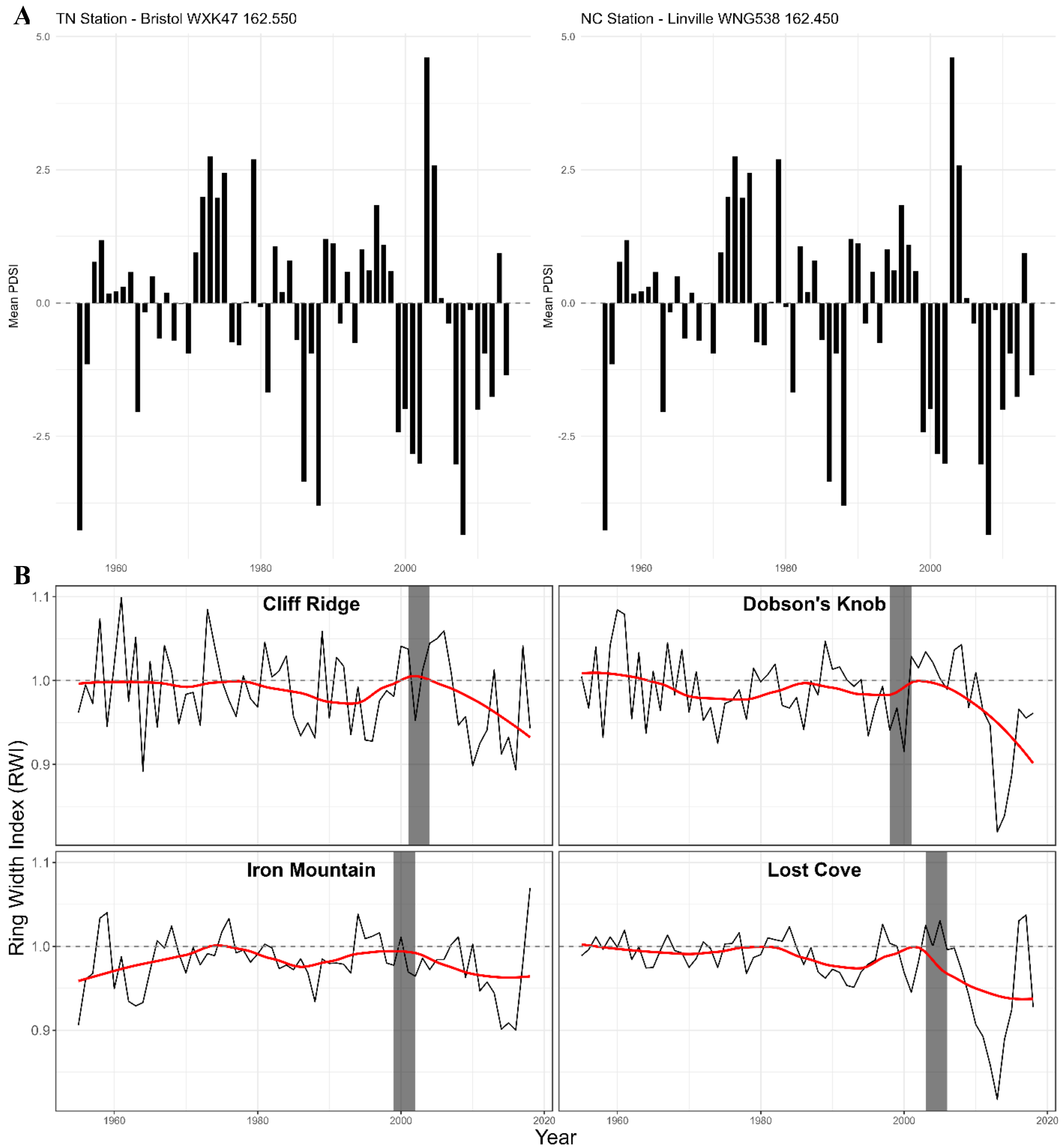

Figure 2.3: (A) Mean PDSI by state with model and correlation between the ring width Index and PDSI from 1955 to 2018. (B) Growth rates over time at each site are characterized by the percentage of cores each year that experienced an increase in growth yearly average ring width values (mm) on the y axis (1.0 = no change) and year on the x axis. The smoothed, red trend lines (LOESS fits) illustrate the trajectory of annual growth index over time, while the gray shaded regions denote sample depth. Vertical shaded lines indicate the three years leading to the first record of HWA in each host county.

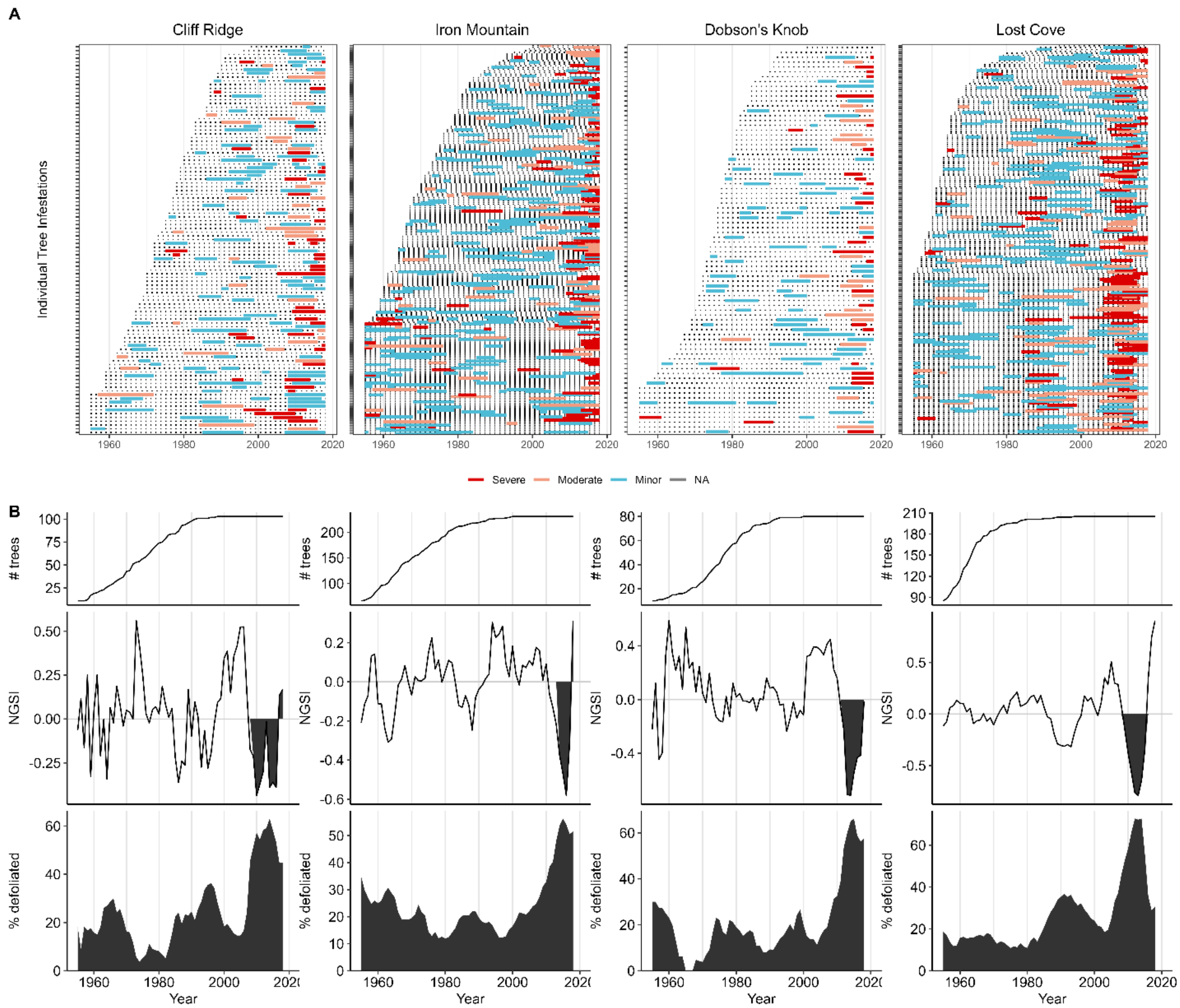

Figure 2.4: (A) Defoliation history of individual trees by site, presented in ascending order of establishment year. The y-axis represents individual tree output, and the x-axis represents year. (B) Sample depth, Normalized Growth Suppression Index (NGSI), and estimate of percent of trees defoliated in two sites in TN on the left and in NC on the right (output produced with Guiterman et al. 2020). Filled sections within NGSI are considered significant outbreaks.

Hurricane Hugo, September 21-22, 1989

Figure 2.5: Map of Hurricane Hugo track that aligns with major disturbances in the area of all four sites.

References

Altman, J., Fibich, P., Dolezal, J., & Aakala, T. (2014). TRADER: a package for Tree Ring Analysis of Disturbance Events in R. Dendrochonologia, 32(2), 107-112.

Austin, D. A., Van De Gevel, S. L., & Soulé, P. T. (2016). Forest dynamics and climate sensitivity of an endangered Carolina hemlock community in the southern Appalachian Mountains, USA. Botany, 94(4), 301–309. https://doi.org/10.1139/cjb-2015-0222

Baumgras, J. E., Sendak, P. E., & Sonderman, D. L. (2000). Ring Shake in Eastern Hemlock: Frequency and Relationship to Tree Attributes. *In: McManus, Katherine A.; Shields, Kathleen S.; Souto, Dennis R., Eds. Proceedings: Symposium on Sustainable Management of Hemlock Ecosystems in Eastern North America; 1999 June 22-24; Durham, NH. Gen. Tech. Rep. NE-267. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station: 156-160.* https://research.fs.usda.gov/treesearch/22179

Bigelow, S. W., Runkle, J. R., & Oswald, E. M. (2020). Competition, Climate, and Size Effects on Radial Growth in an Old-Growth Hemlock Forest. *Forests*, *11*(1), Article 1. https://doi.org/10.3390/f11010052

Brown, M. J., New, B. D., Oswalt, S. N., Johnson, T. G., & Rudis, V. A. (n.d.). *North Carolina's Forests, 2002*.

Bunn, A. G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia*, *26*(2), 115–124. https://doi.org/10.1016/j.dendro.2008.01.002

Bunn A, Korpela M, Biondi F, Campelo F, Klesse S, Mérian P, Qeadan F, Zang C (2025). dplR: Dendrochronology Program Library in R. doi:10.32614/CRAN.package.dplR, R package version 1.7.8, https://CRAN.R-project.org/package=dplR.

Butler, S.M., White, A.S., Elliott, K.J., Seymour, R.S. (2014). *Disturbance history and stand dynamics in secondary and old-growth forests of the Southern Appalachian Mountains, USA 1*. ResearchGate. http://dx.doi.org/10.3159/TORREY-D-13-00056.1

Davis, Donald D., Fromm, Matthew S., Davis, Matthew D. (2007). Impact of the hemlock woolly adelgid on radial growth of Eastern hemlock in Pennsylvania. e-Gen. Tech. Rep. SRS–101. U.S. Department of Agriculture, Forest Service, Southern Research Station: 157-162 [CD-ROM].

Davis, G. A., Havill, N. P., Adelman, Z. N., Caccone, A., Kok, L. T., & Salom, S. M. (2011). DNA barcodes and molecular diagnostics to distinguish an introduced and native *Laricobius* (Coleoptera: Derodontidae) species in eastern North America. *Biological Control. 58(1): 53-59.*, *58*, 53–59. https://doi.org/10.1016/j.biocontrol.2011.03.016

Dharmadi, S. N., Elliott, K. J., & Miniat, C. F. (2019). Lack of forest tree seedling recruitment and enhanced tree and shrub growth characterizes post-*Tsuga canadensis* mortality forests in the southern Appalachians. *Forest Ecology and Management*, *440*, 122–130. https://doi.org/10.1016/j.foreco.2019.03.024

Dodd, D. (n.d.). *Hemlock Woolly Adelgid National Initiative*. Hemlock Woolly Adelgid National Initiative. https://hemlock-woolly-adelgid-national-initiative-gmsts.hub.arcgis.com/

Elliott, K. J., & Swank, W. T. (2008). Long-term changes in forest composition and diversity following early logging (1919–1923) and the decline of American chestnut (Castanea dentata). *Plant Ecology*, *197*(2), 155–172. https://doi.org/10.1007/s11258-007-9352-3

Ellison, A. M., Bank, M. S., Clinton, B. D., Colburn, E. A., Elliott, K., Ford, C. R., Foster, D. R., Kloeppel, B. D., Knoepp, J. D., Lovett, G. M., Mohan, J., Orwig, D. A., Rodenhouse, N. L., Sobczak, W. V., Stinson, K. A., Stone, J. K., Swan, C. M., Thompson, J., Von Holle, B., & Webster, J. R. (2005). Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment*, *3*(9), 479–486. https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2

Ellison, A. M., Orwig, D. A., Fitzpatrick, M. C., & Preisser, E. L. (2018). The Past, Present, and Future of the Hemlock Woolly Adelgid (Adelges tsugae) and Its Ecological Interactions with Eastern Hemlock (Tsuga canadensis) Forests. *Insects*, *9*(4), 172. https://doi.org/10.3390/insects9040172

Fajvan, M. A., & Wood, P. B. (2010). *Maintenance of Eastern Hemlock Forests: Factors Associated with Hemlock Vulnerability to Hemlock Woolly Adelgid*. Proceedings from the conference on the ecology and management of high-elevation forests in the central and southern Appalachian Mountains; 2009 May 14-15; Slatyfork, WV. Gen. Tech. Rep. NRS-P-64. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station: 31-38.

Fraver, S., & White, A. S. (2005). *Identifying growth releases in dendrochronological studies of forest disturbance*. https://doi.org/10.1139/x05-092

Greenberg, C. H., & McNab, W. H. (1998). Forest disturbance in hurricane-related downbursts in the Appalachian mountains of North Carolina. *Forest Ecology and Management*, *104*(1–3), 179–191. https://doi.org/10.1016/S0378-1127(97)00246-6

Guiterman, C. H., Lynch, A. M., & Axelson, J. N. (2020). dfoliatR: An R package for detection and analysis of insect defoliation signals in tree rings. *Dendrochronologia*, *63*, 125750. https://doi.org/10.1016/j.dendro.2020.125750

Hart, J. L., & Kupfer, J. A. (2011). Sapling richness and composition in canopy gaps of a southern Appalachian mixed Quercus forest1. *The Journal of the Torrey Botanical Society*, *138*(2), 207–219. https://doi.org/10.3159/TORREFY-D-11-00006.1

Havill, N. P., Montgomery, M. E., Yu, G., Shiyake, S., & Caccone, A. (2006). Mitochondrial DNA from Hemlock Woolly Adelgid (Hemiptera: Adelgidae) Suggests Cryptic Speciation and Pinpoints the Source of the Introduction to Eastern North America. *Annals of the Entomological Society of America*, *99*(2), 195–203. https://doi.org/10.1603/0013-8746(2006)099[0195:MDFHWA]2.0.CO;2

Havill, N. P., Shiyake, S., Lamb Galloway, A., Foottit, R. G., Yu, G., Paradis, A., Elkinton, J., Montgomery, M. E., Sano, M., & Caccone, A. (2016). Ancient and modern colonization of North America by hemlock woolly adelgid, Adelges tsugae (Hemiptera: Adelgidae), an invasive insect from East Asia. *Molecular Ecology*, *25*(9), 2065–2080. https://doi.org/10.1111/mec.13589

Hepting, G. H. (1964). Forest Pathology in the Southern Appalachians, 1900-1940. *Forest History Newsletter*, *8*(3), 11–13. https://doi.org/10.2307/3983014

Huang, C., Ling, Pui-Yu, & Zhu, Z. (2015). North Carolina's forest disturbance and timber production assessed using time series Landsat observations. *International Journal of Digital Earth*, *8*(12), 947–969. https://doi.org/10.1080/17538947.2015.1034200

Humphrey, L. D. (1989). Life History Traits of Tsuga caroliniana Engelm. (Carolina Hemlock) and Its Role in Community Dynamics. *Castanea*, *54*(3), 172–190.

Jetton, R. (2024). (PDF) Laboratory Studies of Feeding and Oviposition Preference, Developmental Performance, and Survival of the Predatory Beetle, *Sasajiscymnus tsugae* on Diets of the Woolly Adelgids, *Adelges tsugae* and *Adelges piceae*. *ResearchGate*. https://doi.org/10.1673/031.011.6801

Jetton, R. M., Dvorak, W. S., & Whittier, W. A. (2008). Ecological and genetic factors that define the natural distribution of Carolina hemlock in the southeastern United States and their role in *ex situ* conservation. *Forest Ecology and Management*, *255*(8), 3212–3221. https://doi.org/10.1016/j.foreco.2008.01.032

Jubb, C. S. (2019, June). *Jubb_CS_T_2019*.

Keyser, T. L., Styers, D. M., Wind, M., DeWald, L., & Collins, B. (2023). Composition and Structure of Tsuga caroliniana Engelm. Communities in the Southern Appalachian Mountains of Western North Carolina. *Southeastern Naturalist*, *22*(1), 57–77. https://doi.org/10.1656/058.022.0109

Koprowski, M., & Duncker, P. (2012). Tree ring width and wood density as indicators of climatic factors and insect outbreaks affecting spruce growth. *Ecological Indicators*, *23*, 332–337. https://doi.org/10.1016/j.ecolind.2012.04.007

Levy, F., & Walker, E. S. (2014). Pattern and Rate of Decline of a Population of Carolina Hemlock (Tsuga caroliniana Engelm.) in North Carolina. *Southeastern Naturalist*, *13*(6), 46–60. https://doi.org/10.1656/058.013.s605

Martin, K. L., & Goebel, P. C. (2013). The foundation species influence of eastern hemlock (Tsuga canadensis) on biodiversity and ecosystem function on the Unglaciated Allegheny Plateau. *Forest Ecology and Management*, *289*, 143–152. https://doi.org/10.1016/j.foreco.2012.10.040

Matalas, N. C. (1997). Stochastic Hydrology in the Context of Climate Change. *Climatic Change*, *37*(1), 89–101. https://doi.org/10.1023/A:1005374000318

Maxwell, R. S., & Larsson, L.-A. (2021). Measuring tree-ring widths using the CooRecorder software application. *Dendrochronologia*, *67*, 125841. https://doi.org/10.1016/j.dendro.2021.125841

Mayfield, A., Dietschler, N., & Whitmore, M. C. (2021). The Lari-Leuco container: A novel collection arena for separating insects ascending or descending from a plant foliage sample. *Journal of Economic Entomology*, *114*, 2400–2405. https://doi.org/10.1093/jee/toab181

Mayfield, A.E., III; S.M. Salom; K. Sumpter; T. McAvoy; N.F. Schneeberger; R. Rhea. (2020). *Integrating chemical and biological control of the hemlock woolly adelgid: a resource manager's guide*. FHAAST-2018-04. USDA Forest Service, Forest Health Assessment and Applied Sciences Team, Morgantown, West Virginia.

Mayfield III, A. E., Bittner, T. D., Dietschler, N. J., Elkinton, J. S., Havill, N. P., Keena, M. A., Mausel, D. L., Rhea, J. R., Salom, S. M., & Whitmore, M. C. (2023). Biological control of hemlock woolly adelgid in North America: History, status, and outlook. *Biological Control*, *185*, 105308. https://doi.org/10.1016/j.biocontrol.2023.105308

Nowacki, G.J. & Abrams, M.D. (1997). Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. Ecological Monographs, 67, 225-249.

Orwig, D. A., & Foster, D. R. (1998). Forest Response to the Introduced Hemlock Woolly Adelgid in Southern New England, USA. *The Journal of the Torrey Botanical Society*, *125*(1), 60–73. https://doi.org/10.2307/2997232

Orwig, D. A., Foster, D. R., & Mausel, D. L. (2024). Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. *Journal of Biogeography*, *29*(10–11), 1475–1487. https://doi.org/10.1046/j.1365-2699.2002.00765.x

P McCarty, E., & Addesso, K. M. (2019). Hemlock Woolly Adelgid (Hemiptera: Adelgidae) Management in Forest, Landscape, and Nursery Production. *Journal of Insect Science*, *19*(2), iez031. https://doi.org/10.1093/jisesa/iez031

Payton, I. J., Fenner, M., & Lee, W. G. (n.d.). Keystone species: The concept and its relevance for conservation management in New Zealand. *Science for Conservation*, *203*.

Posit team (2024). RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. URL http://www.posit.co/.

Potter, K. M., Jetton, R. M., Bower, A., Jacobs, D. F., Man, G., Hipkins, V. D., & Westwood, M. (2017). Banking on the future: Progress, challenges and opportunities for the genetic conservation of forest trees. *New Forests*, *48*(2), 153–180. https://doi.org/10.1007/s11056-017-9582-8

Radville, L., Chaves, A., & Preisser, E. L. (2011). Variation in plant defense against invasive herbivores: Evidence for a hypersensitive response in eastern hemlocks (Tsuga canadensis). *Journal of Chemical Ecology*, *37*(6), 592–597. https://doi.org/10.1007/s10886-011-9962-z

Rentch, J. S., Adams, H. S., Coxe, R. B., & Stephenson, S. L. (2000). An Ecological Study of a Carolina Hemlock (Tsuga caroliniana) Community in Southwestern Virginia. *Castanea*, *65*(1), 1–8.

Schomaker, M. E., Zarnoch, S. J., Bechtold, W. A., Latelle, D. J., Burkman, W. G., & Cox, S. M. (2007). *Crown-condition classification: A guide to data collection and analysis* (No.

SRS-GTR-102; p. SRS-GTR-102). U.S. Department of Agriculture, Forest Service, Southern Research Station. https://doi.org/10.2737/SRS-GTR-102

Speer, J. H. (2010). *Fundamentals of Tree Ring Research*. The University of Arizona Press. https://www.researchgate.net/publication/259466472_Fundamentals_of_Tree_Ring_Research

Tomback, D. F., & Achuff, P. (2010). Blister rust and western forest biodiversity: Ecology, values, and outlook for white pines. *Forest Pathology,* Retrieved August 9, 2025, from https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1439-0329.2010.00655.x

Vose, J. M., Wear, D. N., Mayfield, A. E., & Dana Nelson, C. (2013). Hemlock woolly adelgid in the southern Appalachians: Control strategies, ecological impacts, and potential management responses. *Forest Ecology and Management*, *291*, 209–219. https://doi.org/10.1016/j.foreco.2012.11.002

Wager-Page, S. A. (n.d.). *Draft Environmental Assessment, December 2009*.

Walker, D. M., Copenheaver, C. A., & Zink-Sharp, A. (2014). Radial growth changes following hemlock woolly adelgid infestation of eastern hemlock. *Annals of Forest Science*, *71*(5), 595–602. https://doi.org/10.1007/s13595-014-0367-3

Wang, D., Gao, X., Wu, S., Zhao, M., Zheng, X., Wang, Z., Zhang, Y., & Fan, C. (2024). A Comprehensive Review on Ecological Buffer Zone for Pollutants Removal. *Water*, *16*(15), Article 15. https://doi.org/10.3390/w16152172

Whittier, W. Andrew; Jetton, Robert M.; Rhea, James R. 2025. Carolina hemlock distribution and health in the Southern Appalachian Mountains. Conkling, B.L.; Pandit, K., eds. Forest Health Monitoring: Evaluation Monitoring project summaries 2023. Gen. Tech.

Rep. WO-105a. Washington, DC: U.S. Department of Agriculture, Forest Service. 31–39. Chapter 5. https://doi.org/10.2737/WO-GTR-105aChap5.

Wilson, C. M., Vendettuoli, J. F., Orwig, D. A., & Preisser, E. L. (2016). Impact of an Invasive Insect and Plant Defense on a Native Forest Defoliator. *Insects*, *7*(3), 45. https://doi.org/10.3390/insects7030045

Wind, M. (2021). *Composition and Structure of Tsuga Caroliniana Stands in the Southern Appalachian Mountains* [M.S., Western Carolina University]. https://www.proquest.com/docview/2567991393/abstract/4B9B90B7B4C247A1PQ/1

Yarnell, S. L. (1998). *The Southern Appalachians: A History of the Landscape*. U.S. Department of Agriculture, Forest Service, Southern Research Station.

APPENDIX A

Figure S1.1: Lari-Leuco container

Figure S1.2: (A) Modified *Laricobius* container and (B) contents