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Demography and Dendrochronology of a Disjunct Population of Eastern Hemlock in Southwestern Ohio

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DEMOGRAPHY AND DENDROCHRONOLOGY OF A DISJUNCT POPULATION OF EASTERN HEMLOCK IN SOUTHWESTERN OHIO

A thesis submitted in partial fulfillment of the
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I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY Marie Johnson ENTITLED Demography and dendrochronology of a disjunct population of eastern hemlock in southwestern Ohio BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Master of Science.

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ABSTRACT

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Edge and isolated plant populations provide information about the resilience and the most basic resource needs of a species. Plant demography examines changes in population size and structure over time. An isolated, disjunct eastern hemlock population in Clifton Gorge State Nature Preserve, Yellow Springs, Ohio consists of two distinct subpopulations each with different environmental characteristics, reproductive capacities, and health ratings. Both subpopulations at Clifton Gorge were found to exhibit significant decreases in average annual ring width through time. Linear regression modeling determined that average annual growing season precipitation and temperature were the strongest predictors of these growth trends. A comparative hemlock population at Cantwell Cliffs, Rockbridge, Ohio within the contiguous range of the species displayed environmental characteristics more typical of hemlock-dominated stands and slight increases in average annual ring width through time, suggesting that the contiguous site is more favorable for eastern hemlock performance.

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I. INTRODUCTION

Obtaining baseline information about plant populations is important for tracking, understanding, and predicting plant responses to environmental change and biotic stress (Eschtruth *et al.*, 2006). Demographic information is especially valuable for populations at the edge of their natural range, as edge populations are often first affected by the progression of biotic and abiotic disturbances such as invasive pests and climate change (Brown *et al.*, 1996). Given the relative inhospitality of the edges of a range relative to the center of the range, populations at the edge likely have access to fewer resources and less favorable weather conditions, making them more susceptible to disturbance (Brown *et al.*, 1996). Isolation and inbreeding contribute to increased genetic uniformity and have negative implications for resistance and resilience in the event of invasive species introduction or disturbance. Alternatively, isolated populations might prove to be useful sources of unique genetics in conservation efforts. Edge plant populations in the Ohio region are commonly glacial relicts, surviving pockets of a once larger, more widespread population (Braun, 1928). In some cases, receding glaciers created topographic features that still provide protected microclimates for a species that had previously relied on the microclimate of the glacier itself. Investigating which environmental factors allow edge populations to survive might provide insight into the adaptability and resilience of a species. The possible presence of rare alleles within isolated populations also warrants study based on the ability of findings to aid in understanding the genetics of the species.

Eastern hemlock (*Tsuga canadensis* (*L.*) *Carriere*) is a long-lived, evergreen member of the pine family (Myers *et al*., 2015). These trees are commonly found in the Appalachian forests of North America, but isolated populations at the edges of their native range are fairly abundant (Myers *et al*., 2015). Due to its widespread ecological impacts, eastern hemlock is considered a foundational species (Myers *et al*., 2015; Quimby, 1996). Eastern hemlock acidifies soil, reduces temperature with its extremely dense canopy, and modifies the humidity of the understory creating a unique microenvironment that acts as a filter in determining which species can colonize hemlock stands (Finzi *et al.*, 1998; Myers *et al.*, 2015). Hemlocks typically populate the sloped areas along streams and exhibit reduced annual ring widths when exposed to increased temperature or reduced moisture (Kessell, 1979; Avery, 1940). In most cases, hemlock stands include very few other tree species (Hessl and Pederson, 2013). Colonization of the understory by saplings and herbaceous plant species is sparse, leaving the forest floor nearly bare except for a thick, slow-decomposing layer of needles. These trees, while possibly limiting land biodiversity, contribute to stream health and aquatic biodiversity (Hessl and Pederson, 2013; Ellison *et al.*, 2005). Due to the narrow regeneration niche of eastern hemlock, seedling establishment and subsequent recruitment into larger size classes may occur only at very low levels (Rooney and Waller, 1998; Rooney *et al.*, 2000). However, seed recruitment and seedling establishment is most successful in areas where the forest floor is largely covered in thin needle leaf litter rather than any depth of broad-leaved litter or some combination of the two litter types (Rooney *et al.*, 2000). Seedlings also occur more often than expected on rotting wood with the opposite finding for tip-up mounds and the forest floor (Rooney and Waller, 1998). This level of specificity in preferred establishment conditions may contribute to difficulty in hemlock reproduction, especially at sites where one or more of the ideal conditions are even periodically absent.

Hemlock woolly adelgid (*Adelges tsugae*; HWA) is an invasive, sap-sucking insect that was accidentally introduced from Japan to the United States in the 1950s (Vose *et al*., 2013). Since its introduction, HWA has spread to 18 states within the range of eastern hemlock (Vose *et al*., 2013). As an aphid-like nymph, HWA either crawls from natal tree to a new host tree or is dispersed by wind or mechanical transport, where it then attaches at the base of the needles and begins feeding on sugar and nutrients from the network of transport tissue (Vose *et al*., 2013). Once attached, the insects lose mobility and continue to feed until they secrete a waxy capsule where they will eventually lay their eggs and die (Vose *et al*., 2013). HWA attacks eastern hemlock trees of all sizes and ages, killing adult trees and halting stand reproduction (Vose *et al.*, 2013). Because eastern hemlock trees in the United States did not evolve alongside HWA, the trees lack effective defense mechanisms, resulting in very high tree mortality rates (Vose *et al.*, 2013). Despite high rates of HWA-induced mortality, resistant hemlock individuals do exist and may provide information about how to better combat this invasive pest (Caswell *et al*., 2008; Ingwell and Preisser, 2011).

We conducted a demographic study of the isolated eastern hemlock population at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio. Baseline information about population density, age frequency distribution, growth rate, and reproductive capacity was collected to determine the status of and predict future threats to the population. Dendrochronological analyses were conducted to assess annual ring width through time to determine what factors predict these trends and how these trends might impact the future success of the population. Our findings might become useful for a comparative study looking at other isolated populations along the edge of the range of eastern hemlock in Ohio and elsewhere. A thorough survey for hemlock woolly adelgid provided insight into the infestation status of the population and might, in combination with demographic, environmental, and dendrochronological observations, help to conserve a local population by providing the foundation for the formulation and implementation of a hemlock management plan at Clifton Gorge.

II. METHODS

STUDY AREA AND SITES

The primary study site located near the village of Clifton (Greene County, Ohio) follows the Little Miami River from the 268-acre Clifton Gorge State Nature Preserve (N39º 48.010', W83º 50.143') to the 752-acre John Bryan State Park. Here the river drains down the escarpment between the underlying Silurian geologic plain and the adjoining Ordovician plain. The flow of the river from the younger, more resistant Silurian rock to the older, less resistant Ordovician rock allows for the rapid erosion of the Ordovician bedrock and the formation of the most salient feature of the site, the gorge itself. Closest to the surface in the Silurian layer is Ceaderville dolomite (50 ft of depth), with Springfield (7ft) and Euphemia dolomite (7ft) beneath. These are the rock layers that form the shaded, north-facing cliffs of the gorge and allow for the relatively humid, "refrigerated" gorge microclimate. Beneath the dolomite layers are softer rock layers: Osgood shale (35 feet), Brassfield limestone (35 ft), and Elkhorn shale (15 ft) (Carmen, 1946; John Bryan State Park Trail Map, 2017). The cutting of the river through the Osgood shale with relatively little resistance and greater speed compared to the dolomite layers results in a hollowing out of the gorge at the Osgood layer. This hallowing leads to the detachment (slumping) of large dolomite blocks from the gorge walls. These blocks are frequent and of varying sizes throughout the gorge portion of the study site, with Steamboat Rock being the most prominent example (Haneberg-Diggs and Waid, 2018;

John Bryan State Park Trail Map, 2017). As the river continues to flow toward John Bryan, it cuts deeper into the softer rock layers, allowing for the widening of the gorge and the softening of the valley slope before reaching the more resistant Brassfield limestone layer, which results in a narrow and steep valley within the broader one. The gorge at the end of the study site is wide and much more gently sloped, as it has eroded through the limestone layer and into the older rock below.

The steep walls of the gorge even in the broader passes provide the shade and shelter necessary for maintaining a cooler, more humid microclimate within the continental climate of the surrounding area. It is within this microclimate that two distinct subpopulations of the study species, eastern hemlock (*Tsuga canadensis*), can survive despite being approximately 50 miles outside of their native range. The Clifton Gorge hemlock subpopulation consists of approximately 110 individuals found mostly on the Southeast, permit-access side of the river between The Falls and Blue Hole (John Bryan State Park Trail Map, 2017). The second subpopulation of about 22 individuals exists downriver in John Bryan along the public-access trail behind the shelter in the lower picnic area. This group of trees progresses toward the bank of the river on the Northwest side. The site is characterized by shallow, rocky soils, extreme slopes in places, and variable leaf litter depths.

GENERAL SAMPLING

Initial interest in the eastern hemlocks at Clifton Gorge stemmed from their brief mention on the Clifton Gorge website and from personal observation of the largest individuals from across the river by several members of the Wright State University faculty during recreational hikes (Ohio Division of Natural Areas & Preserves, 2018). A preliminary scouting mission to locate hemlocks on the research-only side of the Gorge was conducted in September 2016, during which most individuals were found. Additional previously undocumented individuals were discovered and added to the data set throughout the course of the study. Apart from small seedlings clustered on the floodplain at the gorge floor, all individuals were tagged.

Trees were identified and tagged using numbered aluminum disks secured with nails for larger trees and flagging tape for the smallest seedlings and saplings. Data was recorded on a data sheet with a row for each tree and included: tree tag number, rough location relative to the nearest documented hemlock or some landmark, diameter at breast height (DBH), presence or absence of cones, presence or absence of HWA infestation, environmental characteristics (*e.g.* rough description of degree of slope, leaf litter thickness, proximity to the river, rockiness of the substrate, and any other relevant observations), tree condition (*e.g.* condition of needles, absence of branches, relative degree of epicormic sprouting, overall appearance, and any other relevant observations), and the date. No DBH was taken for small seedlings with DBH less than two centimeters, and all such individuals were grouped into their own size class. Binoculars were utilized to determine whether individuals were cone-bearing and to check the upper canopy for dieback. The HWA infestation status of each tree was determined according to the protocol outlined by the Forest Health Technology Enterprise (Costa and Onken, 2006), which calls for the visual inspection of the two lowest tree branches for the presence of HWA individuals. From trees with a DBH greater than 10 cm, a core was taken for dendrochronological analysis. Tree health, site slope, and thickness of leaf litter were each assigned *post hoc* to categories ranging from one to three, with one representing the lowest score and three representing the highest score. For categorization of slope: 1 = flat or nearly flat; 2 = slight to intermediate slope; 3 = steep slope to cliff edge. For categorization of leaf litter depth: 1 = thin leaf litter with most to half of the ground exposed; 2 = more than half of the ground covered, thin accumulation over most or all of the ground; 3 = moderate to thick coverage. For health categorization: 1 = poor health, missing branches, excessive epicormic branching, canopy dieback; 2 = intermediate health, only one to two indicators of decreased health; 3 = very healthy with little to no indication of health issues.

COMPARATIVE SITE SAMPLING – CANTWELL CLIFFS, ROCKBRIDGE, OHIO

The comparative study site is located toward the Northern boundary of Hocking Hills in Southeast Ohio's Hocking County approximately 80 miles from the disjunct site at Clifton Gorge. The Cantwell Cliffs site, which is accessible via pull-off parking along OH-374 (39°31'38.1" N, 82°34'22.2" W), lies within the Cantwell Cliffs portion of Hocking Hills State Park. Climate here is continental. The site is characterized by a stream in a deep valley with steeply sloped sides and large sandstone slump blocks at the top. Most areas are covered in thick mixed deciduous and coniferous leaf litter (Cantwell Cliffs, 2018).

The Cantwell Cliffs sampling method followed the general sampling method apart from sample selection and tag installation. On November 10, 2018, 35 individuals were selected in a haphazard fashion such that the size distribution of the sampled population subset was roughly reflective of the whole population. Tagging of trees was not necessary for the purposes of dendrochronological comparison.

SAMPLING, PROCESSING, AND ANALYSIS OF TREE CORES

Cores were taken from trees with DBH greater than 10 cm using a 20-inch Haglof 3-thread increment borer (4.3 mm diameter). If possible, cores were taken at breast height through the entire diameter of the tree. If large individuals had diameters too great for a core of the entire diameter, efforts were made to avoid reaction wood on the trunk side where the borer would penetrate. This was not always possible, however, depending on whether the desired side of the trunk was safely accessible. The borer was cleaned and lubricated with WD-40 Multipurpose Lubricant before and after each use to prevent jamming and twisting of the core. Each core was loaded into a labeled 10.5 inch Aardvark brand paper straw (5.8 mm diameter) for transport and subsequent drying. Cores were dried on a bench in an air-conditioned laboratory for no fewer than five days before mounting. Wood glue was used to adhere dried core pieces to labeled ¼ inch by ¾ inch pine screen molding, cut to length. Clear adhesive tape was used to temporarily bind the cores to the bases while the glue dried (no fewer than three days). Upon removal of the tape, cores were sanded by hand using sand paper of increasing grit: 180, 220, 320. The width of each growth ring for each prepared core was visualized with an Olympus Tokyo dissecting microscope, measured with Mitutoyo Absolute Digimatic Caliper Series-500 (0.01 mm resolution) calipers, and recorded for cross-comparison. Cores with missing segments, poorly-aligned pieces, or extremely small or blurred rings such that accurate measurements could not be taken were omitted from analysis.

SEED BOX CONSTRUCTION AND PLACEMENT

Ten seed collection boxes were constructed according to the protocol outlined by Herman (1963). Each box had dimensions of 63.5 by 30.48 by 7.62 centimeters with an effective catch area of 626.75 square centimeters and consisted of two stacked frames held together with one 60.96-centimeter bungee cord at each 30.48 centimeter end. Both top and bottom pieces were framed with finger-joint trim board (2.54 cm by 5.08 cm) and 6d hot-galvanized steel box nails. The exterior of the top frame was covered with 3-mesh galvanized hardware cloth secured with ¾ inch hot-galvanized poultry net staples. The collecting layer itself was secured to the top of the bottom frame with T50 ¼ inch crown galvanized steel staples from a T50 staple gun. This layer, consisting of New York Wire FCS9579-M fiberglass solar screen (25 by 12 inches), was sandwiched between the two frames to form the middle layer. T50 staple gun staples were also used to attach 18-mesh aluminum screen to the bottom-most layer of the bottom frame. The resolving layers, from top to bottom, of the completed boxes were galvanized hardware cloth, fiberglass solar screen, and aluminum screen, with the aluminum screen in direct contact with the forest substrate.

Box placement was determined based on proximity to cone-bearing individuals, logistics of box monitoring and retrieval, and clear line of possible seed dispersal. An effort was also made to place boxes at comparable points both on the cliff edge and on the floor of the gorge. Each box was anchored by nearby rocks or branches with as little interference with effective catch area as possible. Boxes were placed on October 24, 2017 and remained in the field until March 19, 2018. Boxes were checked for obstructive leaf litter on October 31, November 7, 17, and 28, and December 20, 2017. Leaf litter accumulation was minimal on all checkup visits and boxes were left largely undisturbed for the remainder of the collection period.

At the time of retrieval on March 19, 2018, the coordinates of each box were recorded with either a Garmin Oregon 400t GPS unit or the Google Maps app on a Galaxy S6 smartphone depending on the ability of the Garmin unit to connect to satellites at a given location. The top frame of each box was removed to reveal the solar screen collecting layer. The screen was detached from the bottom frame, carefully folded to prevent spilling of the seed and cone samples, and placed in a labeled Ziploc bag for transport. In the laboratory, the contents of each Ziploc bag were placed on their own labeled plastic lunch tray and allowed to dry until April 5, 2018. After drying, the contents of each box were sifted through using scoopula and forceps. For each tray of box contents, eastern hemlock cones were separated and their seeds removed and put into a labeled 15 mL conical tube. Loose hemlock seeds were collected from the remaining sample and placed into a separate tube. All seeds were removed from the storage tube and observed under an Olympus Tokyo dissecting microscope to confirm accurate identification and seed counts. In summary, seed box samples were processed and separated into two components per box: one conical tube of seeds from within cones (if cones were present in the sample) and one conical tube of loose seeds.

CUTTINGS PROTOCOL

Fifteen-centimeter branch cuttings were collected from 10 healthy eastern hemlock individuals at each of 11 sites in Ohio and Indiana: Yellow Springs – a Pennsylvania native transplanted to private property (OH), Clifton Gorge State Nature Preserve (OH), private land in Hocking Hills (OH), Clifty Falls State Park (IN), Yellow Birch Ravine Nature Preserve (IN), Hemlock Cliffs National Park (IN), Turkey Run State Park (IN), Shades State Park (IN), Trevlac Bluffs Nature Preserve (IN), Laura Hare Nature Preserve (IN), and Hemlock Bluff Nature Preserve (IN). All sites provide climatically and topographically similar habitat for what are believed to be wild populations of eastern hemlock individuals. Sites were selected to provide comparative representation of both contiguous (*i.e.* the Pennsylvania individual and the private property in Hocking Hills) and disjunct (*i.e.* all Indiana sites) populations. Six of eight disjunct comparative sites in Indiana were selected thanks to their sampling in a genetics study published by Hobbs and Clay in 2013.

Timing of field work as well as materials and methods used in propagation attempts were based on hemlock cuttings trials conducted by Caswell *et al.* (2008). The out-of-state collection trip for this study was conducted February 28 and March 1, 2017. Ten 15-centimeter terminal branch cuttings were taken using pruning shears from the lowest healthy branches of 10 eastern hemlock individuals at each site. Cuttings were stored and transported in five-gallon buckets of tap water for the duration of the trip.

Upon returning to the laboratory, the large cuttings were trimmed down with a razor blade at a 45-degree angle to lengths of approximately seven centimeters. Needles and the majority of twig bark were removed from the bottom third of each cutting and the cut end dipped for approximately 5 seconds in a 1:1 solution of distilled water and Dip 'N' Grow Rooting Hormone. The rooting hormone-saturated end of each cutting was then inserted into a shallow tray of potting soil. Cuttings were misted daily with distilled water from a spray bottle and the soil kept moist as consistently as possible. Approximately every other day dead cuttings were removed from the trays and discarded. Cuttings from the Pennsylvania individual, Clifty Falls, and Hocking Hills were fertilized on April 6, 2017 with a liquid preparation of Plant Marvel Nutriculture General Purpose fertilizer mixed according to the instructions on the bag. On April 27, 2017 all surviving cuttings were treated for spider mites with a batch of Avid insecticide that had been mixed in August of the previous year. Within one year of cuttings harvest and planting, all cuttings had lost their needles and died, including the few that had developed substantial roots.

STATISTICAL METHODS

ENVIRONMENTAL AND DEMOGRAPHY DATA ANALYSIS

When not handled as a single population, the main study population at Clifton Gorge (CG) is split into two subpopulations, the gorge subpopulation upriver toward Clifton and the picnic subpopulation behind the lower picnic shelter in John Bryan. The distance between these two subpopulations and the considerable differences in topography between the sites might suggest that these two groups of trees are ecologically distinct. Thus, separate tests were run on both the entire CG population and on the individual subpopulations. The trees sampled in Cantwell Cliffs (CC) were treated as a single population in all cases.

Data collected for each tree include three ordinal variables: relative slope of the site, relative thickness of leaf litter, and relative health of the individual – all ranked one to three. Binary data for the presence or absence of cones were also recorded per individual. For each of these variables, Chi-square tests for independence were conducted to determine if the frequency distribution of trees placed in different categories varied significantly between sites (R software, R Core Team 2017). Eight chi-square tests were run to compare each environmental (*i.e.* slope and leaf litter) and demographic variable (*i.e.* health) for the entire CG population *versus* Cantwell Cliffs and for the CG gorge subpopulation *versus* the CG picnic subpopulation.

SEED BOX DATA

A two sample Student's t-Tests was performed to elucidate any differences in seed catch between boxes placed on the cliff edge and boxes placed on the gorge floor (R software, R Core Team 2017).

DENDROCHRONOLOGY DATA

Data obtained through dendrochronological methods included growth ring width per year for each cored individual. Widths for each year were averaged over all cored individuals at each site to produce average annual ring width by site. Average annual ring width at each site visualized through time revealed steep peaks in annual ring width followed by stabilization in observed trends. These peaks are believed to represent release events during which one or more resources (*e.g.* light) were uncharacteristically abundant. The oldest individuals at the CG site were found in the gorge subpopulation, one of which was dated back to 1782. Statistics performed to compare average annual ring width to climate variables were limited by the earliest year of available climate data, 1895. For this reason, average annual ring widths for years 1782 through 1894 were excluded from statistical analyses for the only two sites for which data was available during that time, CG overall and the gorge subpopulation at CG. Statistical analyses to describe the overall CG site without release events include only years following the release event at the picnic subpopulation (1949 through 2017), as it occurred more recently than the release event at the gorge subpopulation.

Correlations were run to test for associations between average annual ring width and calendar year at each site, both with and without data from release event years (R software, R Core Team 2017). A correlation was also run to test for associations between time and annual ring width averaged for all cored individuals across all sites (R software, R Core Team 2017).

Multiple regression was utilized to estimate the relationship between average annual ring width and several climate variables (R software, R Core Team 2017). The climate dataset used for this study contains time series data averaged for the entire state of Ohio starting in year 1895 (NOAA National Centers for Environmental information, 2018). Variables considered in this study included: average temperature in May of each year, average temperature over the growing season (April – June) of each year, maximum and minimum temperatures for May of each year and over the growing season of each year, and average precipitation in May and over the growing season of each year. May was isolated as a month in which significant growth typically occurs for hemlock trees in Ohio, as resource allocation begins to shift toward reproduction in following months (Olson *et al.*, 1959). Correlations were run to test for associations between each climate variable and time (R software, R Core Team 2017). A correlation matrix including all independent climate variables was run to aid in model building. For any two independent variables with a correlation coefficient greater than 0.7, the variable spanning the growing season was preferentially selected for inclusion in the models (Dormann *et al.*, 2013). Maximum temperature in May was not strongly correlated with any other climate variables and was included to capture some component of extreme climate events.

Variables and interactions were reduced to produce two general model formulas:

AvgGrowth ~ AvgTempGS + AvgPrecipGS + AvgTempGS*AvgPrecipGS

AvgGrowth ~ AvgTempGS + AvgPrecipGS + MaxTempMay + AvgTemp3*Precip3 + MaxTempMay*Precip3

where AvgGrowth refers to the average yearly ring width, AvgTempGS refers to the average yearly temperature over the growing season, AvgPrecipGS refers to the average yearly precipitation over the growing season, MaxTempMay refers to the maximum temperature in May of each year, and * denotes an interaction between two independent variables. Regressions were run for all cored individuals averaged across the entire CG population, all cored individuals averaged across Cantwell Cliffs, for each CG subpopulation averaged individually, and for the combined average yearly ring widths including all cored individuals at both Cantwell Cliffs and Clifton Gorge. Regressions were also run for each population/subpopulation substituting AvgPrecipGS for a vector containing the average precipitation over the growing season in the previous year (PrevAvgPrecipGS).

Akaike information criterion (AIC) was calculated for all models at sites for which more than one model resulted in a significant overall p-value (R software, R Core Team 2017). The model with the lowest AIC value was selected as the best fit model for that site.

Two sample Student's t-tests were performed to test for differences in average annual ring width between sites (R software, R Core Team 2017). Tests were run comparing Cantwell Cliffs to the entire CG population and separately to each subpopulation both including and excluding release events. t-Tests were also performed to compare average annual ring width between CG picnic and CG gorge subpopulations, both with and without release events. The average annual ring width vector in each t-test for which release events were included consisted of only years for which at least one tree at each site had available core data. Thus, the site with the younger oldest tree provided the limiting data set. The average annual ring width vector in each t-test for which release events were excluded consisted of only years for which neither site was undergoing a release event.

III. RESULTS

DEMOGRAPHY

The eastern hemlock population at Clifton Gorge consists of approximately 132 individuals (Fig. 1), 110 in the gorge subpopulation, 22 in the picnic subpopulation, and two additional individuals that did not clearly belong to either subpopulation and were therefore excluded from statistical analyses (Fig. 2-3). The picnic subpopulation has no small individuals with DBH of zero to 10 cm nor any individuals larger than 51 cm DBH. Distribution of individuals across the size classes that are represented in the picnic subpopulation follows a relatively normal distribution with a slight skew toward smaller size classes (Fig. 2).

Of the 110 individuals in the gorge subpopulation, 95 are small seedlings with DBH less than 2 cm (Fig. 3). The gorge subpopulation consists of no individuals with DBH between 11 and 50 cm and only one to two individuals in each of the remaining, larger size classes (Fig. 3). All size classes for which the picnic subpopulation had no representation contained one or more individuals at the gorge subpopulation with the exception of 41-45, 71-75, 86-90, and 91-95 cm DBH. The gorge subpopulation includes the largest and smallest individuals while the picnic subpopulation includes individuals from the slightly right-skewed intermediate size classes.

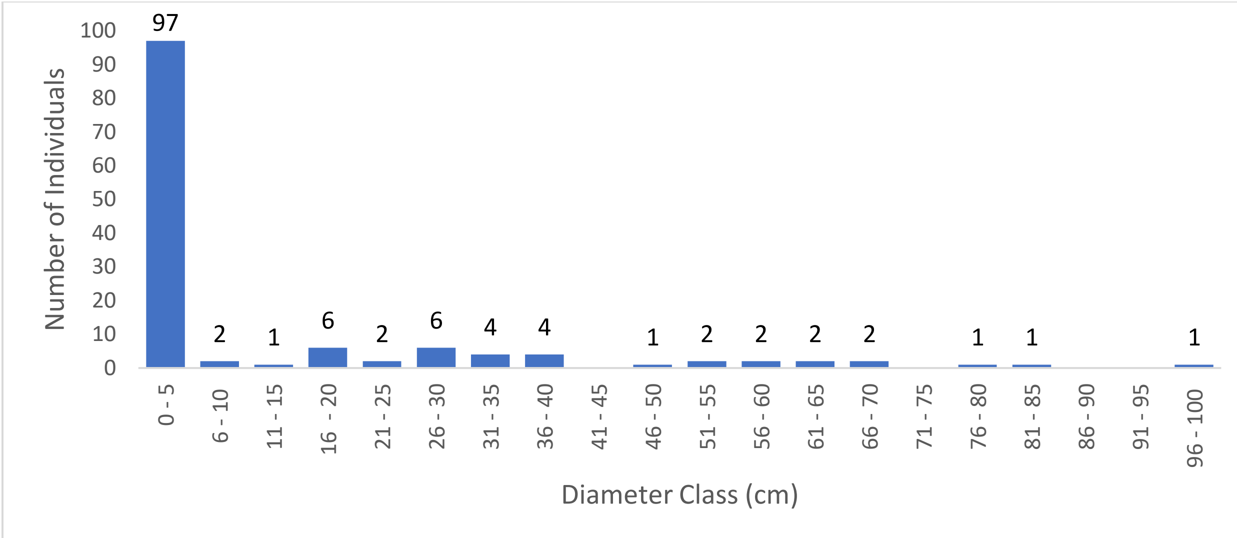

Fig. 1 – Overall size distribution of eastern hemlock individuals at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio (N = 134).

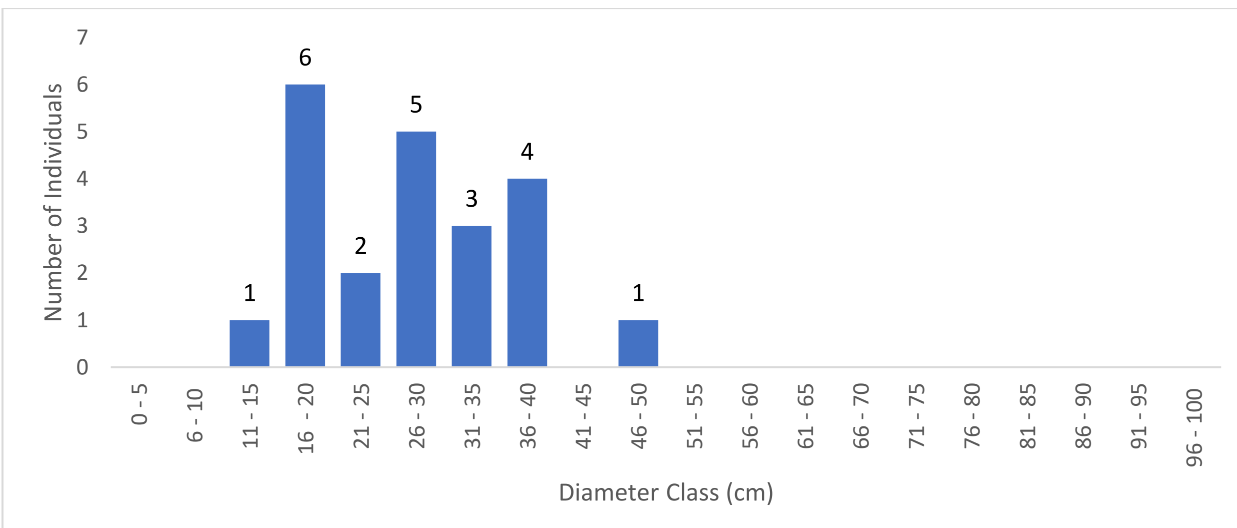

Fig. 2 – Size distribution of eastern hemlock individuals in the picnic subpopulation at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio (N = 22).

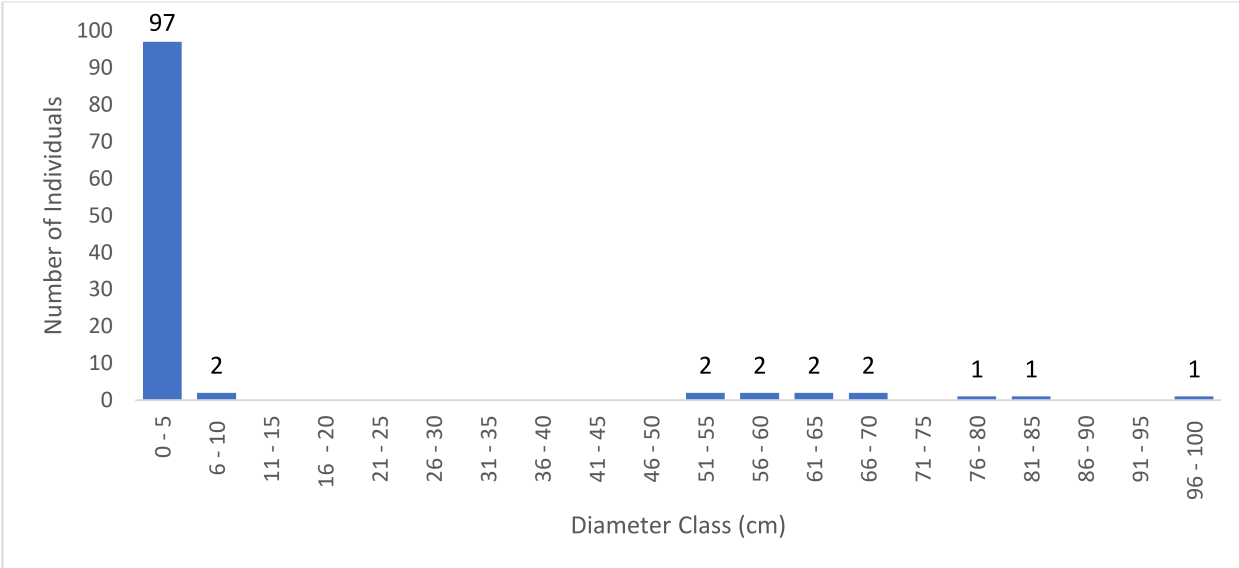

Fig. 3 – Size distribution of eastern hemlock individuals in the gorge subpopulation at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio (N = 110).

ENVIRONMENT CHARACTERISTICS BY SITE

Significant differences among sites in distribution of individuals across the three slope categories were found for CG relative to CC ($X^2 = 86.581$, df = 2, $p < 2.2e\text{-}16$) and for the CG picnic subpopulation relative to the CG gorge subpopulation ($X^2 = 46.497$, df = 2, $p < 8.0e\text{-}12$; Fig. 4 – 5). Individuals growing at Clifton Gorge tend to grow on shallower slopes than individuals at Cantwell Cliffs. Eighty-nine percent of individuals at CG grow on flat or nearly flat ground while all individuals at Cantwell Cliffs grow on either moderately (34%) or steeply (66%) sloped ground.

Individuals in the gorge subpopulation at Clifton Gorge tend to grow on less sloped ground than individuals in the picnic subpopulation at Clifton Gorge. Approximately 91% of individuals grow on flat or nearly flat ground in the gorge subpopulation while only about 32% of individuals grow in the same slope category in the picnic subpopulation.

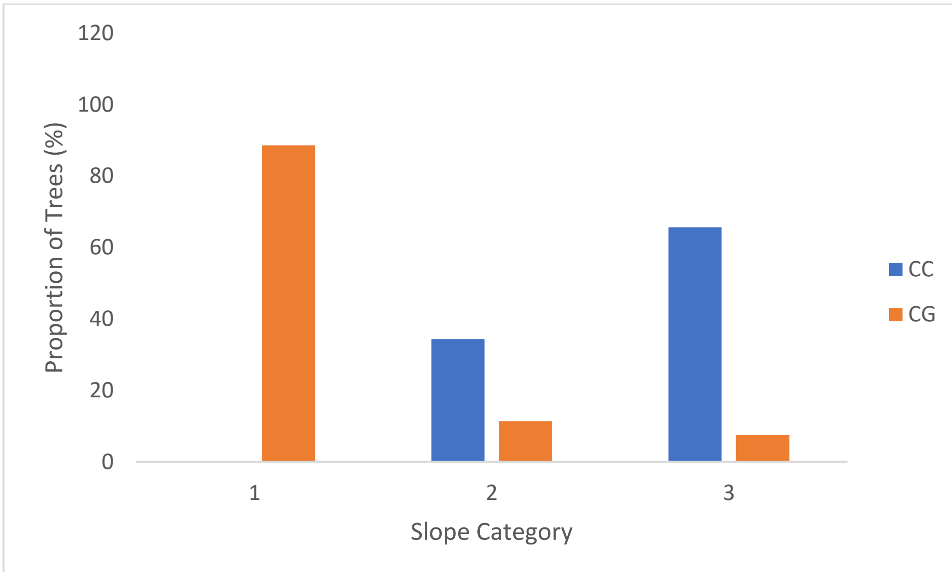

Fig. 4 – Proportion of eastern hemlock individuals in each of three slope categories at Cantwell Cliffs (CC; N = 32) and Clifton Gorge (CG; N = 132), Ohio. 1 = flat or nearly flat; 2 = slight to intermediate slope; 3 = steep slope to cliff edge.

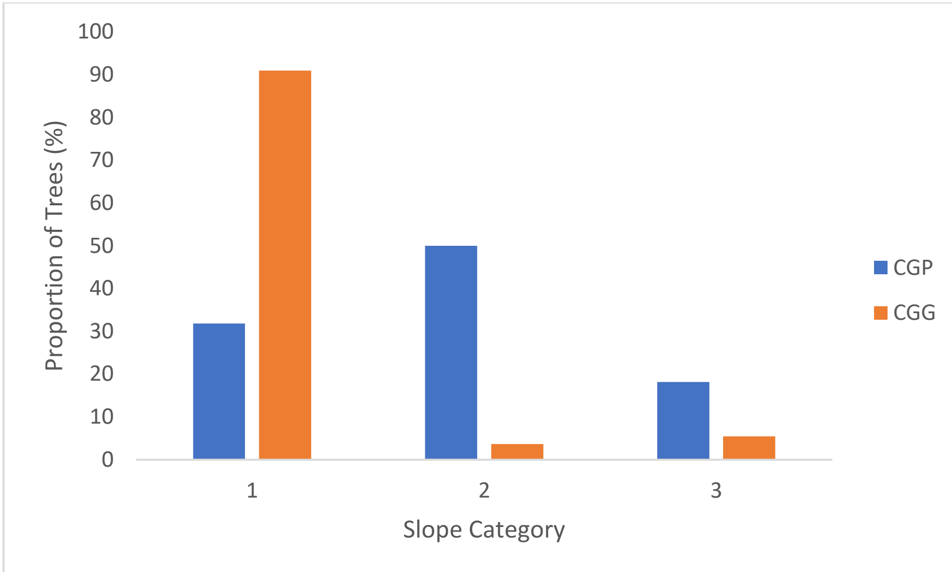

Fig. 5 – Proportion of eastern hemlock individuals in each of three slope categories at Clifton Gorge, Ohio in the picnic (CGP; N = 22) and the gorge (CGG; N = 110) subpopulations. 1 = flat or nearly flat; 2 = slight to intermediate slope; 3 = steep slope to cliff edge.

Significant differences among sites in distribution of individuals across the three leaf litter categories were found for CG relative to CC ($X^2 = 35.77$, df = 2, $p < 1.7e{-8}$) and for the CG picnic subpopulation relative to the CG gorge subpopulation ($X^2 = 41.52$, df = 2, $p < 9.6e{-10}$; Fig. 6 – 7). Individuals at Clifton Gorge tended to grow in shallower leaf litter than individuals at Cantwell Cliffs. Most individuals at CG (approximately 61%) grow in areas with the least amount of leaf litter while the remaining approximately 39% of individuals are split almost evenly between categories two and three (approximately 17 and 22%, respectively). Approximately 66% of individuals at CC grow in the thickest category of leaf litter, with approximately 31% of individuals falling into category two and only about 3% of individuals in the thinnest leaf litter category.

The majority of individuals in the gorge subpopulation at CG (approximately 73%) grow in areas with the thinnest leaf litter, with approximately 16% in category three and approximately 11% in category two. Overall, individuals in the gorge subpopulation grow in thinner leaf litter than individuals in the picnic subpopulation, where all individuals are evenly split between categories two and three.

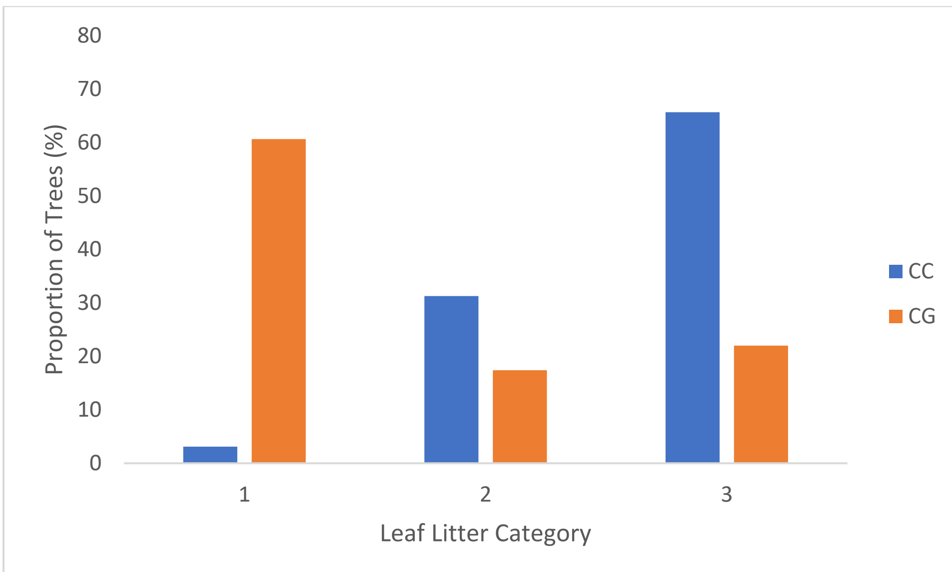

Fig. 6 – Proportion of eastern hemlock individuals in each of three leaf litter categories at Cantwell Cliffs (CC; N = 32) and Clifton Gorge (CG; N = 132), Ohio. 1 = thin leaf litter with most to half of the ground exposed; 2 = more than half of the ground covered, thin accumulation over most or all of the ground; 3 = moderate to thick coverage.

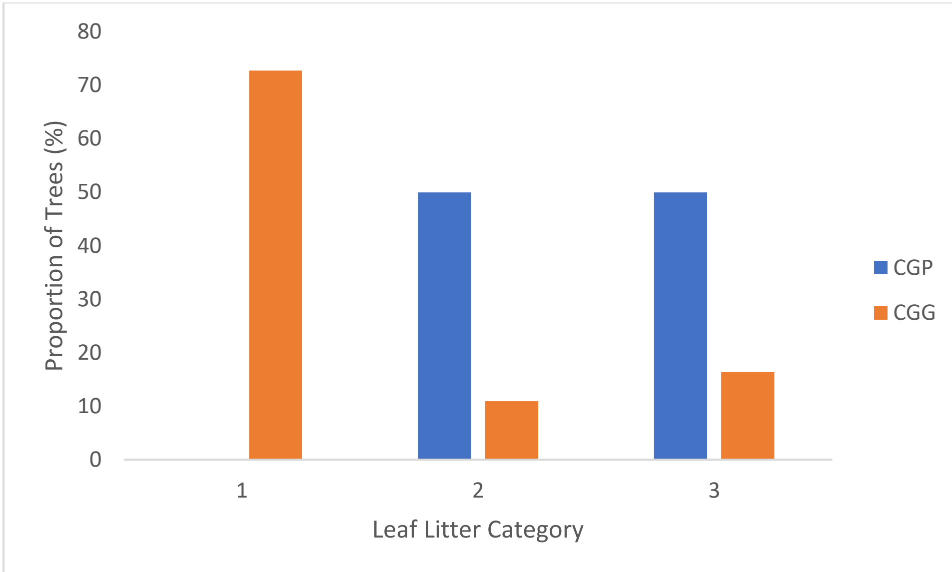

Fig. 7 – Proportion of eastern hemlock individuals in each of three leaf litter categories at Clifton Gorge, Ohio in the picnic (CGP; N = 22) and the gorge (CGG; N = 110) subpopulations. 1 = thin leaf litter with most to half of the ground exposed; 2 = more than half of the ground covered, thin accumulation over most or all of the ground; 3 = moderate to thick coverage.

TREE HEALTH BY SITE

Significant differences among sites in the distribution of individuals across the three health categories were found for CG relative to CC ($X^2 = 17.567$, df = 2, $p < 0.001$) and for the CG picnic subpopulation relative to the CG gorge subpopulation ($X^2 = 17.123$, df = 2, $p < 0.001$); Fig. 8 – 9).

Both CC and CG had the greatest number of individuals in the intermediate health category, followed by the good and the poor health categories, respectively. With approximately 96% of individuals in either the second or third health category, CG scores higher for overall health than CC (approximately 78% in categories 2 and 3).

Both the picnic and the gorge subpopulations at Clifton Gorge have very few individuals in the lowest health category relative to either of the two higher health categories. While both subpopulations have a very similar proportion of individuals in either of the two highest health categories (approximately 97 and 95% for the gorge and picnic subpopulations, respectively), the picnic subpopulation has more individuals in the best health category. Thus, the picnic subpopulation scores higher in overall health than the gorge subpopulation.

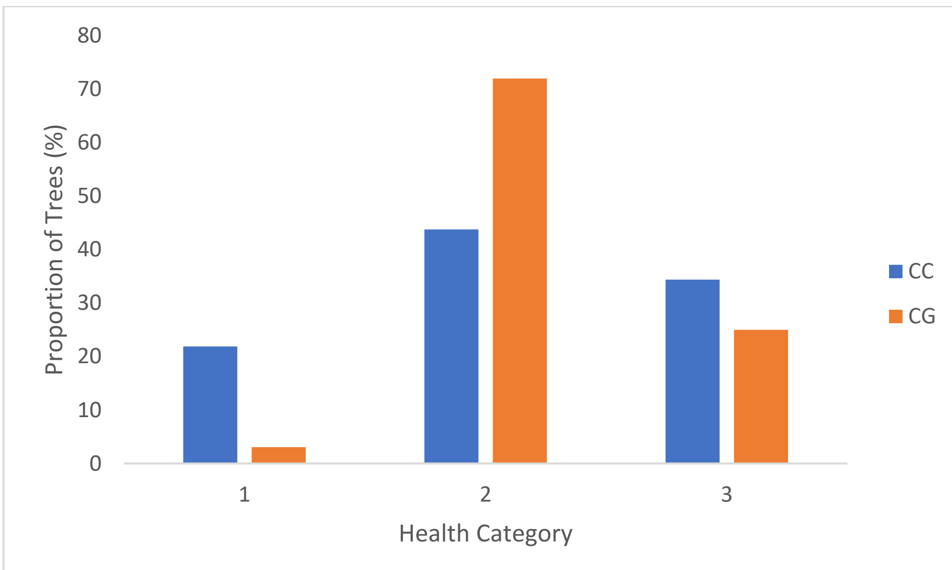

Fig. 8 – Proportion of eastern hemlock individuals in each of three health categories at Cantwell Cliffs (CC; N = 32) and Clifton Gorge (CG; N = 132), Ohio. 1 = poor health, missing branches, excessive epicormic branching, canopy dieback; 2 = intermediate health, only one to two indicators of decreased health; 3 = very healthy with little to no indication of health issues.

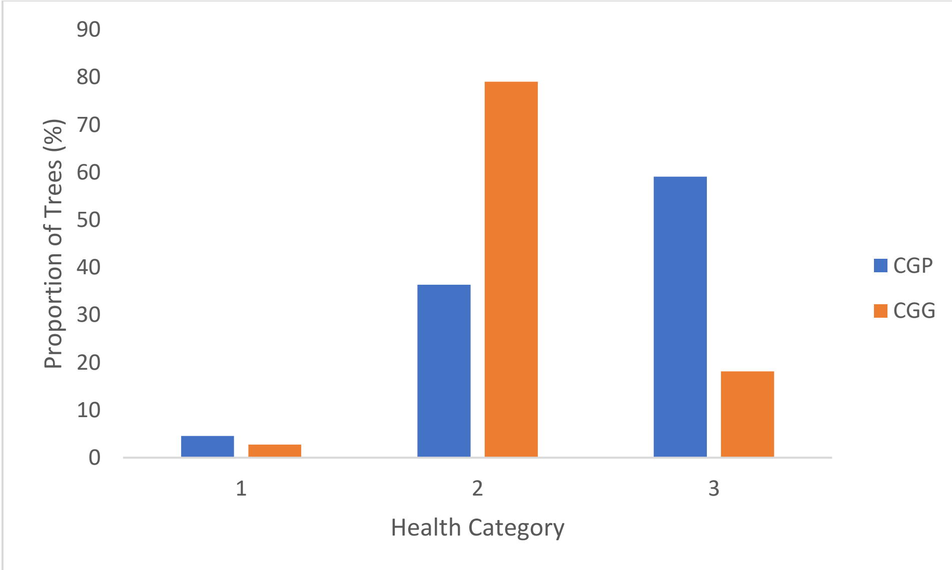

Fig. 9 – Proportion of eastern hemlock individuals in each of three health categories at Clifton Gorge, Ohio in the picnic (CGP, N = 22) and the gorge (CGG; N = 110) subpopulations. 1 = poor health, missing branches, excessive epicormic branching, canopy dieback; 2 = intermediate health, only one to two indicators of decreased health; 3 = very healthy with little to no indication of health issues.

SEED PRODUCTION AT CLIFTON GORGE

Significant differences among sites in the frequency of cone-bearing individuals were found at CG, where the picnic subpopulation had a significantly larger proportion of cone-bearing individuals (36%) than the gorge subpopulation (10%; $X^2 = 9.379$, df = 1, $p < 0.003$).

Seed boxes positioned at Clifton Gorge on the gorge floor caught significantly more seeds ($\bar{x} = 104 \pm 53$ seeds; N = 6) than boxes positioned along the cliff edge above ($\bar{x} = 37 \pm 10$ seeds; N = 4; $t = -3.052$, df = 5.498, $p < 0.03$).

CLIMATE DATA

Average yearly temperature over the growing season, average yearly precipitation over the growing season, and average yearly minimum temperature over the growing season were the only climate variables for which data was analyzed that displayed statistically significant trends over time. Average yearly temperature over the growing season ($r = 0.236$, $df = 121$, $p < 0.01$; Fig. 10) and average yearly precipitation over the growing season ($r = 0.239$, $df = 121$, $p < 0.01$; Fig. 11) increase slowly but significantly over time for the state of Ohio. Average minimum temperature over the growing season increases significantly over time for the state of Ohio ($r = 0.314$, $df = 121$, $p < 0.001$; Fig. 12).

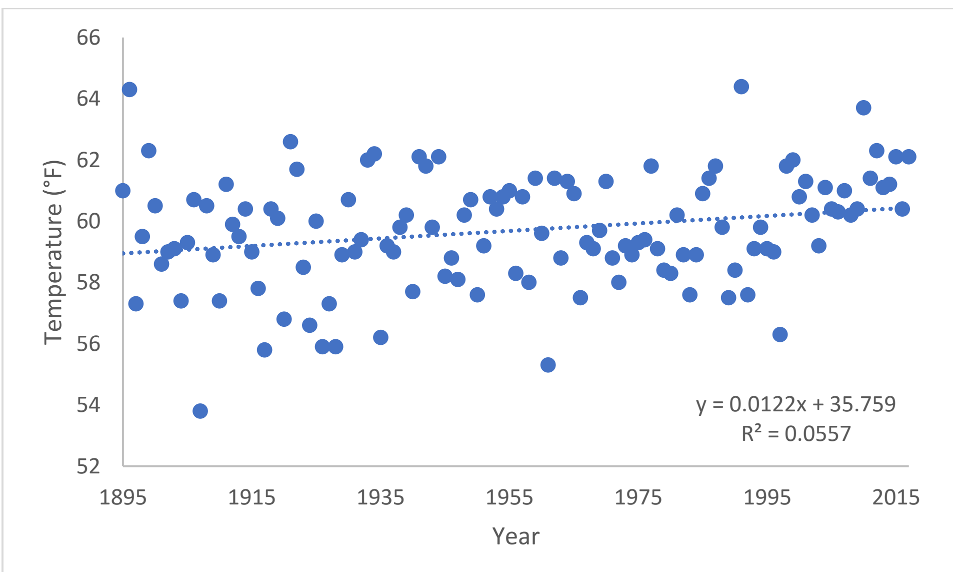

Fig. 10 – Average three-month temperature (April – June) for each year in the state of Ohio from 1895 through 2017 (NOAA National Centers for Environmental information, 2018).

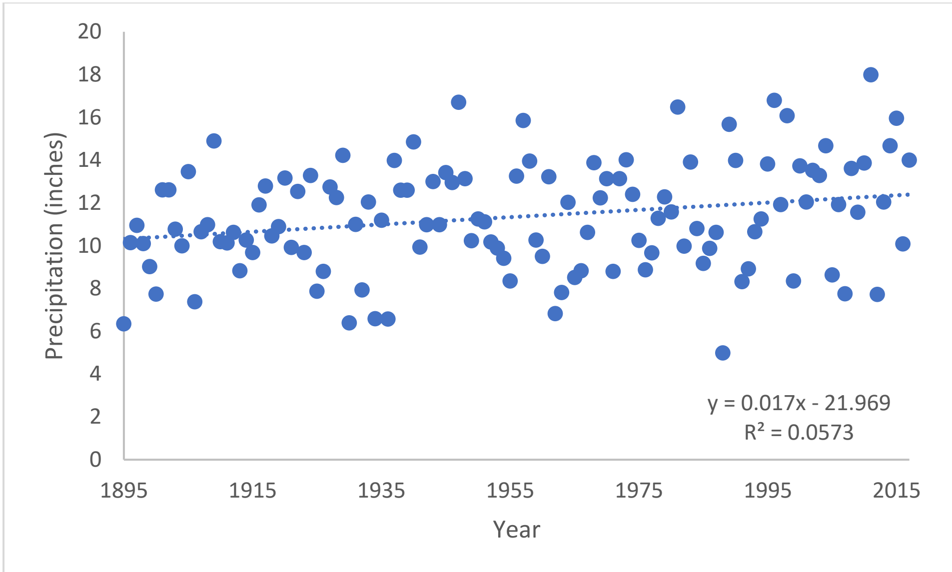

Fig. 11 – Average three-month precipitation (April – June) for each year in the state of Ohio from 1895 through 2017 (NOAA National Centers for Environmental information, 2018).

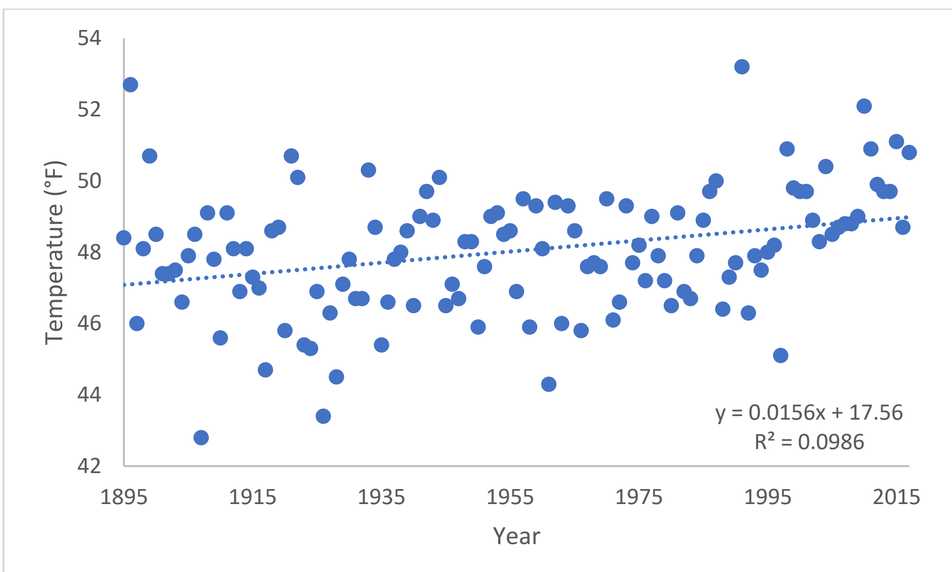

Fig. 12 – Average three-month minimum temperature (April – June) for each year in the state of Ohio from 1895 through 2017 (NOAA National Centers for Environmental information, 2018).

GROWTH TRENDS

Time periods in average yearly ring width during which release events are believed to have taken place include 1898 through 1940 for Cantwell Cliffs, 1931 through 1948 for the picnic subpopulation at Clifton Gorge, and 1827 through 1848 for the gorge subpopulation at Clifton Gorge (Fig. 13). When both CG subpopulations are averaged together to obtain overall average yearly ring width for the CG site, statistics specified to exclude release events use only data from time periods for which neither subpopulation was experiencing a release event (*i.e.* 1949-2017).

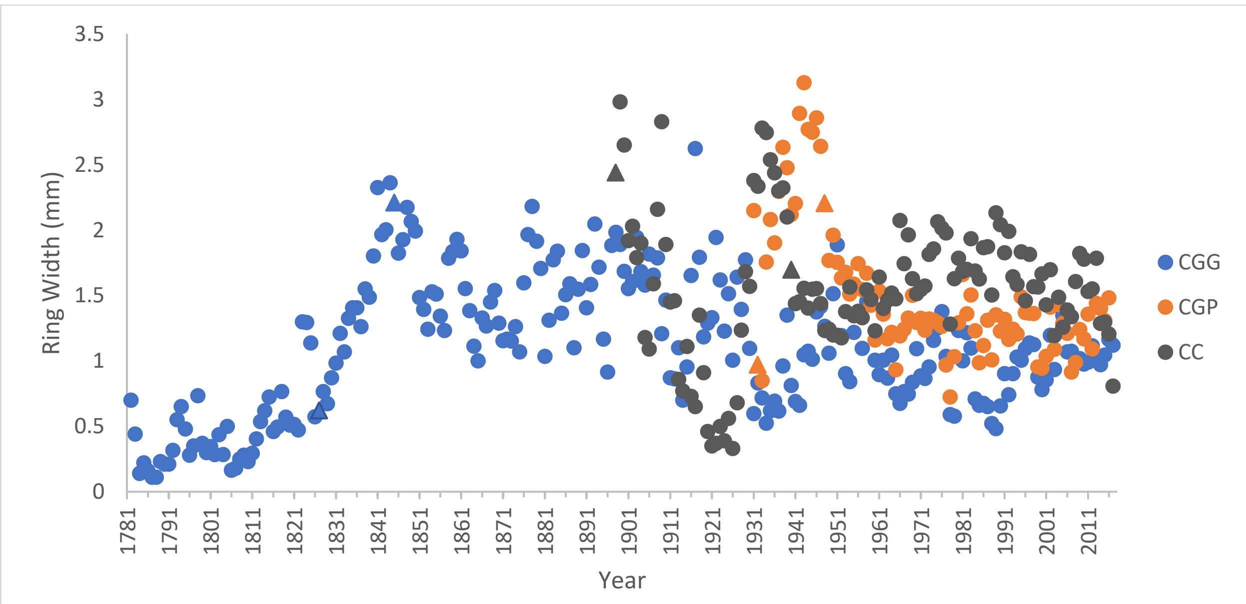

Fig. 13 – Yearly ring width averaged separately across all eastern hemlock individuals cored from the gorge (CGG; N = 30) and picnic (CGP; N = 22) subpopulations at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio and from Cantwell Cliffs (CC, N = 28), Rockbridge, Ohio. First and last years of release events for each site/subpopulation are marked with triangles in each data series (1827 and 1848 for CG gorge; 1898 and 1940 for CC; 1931 and 1948 for CG picnic).

No significant long-term changes in average ring widths were detected through time at CC either with ($r = 0.163$, $df = 118$, $p > 0.05$; Fig. 14) or without ($r = 0.118$, $df = 75$, $p > 0.3$; Fig. 15) release events despite the very slight increase in ring width in both cases.

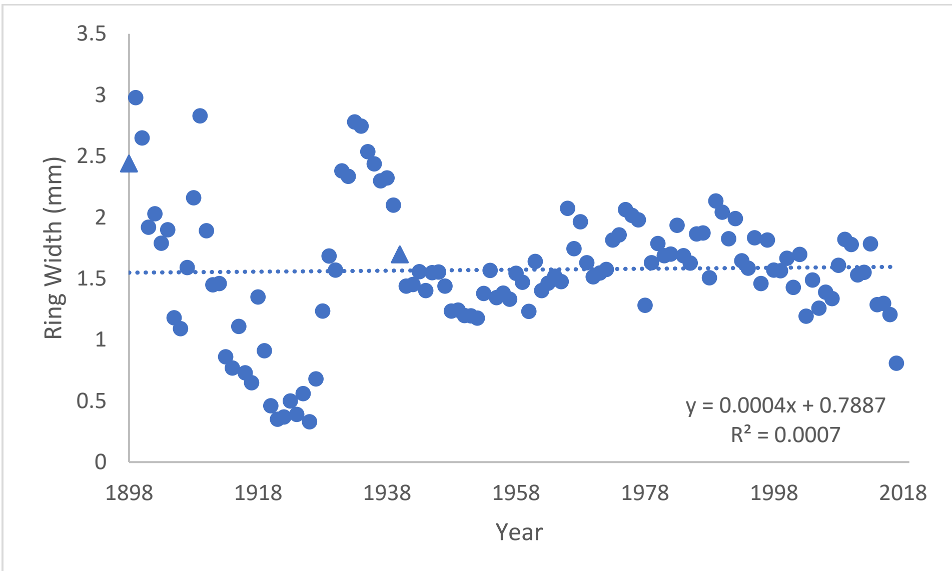

Fig. 14 – Yearly ring width averaged across all eastern hemlock individuals cored at Cantwell Cliffs, Rockbridge, Ohio (N = 28). Data series was truncated at year 1898 based on the first available ring width from the oldest cored individual. First and last years of release events are marked with triangles (1898 and 1940).

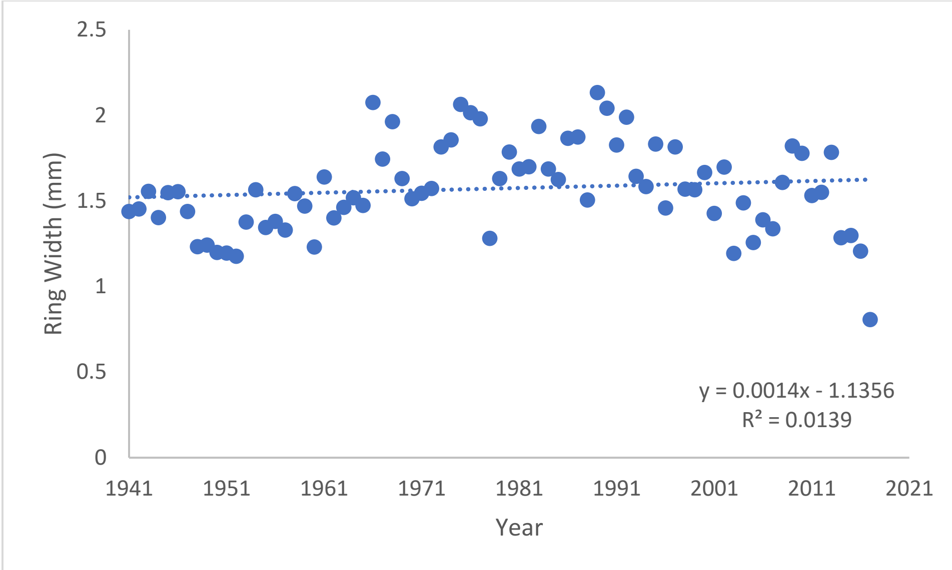

Fig. 15 – Yearly ring width averaged across all eastern hemlock individuals cored at Cantwell Cliffs, Rockbridge, Ohio, excluding years during which release events are believed to have occurred (N = 28). Data series was truncated at year 1941 based on the first year following the end of the release event time frame.

Average yearly ring width for the entire CG population (Fig. 16) decreased significantly over time both when release events were included ($r = -0.267$, $df = 121$, $p < 0.01$; Fig. 17) and excluded ($r = -0.376$, $df = 67$, $p < 0.01$; Fig. 18).

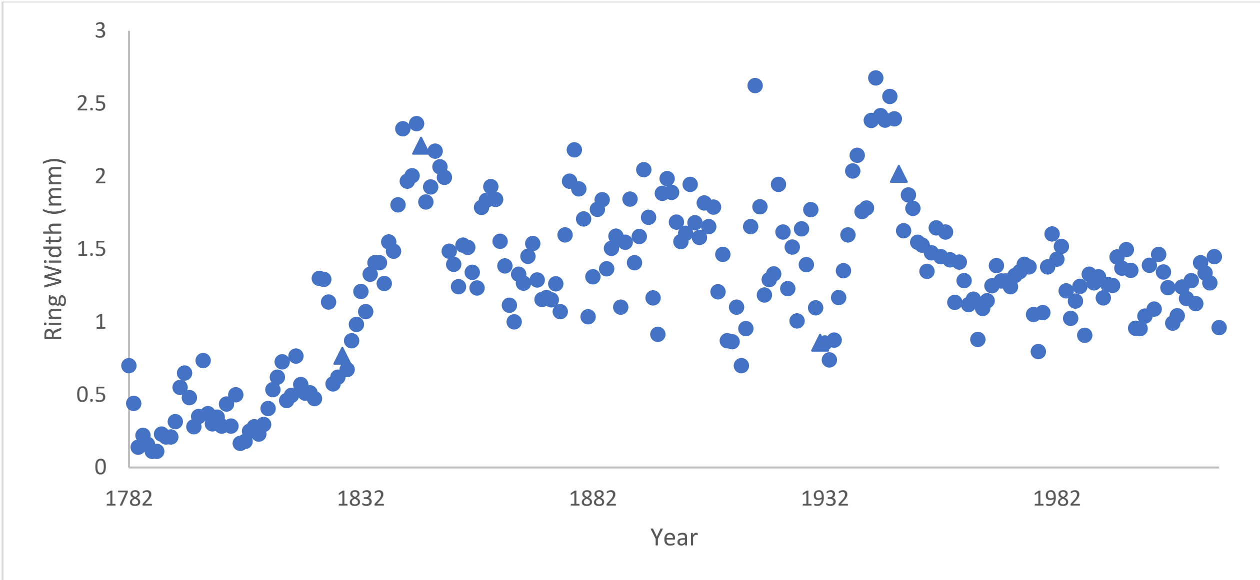

Fig. 16 – Yearly ring width averaged across all eastern hemlock individuals cored at Clifton Gorge, Yellow Springs, Ohio (N = 30). Data series stretches back to year 1782 based on the first available ring width from the oldest cored individual from the gorge subpopulation. First and last years of release events are marked with triangles (1827 and 1848 for the gorge subpopulation; 1931 and 1948 for the picnic subpopulation).

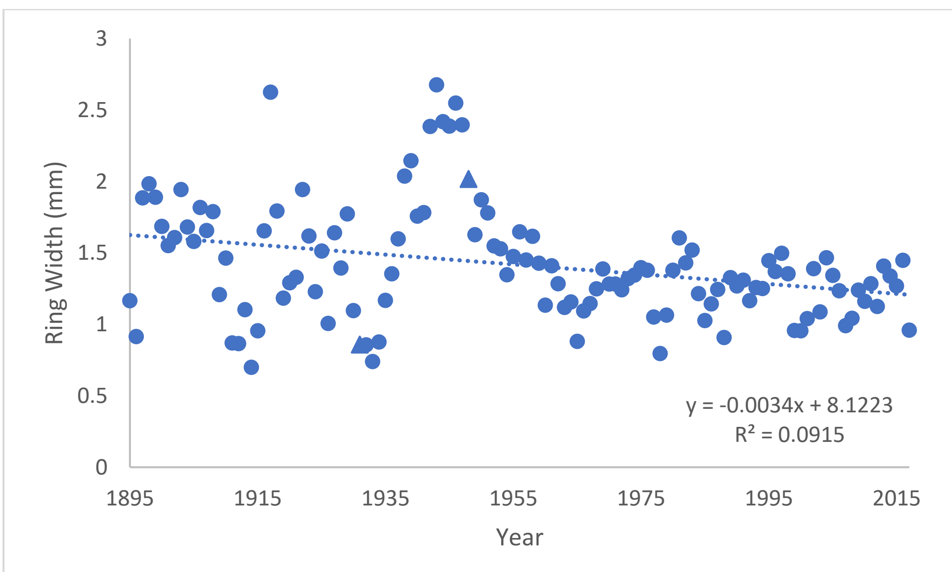

Fig. 17 – Yearly ring width averaged across all eastern hemlock individuals cored individuals at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio (N = 30). Data series was truncated at year 1895 based on the earliest year of available climate data (NOAA National Centers for Environmental information, 2018). First and last years for which either subpopulation experienced release events are marked with triangles (1931 and 1949 for the picnic subpopulation; gorge subpopulation release event excluded by availability of climate data).

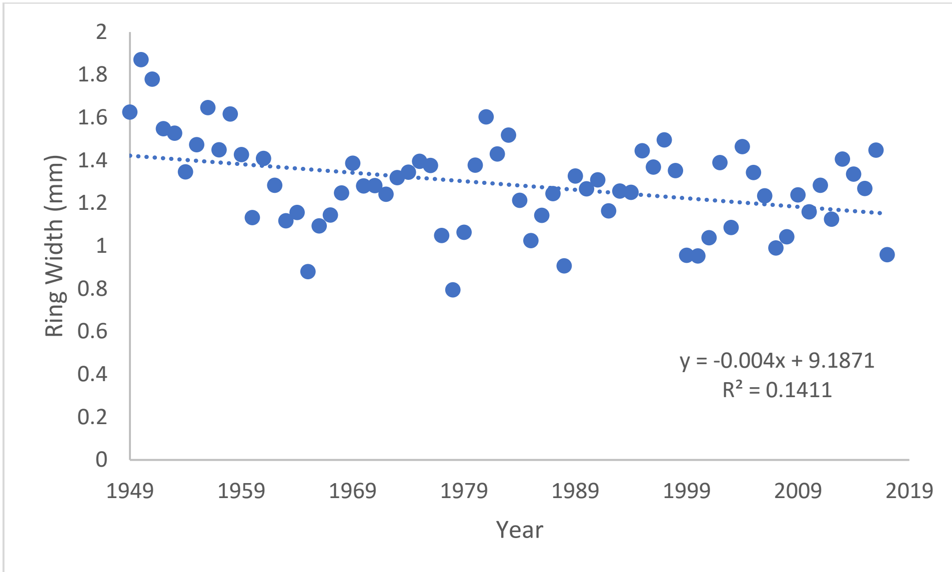

Fig. 18 – Yearly ring width averaged across all eastern hemlock individuals cored individuals at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio, excluding years during which release events are believed to have occurred (N = 30). Data series was truncated at year 1949 based on the latest release in either CG subpopulation, which occurs for the picnic subpopulation at CG from 1931 until 1948.

Average annual ring width for the picnic subpopulation at CG decreased significantly over time both with ($r = -0.603$, $df = 85$, $p < 6.13e-10$; Fig. 19) and without ($r = -0.477$, $df = 57$, $p < 3.5e-5$; Fig. 20) release events.

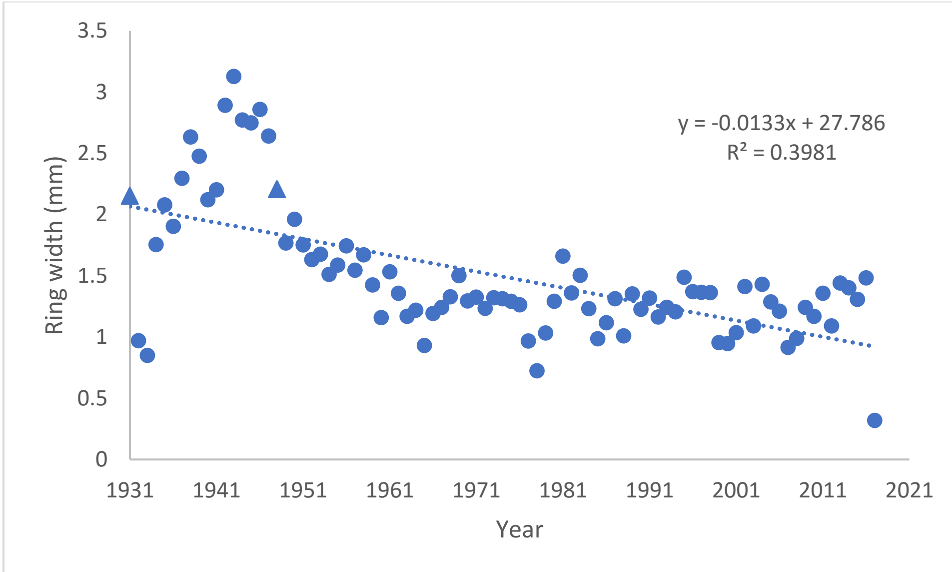

Fig. 19 – Yearly ring width averaged across all eastern hemlock individuals cored from the picnic subpopulation at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio (N = 22). The data series was truncated at 1931 based on the first available ring width from the oldest cored individual. First and last years of release events are marked with triangles.

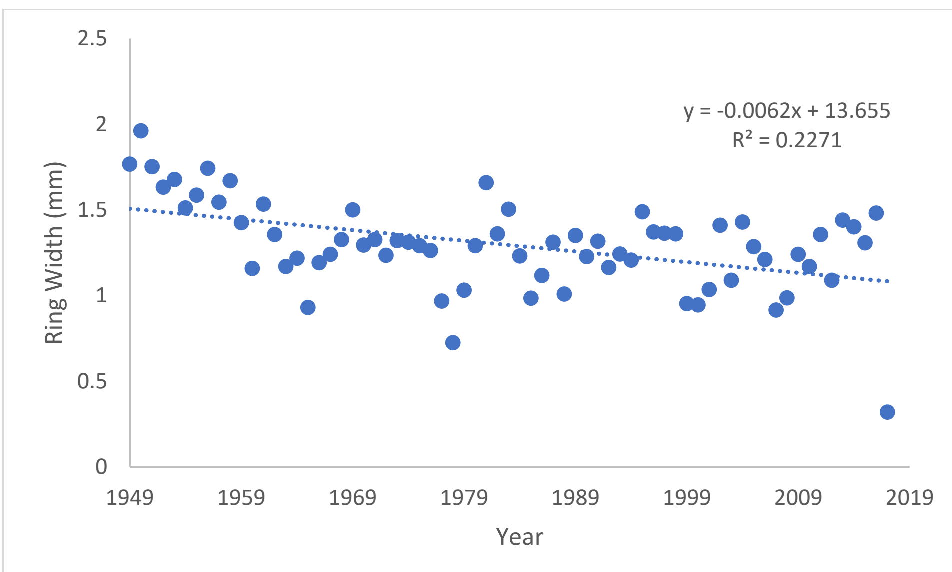

Fig. 20 – Yearly ring width averaged across all eastern hemlock individuals cored from the picnic subpopulation at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio, excluding years during which release events are believed to have occurred (N = 22). Data series was truncated at year 1949 based on the first year following the release event time period.

Ring width data was available for the gorge subpopulation at CG from 1782 to 2017 (Fig. 21). The release event for this site was excluded from statistical analyses due to the first available year of climate data. Average yearly ring width for the gorge subpopulation at CG following the release event from 1827 through 1848 decreases significantly over time ($r = -0.560$, $df = 167$, $p < 2.85e-15$; Fig. 22). This significant decline is maintained when data for the gorge subpopulation is further restricted to match available climate data ($r = -0.458$, $df = 121$, $p < 9.98e-8$; Fig. 23).

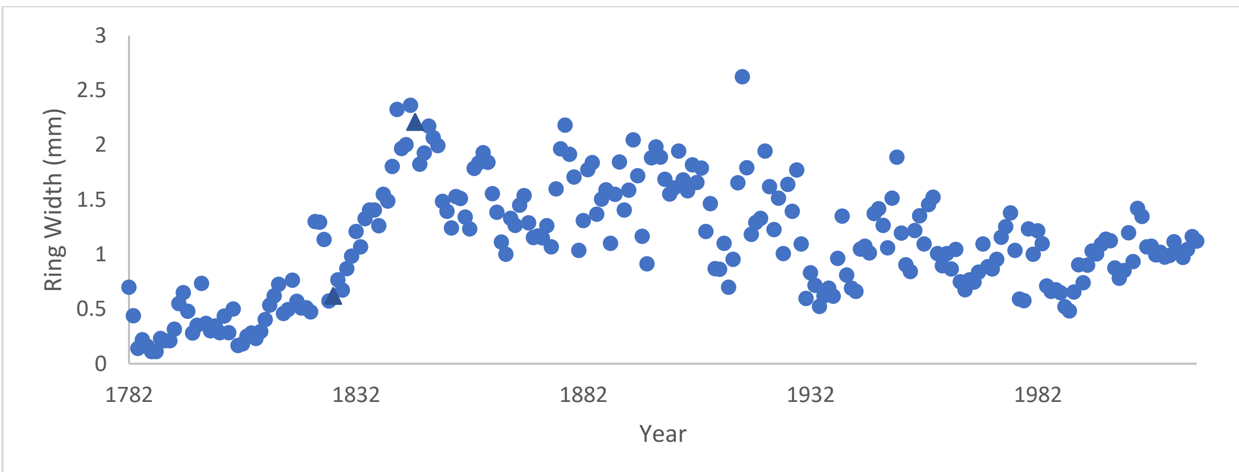

Fig. 21 – Yearly ring width averaged across all eastern hemlock individuals cored from the gorge subpopulation at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio (N = 6). The data series was truncated at 1782 based on the first available ring width from the oldest cored individual. Triangles indicate the first and last years of the release event time period (1827 and 1848).

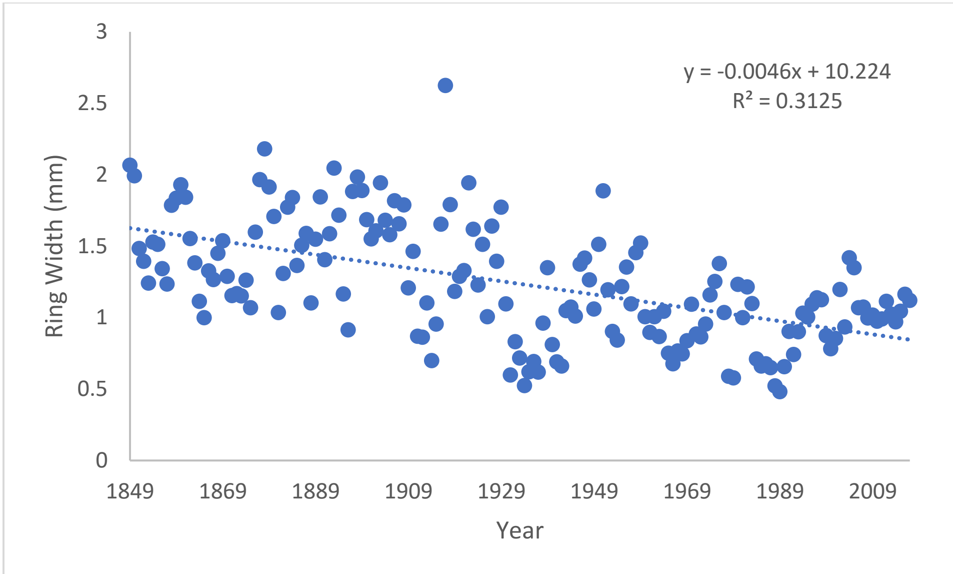

Fig. 22 – Yearly ring width averaged across all eastern hemlock individuals cored from the gorge subpopulation at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio, excluding years during which release events are believed to have occurred (N = 6). Data series was truncated at year 1849 based on the first year following the release event time period.

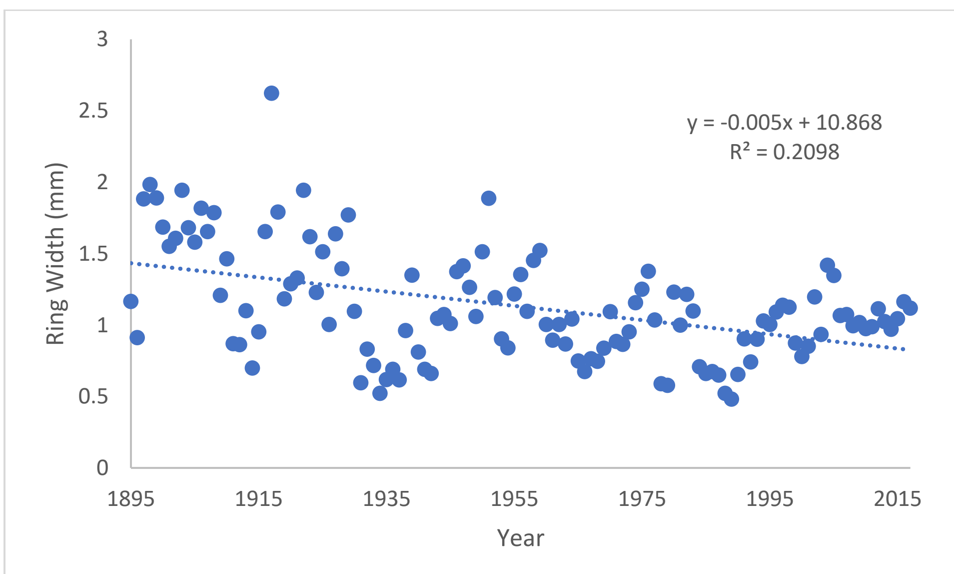

Fig. 23 – Yearly ring width averaged across all eastern hemlock individuals cored from the gorge subpopulation at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio (N = 6). Data series was truncated at year 1895 based on the earliest year of available climate data (NOAA National Centers for Environmental information, 2018).

Collective yearly ring width averaged across all cored individuals from both CG and CC (Fig. 24) decreases significantly over time ($r = -0.207$, $df = 121$, $p < 0.03$; Fig. 25). When time periods for which one or more of the sites are experiencing release events are removed, the slight decrease in overall yearly ring width is no longer significant ($r = -0.098$, $df = 57$, $p > 0.4$; Fig. 26).

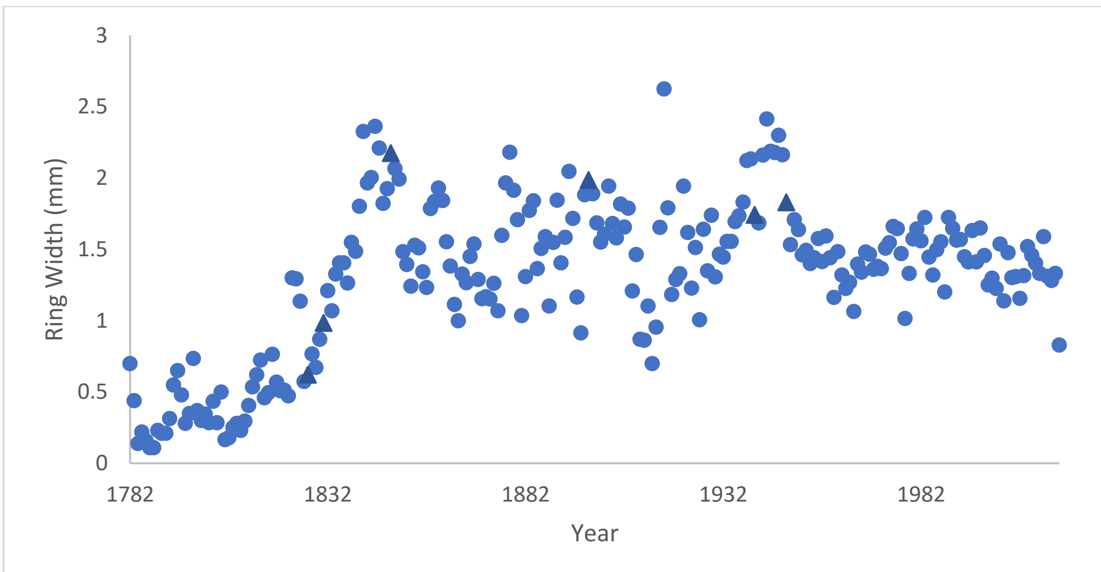

Fig. 24 – Yearly ring width averaged across all eastern hemlock individuals cored at both Cantwell Cliffs, Rockbridge, Ohio and Clifton Gorge State Nature Preserve, Yellow Springs, Ohio (N = 58). Data series stretches back to year 1782 based on the first available ring width from the oldest cored individual from the gorge subpopulation at Clifton Gorge. First and last years of release events are marked with triangles (1827 and 1848 for the gorge subpopulation; 1898 to 1940 for Cantwell Cliffs; 1931 and 1948 for the picnic subpopulation).

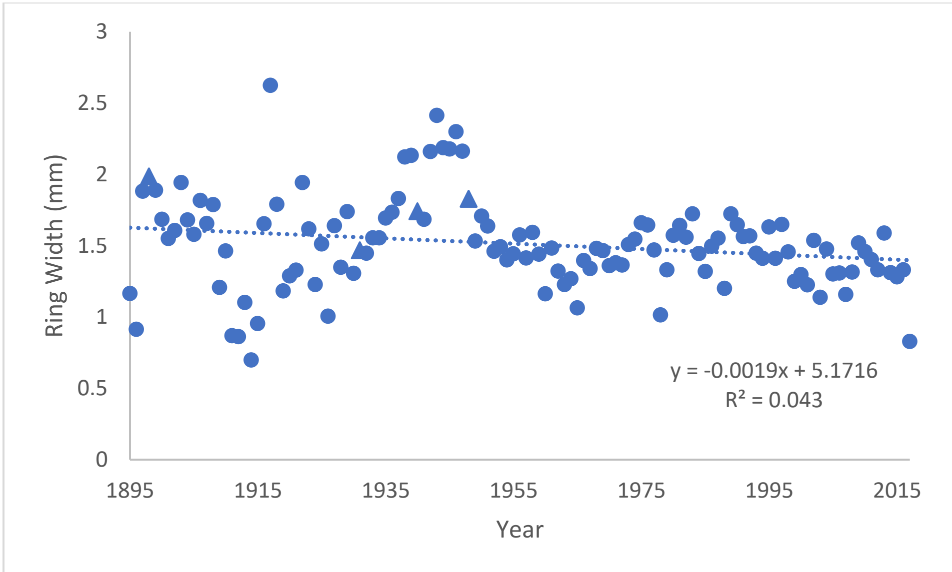

Fig. 25 – Yearly ring width averaged across all eastern hemlock individuals cored at both Cantwell Cliffs, Rockbridge, Ohio and Clifton Gorge State Nature Preserve, Yellow Springs, Ohio (N = 58). Data series was truncated at year 1895 based on the earliest year of available climate data (NOAA National Centers for Environmental information, 2018). First and last years of release events are marked with triangles (1898 to 1940 for Cantwell Cliffs; 1931 and 1948 for the picnic subpopulation).

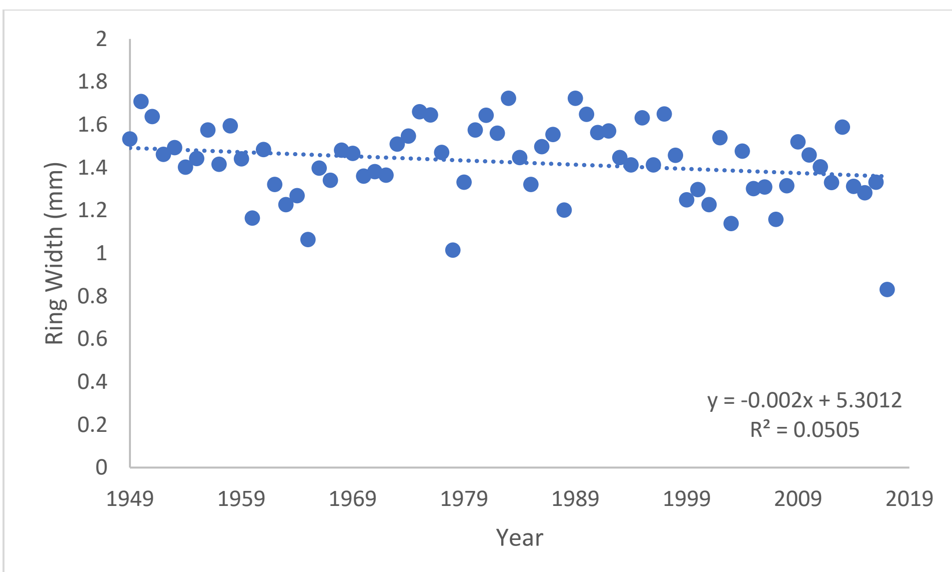

Fig. 26 – Yearly ring width averaged across all eastern hemlock individuals cored at both Cantwell Cliffs, Rockbridge, Ohio and Clifton Gorge State Nature Preserve, Yellow Springs, Ohio, excluding years during which release events are believed to have occurred (N = 58). Data series was truncated at year 1949 based on the first year following the most recent release event time period, which occurs from 1931 to 1948 in the CG picnic subpopulation.

One or more significant linear models were produced to predict average yearly ring width at all sites except Cantwell Cliffs, where ring width was not predicted by any models (Table 1 – 2). Significant models were also produced to predict average yearly ring width across all cored trees, collectively, from all sites.

When the CG population was taken as a whole and considered over the entire time frame for which environmental data was available from the NOAA National Centers for Environmental Information, average ring width was best predicted by the independent effects of average temperature and precipitation over the growing season (April through June) and the interactive effect of the two (AIC = 121; Table 1). The overall statistical significance of this model and all other models lacking statistically significant coefficients was due to the combined small effects of several variables (Table 1 – 2). The lowest coefficient p-value in the CG population model was attributed to the independent effect of average precipitation over the growing season ($p < 0.085$; Table 2). The positive coefficient for this effect indicates that as average growing season precipitation increased, so did average annual ring width. The negative coefficient for the interactive effect of average growing season temperature with average growing season precipitation ($p < 0.098$; Table 2) suggests that increased growing season temperature dampened the positive impact of increased growing season precipitation on ring width.

When release events were excluded from the analysis of CG, ring width across the entire CG population was best predicted by the independent effects of average growing season temperature, average growing season precipitation, and maximum temperature in

May of each year along with the interactive effects of average growing season temperature with average growing season precipitation and maximum May temperature with average growing season precipitation (AIC = -21; Table 1). This model produced no statistically significant coefficients, but the interactive effect of average growing season temperature with average growing season precipitation resulted in the smallest p-value ($p < 0.07$; Table 2). This model lacked significant or nearly significant coefficients for any of the independent effects. In this case, the negative coefficient for the interactive effect of average growing season temperature with average growing season precipitation indicates that as either growing season temperature or growing season precipitation changed, the effect of the other variable on ring width was dampened. The positive coefficient for the interactive effect of average growing season precipitation with maximum annual temperature in May ($p < 0.094$; Table 2) indicates that change in either climate variable enhanced the effect of the other variable on ring width.

The model including average growing season temperature, average growing season precipitation, and the interaction of average growing season temperature with average growing season precipitation best predicted average yearly ring width for the picnic subpopulation at CG when release events were included (no AIC, single significant model). The CG picnic ring width model including release events contained no statistically significant coefficients, but the p-value for the independent effect of average growing season precipitation was the closest to significance ($p < 0.07$; Table 2). The positive coefficient for this independent effect indicates that increased growing season precipitation leads to increased ring width. The negative coefficient for the interactive effect of average growing season temperature with average growing season precipitation ($p < 0.076$; Table 2) suggests that an increase in growing season temperature dampened the positive impact of increased growing season precipitation on ring width.

When release events were excluded from the model to predict ring width for the picnic subpopulation at Clifton Gorge, the only statistically significant model included the independent effects of average growing season temperature, average growing season precipitation, and maximum yearly temperature in May as well as the interactive effects of average growing season temperature with average growing season precipitation and average growing season precipitation with maximum yearly temperature in May. For this model, the interactive effect of average growing season temperature with average growing season precipitation was nearly significant ($p < 0.051$; Table 2). The negative coefficient for this interactive effect indicates, with an absence of statistically significant or nearly significant independent effect coefficients, that as either growing season temperature or growing season precipitation changes, the effect of the other variable on ring width is dampened. The positive coefficient for the interactive effect of average growing season precipitation with maximum annual temperature in May ($p < 0.067$; Table 2) indicates that change in either climate variable enhances the effect of the other variable on ring width.

Due to the limitations of the climate data, it was not possible to run iterations of the models for the gorge subpopulation at Clifton Gorge to include release events. Even the earliest available climate data excludes the release event for that subpopulation. Thus, the single set of models for the gorge subpopulation describe only post-release ring width. Average yearly ring width for the gorge subpopulation at Clifton Gorge was best predicted by the independent effects of average growing season temperature for a given year and average growing season precipitation in the previous year and the interactive effect of the two (no AIC, single significant model). This model did not result in statistically significant coefficients, but the coefficient for average growing season precipitation in the previous year was closest to significance ($p < 0.3$; Table 2). The positive coefficient for this effect indicates that increased growing season precipitation in the previous year leads to increased ring width the following year.

The model including average growing season temperature, average growing season precipitation, and the interaction of average growing season temperature with average growing season precipitation best predicted collective average ring width for all trees at both CG and CC both when years for which one or more site was experiencing release events were included (AIC = 66; Table 1) and excluded (AIC = -51; Table 1). The model to predict average ring width for all trees across both sampled populations with release events included was the only model to include statistically significant coefficients. For this model, both the independent effect of average growing season precipitation ($p < 0.04$; Table 2) and the interactive effect of average growing season temperature with average growing season precipitation ($p < 0.05$; Table 2) were significant contributors to the overall model. The positive coefficient for the effect of growing season precipitation indicates that an increase in growing season precipitation leads to an increase in ring width. The negative coefficient for the significant interactive effect indicates that an increase in growing season temperature dampened the positive impact of increased growing season precipitation on ring width.

When release events were removed from the data set, the independent effect of average growing season precipitation ($p > 0.053$; Table 2) and the interactive effect of average growing season temperature with average growing season precipitation ($p > 0.058$; Table 2) were no longer statistically significant but were still nearly significant. The positive coefficient for the effect of growing season precipitation indicates that an increase in growing season precipitation leads to an increase in ring width. The negative coefficient for the interactive effect indicates that an increase in growing season temperature dampened the positive impact of increased growing season precipitation on ring width.

Table 1 – Significant Linear Models to Predict Average Yearly Ring Width of Eastern Hemlock Trees at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio and across all Ohio Sites – Summary of Akaike Information Criterion (AIC) Values Used to Select Best-Fit Models

Site	Years	Significant Models (Independent Variables)	AIC Values	AIC df
CG All	1896 - 2017	AvgTempGS + AvgPrecipGS + AvgTempGS*AvgPrecipGS	121.5	5
		AvgTempGS + AvgPrecipGS + MaxTempMay + AvgTempGS*AvgPrecipGS + MaxTempMay*AvgPrecipGS	123.0	7
		AvgTempGS + PrevAvgPrecipGS + AvgTempGS*PrevAvgPrecipGS	122.7	5
		AvgTempGS + PrevAvgPrecipGS + MaxTempMay + AvgTempGS*PrevAvgPrecipGS + MaxTempMay*PrevAvgPrecipGS	126.7	7
CG All	1949 - 2017	AvgTempGS + AvgPrecipGS + AvgTempGS*AvgPrecipGS	-18.9	5
		AvgTempGS + AvgPrecipGS + MaxTempMay + AvgTempGS*AvgPrecipGS + MaxTempMay*AvgPrecipGS	-20.7	7
		AvgTempGS + PrevAvgPrecipGS + AvgTempGS*PrevAvgPrecipGS	-17.0	5
CGP	1931 - 2017	AvgTempGS + AvgPrecipGS + AvgTempGS*AvgPrecipGS	NA	NA
CGP	1949 - 2017	AvgTempGS + AvgPrecipGS + MaxTempMay + AvgTempGS*AvgPrecipGS + MaxTempMay*AvgPrecipGS	NA	NA
CGG	1896 - 2017	AvgTempGS + AvgPrecipGS + MaxTempMay + AvgTempGS*AvgPrecipGS + MaxTempMay*AvgPrecipGS	117.3	7
		AvgTempGS + PrevAvgPrecipGS + AvgTempGS*PrevAvgPrecipGS	113.7	5
		AvgTempGS + PrevAvgPrecipGS + MaxTempMay + AvgTempGS*PrevAvgPrecipGS + MaxTempMay*PrevAvgPrecipGS	115.9	7
OH All	1896 - 2017	AvgTempGS + AvgPrecipGS + AvgTempGS*AvgPrecipGS	66.1	5
		AvgTempGS + AvgPrecipGS + MaxTempMay + AvgTempGS*AvgPrecipGS + MaxTempMay*AvgPrecipGS	69.8	7
		AvgTempGS + PrevAvgPrecipGS + AvgTempGS*PrevAvgPrecipGS	70.4	5
OH All	1949 - 2017	AvgTempGS + AvgPrecipGS + AvgTempGS*AvgPrecipGS	-50.8	5
		AvgTempGS + AvgPrecipGS + MaxTempMay + AvgTempGS*AvgPrecipGS + MaxTempMay*AvgPrecipGS	-49.7	7
		AvgTempGS + PrevAvgPrecipGS + AvgTempGS*PrevAvgPrecipGS	-45.2	5

CG All = Including trees from both CGP and CGG subpopulations; CGP = Picnic subpopulation at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio; CGG = Gorge subpopulation at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio; OH All = Including trees from both Clifton Gorge State Nature Preserve and Cantwell Cliffs, Ohio; AvgTempGS = Average temperature for the growing season (April – June) of each year; AvgPrecipGS = Average precipitation for the growing season of each year; MaxTempMay = Maximum temperature in May of each Year; PrevAvgPrecipGS = Average precipitation for the growing season of the previous year; * = Interactive effect of two independent variables

Table 2 – Significant Linear Models to Predict Average Yearly Ring Width of Eastern Hemlock Trees at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio and across all Ohio Sites – Summary of Model Coefficients

Site	Years	Model p-Value	Multiple R-Squared	Adjusted R-Squared	Independent Variables in Best-Fit Model	Coefficient	Coefficient p-Value
CG All	1896 - 2017	0.004976	0.1028	0.07995	AvgTempGS	0.135565	0.1877
					Avg PrecipGS	0.918149	0.0846
					AvgTempGS*AvgPrecipGS	-0.01469	0.0971
CG All	1949 - 2017	0.01069	0.2067	0.1437	AvgTempGS	0.131643	0.1941
					AvgPrecipGS	0.5171	0.1634
					MaxTempMay	-0.05357	0.1928
					AvgTempGS*AvgPrecipGS	-0.01549	0.068
					MaxTempMay*AvgPrecipGS	0.006081	0.0935
CGP	1931 - 2017	0.0512	0.08877	0.05584	AvgTempGS	0.24144	0.1406
					AvgPrecipGS	1.48942	0.0695
					AvgTempGS*AvgPrecipGS	-0.02417	0.0757
CGP	1949 - 2017	0.02803	0.1769	0.1115	AvgTempGS	0.185399	0.1462
					AvgPrecipGS	0.672375	0.1494
					MaxTempMay	-0.077	0.1371
					AvgTempGS*AvgPrecipGS	-0.02087	0.0507
					MaxTempMay*AvgPrecipGS	0.008393	0.066
CGG	1896 - 2017	0.01258	0.08748	0.06428	AvgTempGS	0.017406	0.806
					PrevAvgPrecipGS	0.396616	0.294
					AvgTempGS*PrevAvgPrecipGS	-0.00612	0.334
OH All	1896 - 2017	0.008449	0.09409	0.07106	AvgTempGS	0.134063	0.1027
					AvgPrecipGS	0.873858	0.0399
					AvgTempGS*AvgPrecipGS	-0.0142	0.0448
OH All	1949 - 2017	0.00293	0.1922	0.155	AvgTempGS	0.074015	0.2033
					AvgPrecipGS	0.564078	0.0538
					AvgTempGS*AvgPrecipGS	-0.00915	0.0585

CG All = Including trees from both CGP and CGG subpopulations; CGP = Picnic subpopulation at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio; CGG = Gorge subpopulation at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio; OH All = Including trees from both Clifton Gorge State Nature Preserve and Cantwell Cliffs, Ohio; AvgTempGS = Average temperature for the growing season (April – June) of each year; AvgPrecipGS = Average precipitation for the growing season of each year; MaxTempMay = Maximum temperature in May of each Year; PrevAvgPrecipGS = Average precipitation for the growing season of the previous year; * = Interactive effect of two independent variables

AVERAGE ANNUAL RING WIDTH BY SITE

The average yearly ring width vector in each t-test for which release events were included consisted of only years for which at least one tree at each site had available core data. Thus, the site with the younger oldest tree provided the limiting data set. Comparisons between Cantwell Cliffs and either all of Clifton Gorge or the gorge subpopulation at Clifton Gorge consisted of average yearly ring width for 1898 through 2017, with the year-limiting data set attributed to Cantwell Cliffs. Comparisons between the picnic subpopulation at Clifton Gorge and either Cantwell Cliffs or the gorge subpopulation at Clifton Gorge consisted of average yearly ring width for 1931 through 2017, with the year-limiting data set attributed to the picnic subpopulation at Clifton Gorge. The average yearly ring width vector in each t-test for which release events were excluded consisted of only years for which neither site was undergoing a release event. These time periods were 1949 through 2017 for Cantwell Cliffs against Clifton Gorge overall, 1949 through 2017 for Cantwell Cliffs against the picnic subpopulation at Clifton Gorge, 1941 through 2017 for Cantwell Cliffs against the gorge subpopulation at Clifton Gorge, and 1949 through 2017 for the Clifton Gorge subpopulations against one another.

Overall average yearly ring width varied significantly across all sites compared. When release events were removed from the analysis, all tests became more significant with increased t-statistics except for the comparison between CG picnic and CG gorge subpopulations (Table 3). Average ring width at CC was always found to be greater than average ring width at CG, either overall or relative to each subpopulation individually. The CG picnic subpopulation was always found to have greater average ring width than the gorge subpopulation.

Table 3 – Differences in Grand Ring Width Average between Sites – Summary of t-Test Results

Site x	Site y	Release Events	Grand Ring Width Average (mm) - Site x	Grand Ring Width Average (mm) - Site y	t	df	p
CC	CG	Included	1.57 ± 0.52	1.42 ± 0.40	2.54	223.38	0.01
CC	CGP	Included	1.66 ± 0.37	1.49 ± 0.53	2.44	152.37	0.02
CC	CGG	Included	1.57 ± 0.52	1.12 ± 0.39	7.53	218.61	1.34e-12
CGP	CGG	Included	1.49 ± 0.53	0.98 ± 0.25	8.00	126.65	6.87e-13
CC	CG	Excluded	1.59 ± 0.27	1.29 ± 0.21	7.27	129.18	3.00e-11
CC	CGP	Excluded	1.59 ± 0.26	1.29 ± 0.22	6.46	135.92	1.69e-09
CC	CGG	Excluded	1.57 ± 0.26	1.01 ± 0.26	13.45	152.00	2.20e-16
CGP	CGG	Excluded	1.29 ± 0.26	1.00 ± 0.26	6.57	135.96	1.01e-09

CC = Cantwell Cliffs, Rockbridge, Ohio; CG = Clifton Gorge State Nature Preserve, Yellow Springs, Ohio; CGP = Picnic subpopulation at Clifton Gorge; CGG = Gorge subpopulation at Clifton Gorge

CUTTINGS FAILURE

By the end of summer 2017, all cuttings had died either due to desiccation and needle abscission or root rot. This loss of data prevented any statistical analyses for the cuttings objective, and the loss of the specimens themselves prevented completion of the intended HWA-resistance trials.

IV. DISCUSSION

To predict future threats, I assessed the status of a small, disjunct, and geographically isolated population of eastern hemlock trees at Clifton Gorge State Nature Preserve (CG) in Yellow Springs, Ohio. The establishment of the population in the gorge is believed to have resulted from the shifting of the range of the species as glaciers advanced and the formation the gorge as glaciers receded. The moist, shaded, and “refrigerated” microclimate of the gorge would have allowed the trees to survive even after the favorable effect of the glacier on local climate had long dissipated (Delcourt *et al.*, 1983). Previously, little was known about the number of individuals in the population, their health and reproductive capacity, or their size and age distributions. The incidence of hemlock woolly adelgid (HWA) in the population had not yet been systematically examined. Observations of the population at this site indicate that it consists of two distinct subpopulations – one at Clifton Gorge State Nature Preserve and one at John Bryan State Park – each with their own size distributions and reproductive outlooks. The use of dendrochronology has revealed that the CG population over all as well as each subpopulation individually has experienced a significant decrease in average annual ring width over time. This decline in average annual ring width over time is not apparent in a comparative population from the contiguous range of hemlock at Cantwell Cliffs (CC), Rockbridge, Ohio, where an insignificant but slight increase in ring width was observed over time. Clear differences between sites in environmental characteristics and health metrics were also observed.

SITE CHARACTERISTICS AND DEMOGRAPHY

Individuals at the CC site grow on steeper slopes and in thicker leaf litter overall than individuals at CG. These ratings and the higher needle content in leaf litter at CC suggest that this site is more characteristic of the microenvironments common in hemlock-dominated stands (Goerlich and Nyland, 2000). However, individuals at CC were rated to be less healthy overall than individuals at CG. This might seem to contradict the commonly held belief that habitat within the contiguous range of a species is typically more favorable with greater provision of resources, thus enabling increased fitness (Kincaid and Parker, 2008; Kessell, 1979). While the favorability of the site is not clearly reflected in the health rating for individuals, which considers only the outward appearance of the tree at the time of survey and does not fully capture their performance, favorability does seem to be supported by the slight positive trend in annual ring width and the significantly greater grand ring width average at this site. The site at Cantwell Cliffs is far more densely populated than the Clifton Gorge site, likely reflecting site favorability, and this increased competition for resources such as light may contribute to decreased health ratings in these individuals. The high abundance of young, healthy seedlings at CG may also skew the health ratings for that site toward a higher overall score, as individuals in a similar size class were not only entirely absent from the CC location, possibility due to the thick mixed leaf litter (Rooney *et al.*, 2000), but also would have been excluded from the sample due to the selection of only individuals greater than 10 cm DBH for coring. It is important to note, however, that individuals sampled at Cantwell Cliffs were in close proximity to a highway at the edge of the population. It is possible that edge effects in combination with increased competition contribute to decreased health ratings at CC relative to CG despite increased annual ring width over time.

While the area surrounding the gorge subpopulation at CG has many sheer cliffs and steep slopes, individuals in the gorge subpopulation grow on shallower slopes and in thinner leaf litter than individuals in the picnic subpopulation and score lower for health. At the gorge subpopulation site, hemlock trees are commonly found growing on or around large, relatively flat rocks and on mostly level areas along the riparian zone or a short distance from the cliff edge. It is possible that the shallower slope and differences in slope aspect and/or configuration at the gorge population site contribute to reduced soil moisture, thus decreasing health and grand ring width average relative to the picnic subpopulation (Parker, 1982; Avery *et al.*, 1940). The observation of thinner leaf litter for the gorge subpopulation may explain, in part, the greater number of seedlings in the gorge subpopulation relative to the picnic subpopulation, as leaf litter is a major obstacle to germination in eastern hemlock (Olson *et al.*, 1959; Rooney *et al.*, 2000).

The gorge subpopulation at CG is overly represented by seedlings in the smallest size category. Nearly all the seedlings were found within a floodplain on the gorge floor, which is consistent with the greater number of large, reproductive individuals in the gorge relative to the cliff edge and the significantly larger number of seeds caught by boxes on the gorge floor relative to the cliff ledge above. Periodic flooding keeps the floodplain area mostly free of leaf litter and continuously moist, two requirements of eastern hemlock seed germination and subsequent seedling success that are not as readily available along the cliff edge. The picnic subpopulation has no individuals in either of the two smallest size categories despite having a similar number of cone-bearing individuals as the gorge subpopulation. This might be attributed in part to the thicker mixed deciduous-coniferous leaf litter at the picnic subpopulation preventing germination and seedling survival. Another explanation might be increased accessibility of the site to whitetail deer compared to the gorge subpopulation. Topography at the picnic subpopulation has fewer loose rocks, steep cliffs, and narrow passes that may contribute to the exclusion of deer from areas in the gorge subpopulation. In the 1900s, deer were extirpated from Ohio. The average age of cored individuals in the picnic subpopulation is 78 years. This corresponds roughly with the deer restocking program in Ohio in the 1920s and 1930s and might help to explain how the existing trees could have germinated and grown relatively free of deer for some time, but now fail to recruit seedlings under the steady pressure of deer herbivory. The combined effect of increased deer browse with possibly reduced germination as the hardwood canopy has developed and produced more leaf litter over time may be responsible for the lack of small individuals in the current population. The characteristics of the gorge site or the trees located there are currently less favorable than those of the picnic subpopulation for supporting cone production but, at least in the floodplain area, the gorge site appears to be better at supporting seed germination and initial seedling growth. The picnic site also lacks exceptionally old individuals, either due to the inability of the site to support them or simply due to the relatively young age of the population.

The large gap in size class representation in the gorge subpopulation raises the question as to what factors prevent seedlings from advancing to the next life stage and eventually contributing to the sparsely-represented larger size classes. It is possible that the seedlings currently inhabiting the floodplain are the result of a massive reproductive event that has not occurred for many years and that these individuals will in fact survive to reach cone-bearing age. If we assume, however, that mature trees in the gorge area reproduce in this way every few years, it is possible that, like the picnic subpopulation, deer grazing contributes to the lack of recruitment. This is more likely the case for seedlings along the cliff ledge, where deer can easily access the site and browse on any individuals tall enough to emerge above the leaf litter. The descent to the lower flood plain where most seedlings are found is steep and winding, likely greatly reducing or even completely preventing deer grazing, especially during times when increased water volume would make crossing the river difficult. In the absence of deer herbivory, some other factor or combination of factors must be responsible. While periodic flooding might keep the soil continuously moist for germination and early seedling growth, perhaps the periodic submersion and constant wetness resulting from poor soil drainage is not ideal for seedlings after they have reached a certain size. After seedlings have grown to a size where desiccation is no longer an immediate threat, constant soil moisture might contribute to root rot and tissues damage (Kincaid and Parker, 2008). Periodic submersion might damage needles, causing reduced photosynthetic capacity and/or needle abscission. Periodic flooding might be responsible for washing away small, shallowly-rooted individuals growing in susceptible areas. It is also possible that the large gap in representation of small size classes in the gorge subpopulation is largely attributed to the episodic recruitment patterns characteristic of the species and that this reproductive unpredictability in combination with extremely variable substrates within the gorge and local variation in climate through time simply reduces the chance that all factors will align and allow individuals of this sensitive species to make it past 5 cm DBH (Myers *et al.*, 2015; Hett and Loucks, 1976).

DENDROCHRONOLOGY

When ring widths were plotted against time for all sites, it became apparent that ring width does not increase or decrease linearly over the entire time frame for which data is available. Instead, all sites displayed periods of drastically increased growth followed by drastic decreases in growth and a leveling off into a roughly linear trend. We consider these peaks in growth "release events", which correspond to the sudden and dramatic increases in one or more resources that quickly impacted ring width in these trees. In the case of the sites included in this study, sudden increases in light availability are the most likely contributor to the increased ring width observed during release events (Finzi and Canham, 2000). Due to the lack of information available about the historical land use at Cantwell Cliffs, it is difficult to speculate about what might have happened there to initiate the release events. It is possible, however, that release events in the Cantwell Cliffs population were related to hardwood and some conifer logging through the 1800s and into the early 1900s for building and for wood burning in a nearby iron furnace (Conway, 2018). Alternatively, it is possible that release events resulted from natural successional changes within the forest or from one of the many disturbance regimes commonly associated with edge habitats.

The detailed history of the hemlocks at Clifton Gorge is not well documented, but several key pieces of information seemingly connected to release events in the CG subpopulations are readily available. A series of mills along the river upstream of the Clifton Gorge hemlocks was built starting in the early 1800s. It is likely that some of the lumber used for the buildings came from trees growing in the gorge, opening the canopy and increasing light availability. The largest and closest of the mills to the CG gorge subpopulation was the four-story paper mill, which would have required a great deal of clearing and lumber preparation leading up to its construction and likely required local lumber for paper production. Additionally, one of the mills further upstream was a saw mill, which would have produced a sustained demand for local timber. The construction of this mill and the other mills along the Little Miami river corresponds well with the period determined to be a release event at the gorge subpopulation (1827 – 1848). While hemlock is not a preferred timber species, the use of eastern hemlock in the leather tanning industry during this period of history is well documented (Hergert, 1983). The oldest of the hemlocks at Clifton Gorge are found deep within the gorge or, in the case of one individual, growing off the side of the cliff into the opening above the river. These individuals would have been difficult and dangerous to harvest for either timber or bark tannins, which might explain why they were never felled.

The release event observed in the average ring width pattern of the CG picnic subpopulation took place from the first available ring width year, 1931, through 1948. This corresponds to the construction of the nearby shelter house by the Civilian

Conservation Corps in the 1930s. Across the parking lot from the shelter house and the picnic subpopulation is an old foundation with a large hemlock at each corner. There was some speculation as to whether these individuals were planted and subsequently seeded the group of individuals behind the shelter, but it would seem as though the shelter individuals are not the offspring of one or both of the foundation trees. For this to have been the case, at least one of the individuals by the foundation would have had to reach cone-bearing age (approximately 15 years in vigorous individuals) and spread seed to the shelter area. Picnic individuals would therefore be at least 15 years younger than either of the foundation trees. The oldest individual in the picnic subpopulation (87 years) is near the shelter itself rather than by the foundation. It does not appear that the picnic population spread from one or more planted individuals near the shelter despite the age of the oldest individual roughly matching the time of shelter construction, as the distinct 15-year gap in age of individuals is not apparent by the shelter, either (several individuals aged late to mid-70s). What is more likely is that clearing of the area for construction of the shelter house and possibly the building that was reduced to a foundation across the parking lot increased light availability and allowed for the rapid growth of individuals that had already been struggling to grow in the area.

Following release events, ring width patterns for all sites settled into a less variable and roughly linear trend through time. It is the period following release during which canopy gaps closed and variables for which data were unavailable (*e.g.* light) remained more constant, allowing for more meaningful comparison of ring widths with climate conditions over time. As a species, eastern hemlock generally prefers cool to moderate temperatures and reliable moisture, especially in germination and early growth

(Goerlich and Nyland, 2000). It makes sense, then, that as average growing season temperature increases, average ring width across all sites decreases and that ring width increases with average growing season precipitation in the model predicting average annual ring width for all sampled individuals. These findings are consistent with past studies of ring width in eastern hemlock (Avery *et al.*, 1940; Kessell, 1979). Growing season precipitation was the single variable that most consistently predicted ring width. It would seem contradictory, then, that average growing season precipitation across Ohio was found to increase over time while average annual ring width decreased at all sites except Cantwell Cliffs. Since it is unlikely that precipitation has become so great in Ohio that mature trees are overwatered, the widespread and long-term decrease in ring width at Clifton Gorge despite increases in annual growing season precipitation can likely be attributed to the cumulative effect of increases in annual growing season temperature, the decrease in light availability as the hardwood canopy has developed, slight decreases in ring width as trees age, and other factors for which data was not collected outweighing the positive impact of precipitation on growth. This is supported by the significance or near significance of the negative interactive effect of growing season temperature with growing season precipitation in models to predict ring width in both the picnic subpopulation at CG and averaged across all individuals cored in this study. The nature of the increased precipitation over time might also come into play, with the rate of precipitation determining in part the ability of the soil and tree roots to absorb the moisture and the timing of the precipitation with temperature determining how fast the precipitation will evaporate and become unavailable for absorption.

The increased average annual ring width over time at Cantwell Cliffs despite increases in annual growing season temperature might be attributed to characteristics of the eastern hemlock microhabitat. Hemlocks at the CC site are far more numerous and in closer proximity to one another than individuals at CG. The increased production of needle litter and the resultant changes in pH might make the site more favorable for growth, outweighing the effect of increased temperature (Fenzi *et al*., 1998). It is also possible that the dense hemlock canopy and surrounding topography creates a more effective and absolute microclimate at CC relative to CG such that precipitation at CC is shaded and allowed longer to absorb into soil for utilization by the trees. This same microhabitat/microclimate effect might be part of the explanation for the larger average ring width observed at the picnic subpopulation at Clifton Gorge relative to the gorge subpopulation. It is important to note as well that climate data was averaged across the state of Ohio. Microenvironmental data collected at each location would help to better resolve the relationship of such variables with growth. It is possible that the site at Cantwell Cliffs gets more precipitation than is reflected in the averaged data and that this accounts at least in part for both increased ring width over time and greater average ring width overall at Cantwell Cliffs compared to Clifton Gorge.

OVERALL STATUS AND MANAGEMENT PLAN

The systematic treatment of all individuals in the Clifton Gorge population with HWA insecticide is feasible considering the low number of large individuals and the clustered nature of seedlings. The survey portion of this study did not find any HWA on any hemlocks either in the gorge or the picnic subpopulation, likely due to the provision of a geographic barrier by the gorge topography. The lack of HWA at the site and the longevity of imidacloprid applications strengthens the argument for preemptive treatment of all trees (Smitley and McCullough). Possible solutions to close the size gap in the gorge subpopulation and increase the number of reproductive individuals over time might include installation of seed beds and deer exclosures at the top of the gorge where deer have access and leaf litter is thicker. Seed box data suggests that seeds are distributed to the top of the gorge but that those seeds, which are less numerous than those reaching the gorge floor, either rarely establish or do not survive the seedling stage. Installation of fences around seedbeds would serve a dual purpose: to reduce leaf litter and make the ground more suitable for germination and to eliminate the possibility of deer eating any seedlings that were able to establish. Thinning of the hardwood canopy, while labor intensive and logistically challenging, would increase the availability of light at the gorge floor. Even small increases in light availability might increase growth and vitality, allowing seedlings in the floodplain to have increased resilience against flooding and other challenges (Singer and Lorimer, 1997). The increased light availability might also increase the rate of evaporation and decrease the likelihood of root rot in seedlings. Canopy thinning might have some negative consequences, however. Invasive species such as honeysuckle and burning bush, both of which are prevalent at the site, are also likely to take advantage of the increase in light, requiring that park managers develop a strategy to keep these species under control. The increased temperature and evaporation resulting from increased light might be detrimental to annual hemlock growth despite possibly improving conditions for the survival of floodplain seedlings (Avery, 1940). The success of a canopy thinning operation would require that these and other negative effects be outweighed by the ability of increased light to increase recruitment in the gorge subpopulation.

A similar management plan including treatment of all individuals with HWA insecticide, installation of deer exclosures and seed beds, and thinning of the hardwood canopy would likely benefit the picnic subpopulation at CG for the same reasons.

While the population at Cantwell Cliffs scored lower for health, the vast number of individuals in the population shields it from some degree of risk. Increased average annual ring width over time suggests that the outlook of existing mature trees is good. The identification of hemlock woolly adelgid at the site following my survey in 2017, during which I found no instances of the insect on the individuals cored in this study, however, significantly decreases both the likelihood of future success for the population and the effectiveness of any management plan that might be put into place. The large size of the population and the existing HWA presence there are arguments against treatment of all individuals with insecticide. The selective treatment of healthy, cone-bearing individuals might allow the population to persist even after HWA has killed untreated individuals.

V. CONCLUSION

Variation in environmental characteristics, health, and average annual ring width were found between eastern hemlock at Clifton Gorge State Nature Preserve, Yellow Springs, Ohio and a comparative site within the contiguous range of the species at Cantwell Cliffs, Rockbridge, Ohio. Variation in these factors was also present between two subpopulations at Clifton Gorge. Individuals at Cantwell Cliffs tend to grow on steeper slopes and in thicker leaf litter than individuals at Clifton Gorge. Despite an outward appearance of reduced health at CC, larger grand ring width average and slight positive increases in annual ring width through time indicate that this site from the contiguous range of the species is more favorable for growth than the site at Clifton Gorge.

Of the two subpopulations at Clifton Gorge, the picnic subpopulation is the most similar to the Cantwell Cliffs site with individuals growing on steeper slopes and in thicker leaf litter. Picnic individuals score higher for health than gorge individuals and have a larger grand ring width average. Both subpopulations exhibit decreased average annual ring width over time, however, with average growing season temperature, average growing season precipitation, and the interactive effect of the two being the most likely predictors of this trend.

The CG population is viable but at risk due to low number of individuals and the complex effect of regional and local climate, disturbance history, and stand dynamics on this population and the species in general (Myers *et al*., 2015). The major threats to the population include reduced reproduction, reduced tree growth and changes in the microclimate of the gorge in response to increasing temperature (Avery, 1940), reduced recruitment due to deer herbivory, and hemlock woolly adelgid-associated mortality if the insect reaches the gorge. Implementation of a management plan with aims to increase germination and seedling recruitment and to prevent HWA-infestation has a much higher likelihood of success given the current HWA-free status at the site.

As is the case with many threatened populations, the trajectory of the Clifton Gorge hemlock population is difficult to project. Only the continued study of and interaction with this population will reveal its usefulness to the scientific community, possibly as a source of rare alleles for HWA-resistance, a comparative site for the continued study of disjunct populations and their unique characteristics relative to contiguous populations, or as an example of successful eastern hemlock management.

For those who have grown up enjoying the distinctive beauty of the hemlocks, the slow extinction of the population from the Clifton Gorge site would mean more than simply the loss of biodiversity. The Clifton Gorge site contributes to quality of life and offers a break from the industrialized world we live in. Failure to characterize and protect this population might result in the loss of countless opportunities for ecologists as well as the loss of a beautiful piece of natural history.

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