Southeastern Ohio Hemlock Stands Prior to Hemlock Woolly Adelgid Infestation: Baseline Conditions from 2 Surveys a Decade Apart

JORDAN K. KNISELY and JAMES M. DYER[1], Ohio University, Athens, OH, USA.

ABSTRACT. The Hocking Hills of southeastern Ohio are situated at the western range boundary of eastern hemlock, where this foundation species occurs in isolated pockets in ravines and on steep slopes. The goal of this study is to characterize these hemlock stands prior to infestation by hemlock woolly adelgid (HWA), which recently entered the state and is likely to cause high mortality if untreated. Individuals in 30 plots established from 2008 to 2011 were resurveyed in 2020, allowing determination of growth rates and mortality rates. Each plot was paired with an upslope transect in the resurvey to record non-hemlock species likely to seed in from above. Tree species diversity in the plots is low (Shannon H′ < 1), as eastern hemlock remained the dominant species in all plots; storm damage and competitive thinning appeared to account for most mortality across all species. Hemlock growth rates were comparable to deciduous species. Common co-occurring species are statistically associated with particular topographic and soil properties on the plots. Following future hemlock mortality, tulip-poplar, chestnut oak, white oak, sweet birch, and red maple may be among the first species to dominate the canopy; Japanese stiltgrass currently appears to be the invasive species of greatest concern. An understanding of pre-HWA composition, structure, and forest dynamics can inform restoration efforts, if in the future long-term, sustainable HWA control or host-tree resistance is developed; this understanding can also apprise management and conservation efforts in the unique hemlock stands of southeast Ohio.

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INTRODUCTION

Eastern hemlock (*Tsuga canadensis*) is the most shade-tolerant tree species in the eastern deciduous forest (Godman and Lancaster 1990). This long-lived evergreen occurs across the Appalachian Mountains and the northern hardwoods region of the United States into southern Canada, where it often grows in dense stands and dominates the canopy. The dense growth and high leaf area index of eastern hemlock create shaded, cool, and, moist conditions perpetuating its dominance, while inhibiting other tree species and lowering the density and diversity of understory herbs (Rogers 1980). Owing to the distinctive microclimate and unique habitat associated with it, eastern hemlock is considered a foundation species (i.e., a plentiful species which changes or stabilizes local conditions, often providing habitat for other species in the process) (Ellison et al. 2005). Eastern hemlock exerts strong control on the abundance and diversity of numerous organisms including soil fungi (Fassler et al. 2019), aquatic and amphibious species (Snyder et al. 2002; Ross et al. 2003), and migratory birds (Tingley et al. 2002). The loss of this foundation species would have profound and wide-reaching ecological effects.

Hemlock woolly adelgid (HWA) (*Adelges tsugae*) is an invasive aphid-like insect causing widespread hemlock mortality in the eastern United States. First reported in Virginia in 1951, HWA has spread throughout much of the native range of both eastern hemlock and Carolina hemlock (*Tsuga caroliniana*) of the central and southern Appalachian Mountains. Deriving its common name from its woolly ovisac, HWA reproduces parthenogenetically and biannually in eastern North America. It infests hemlock trees of any size, feeding on the xylem cells at the base of the needles, which disrupts photosynthesis, causes nutrient deficiencies, and leads to needle loss (Williams et al. 2016). HWA has also been shown to induce water stress and negatively impact the tree's carbon balance, potentially leading to carbon starvation (Brantley et al. 2017). Mortality can occur in as little as 4 years (McClure 1991),

[1] Address correspondence to James M. Dyer, Department of Geography, Ohio University, Athens, OH 45701, USA. Email: dyer@ohio.edu

although resistance has been demonstrated in a few trees (Kinahan et al. 2020). The use of insecticides and the release of predatory beetles has provided effective protection against infestation in certain locations and at localized scales (Sumpter et al. 2018). However, without the implementation of such control measures, high mortality is a likely outcome for infested hemlock stands.

The severe decline of eastern hemlock across much of its range has begun a transition toward forests dominated by other species in many affected areas. Non-hemlock species already present in the canopy are among the first to dominate stands following decline and mortality of hemlocks. For example, 12 years after the arrival of HWA in Connecticut, Orwig and Foster (1998) noted that hemlock mortality had resulted in a shift toward canopy dominance by sweet birch (*Betula lenta*), red maple (*Acer rubrum*), and several species of oak (*Quercus* spp.). Of these, sweet birch and oak were already important in the overstory, with red maple increasing in importance in the understory as a result of gaps left by dead hemlock. An abundance of sweet birch was noted in declining hemlock stands in central Connecticut (Stadler et al. 2005), and an increase in sweet birch and yellow birch (*B. alleghaniensis*) was also observed in the Delaware Water Gap of Pennsylvania and New Jersey (Eschtruth et al. 2006). Post-HWA simulation modeling in Kentucky predicted a shift to oak dominance following hemlock mortality (Spaulding and Rieske 2010). Which species become dominant in the absence of eastern hemlock depends upon topographic and elevational variation within a forest. Twenty years after the arrival of HWA at Connecticut College Arboretum, an increase in the basal area of oak species including black oak (*Quercus velutina*), scarlet oak (*Q. coccinea*), and northern red oak (*Q. rubra*) was observed along dry ridge environments. In the more mesic valleys below, a mixture of hardwoods came to dominate the canopy, including yellow birch and American beech (*Fagus grandifolia*) in addition to the oak species (Small et al. 2005). Following a slow hemlock decline at lower elevations in the central Appalachian Mountains of Virginia and West Virginia, a transition to deciduous trees, particularly yellow birch, sweet birch, and beech was observed in the canopy (Martin and Goebel 2012). In the US Forest Service's Coweeta Hydrologic Laboratory in North Carolina, a shift toward a mixed deciduous forest dominated by yellow birch, red maple, and tulip-poplar (*Liriodendron tulipifera*) was observed on the lower slopes (Brantley et al. 2013). However, in riparian settings in the central and southern Appalachians, rosebay rhododendron (*Rhododendron maximum*) has increased in the understory, which can prevent the establishment of trees following hemlock decline (Martin and Goebel 2012; Brantley et al. 2013). These observations demonstrate that throughout the range of eastern hemlock, insights into post-HWA forest composition can be gleaned from an examination of the current composition of these forests.

Hemlock and HWA in Southeastern Ohio

Ohio is situated at the western edge of the range of eastern hemlock, with the eastern half of the state lying completely within its contiguous range (Fig. 1A). The habitat occupied within this area is very restricted. Hemlock forests occupy isolated pockets which, particularly in the unglaciated southeastern part of the state, occur in steep ravines and gorges with shallow soils (Fig. 1B). These stands are floristically distinct compared to more northern forests of New England and Canada, lacking trees with boreal affinities such as red pine (*Pinus resinosa*) and northern white-cedar (*Thuja occidentalis*) (Black and Mack 1976). These southeastern Ohio hemlock stands also differ considerably from higher elevation stands in the central and southern Appalachian Mountains, lacking rhododendron thickets and higher elevation red spruce (*Picea rubens*) communities (Martin and Goebel 2012; Brantley et al. 2013). In highly dissected southeastern Ohio, Martin and Goebel (2013) reported that eastern hemlock dominated all forest layers, and was most dominant in the overstory at the bottom of slopes, particularly near streams. At these settings it was often accompanied by beech, sweet birch, and tulip-poplar, with only tulip-poplar and beech representing more than 10% of the basal area. These species decreased upslope, while white oak (*Quercus alba*), chestnut oak (*Q. montana*), and red maple increased moving upslope.

HWA was first observed in southeastern Ohio in 2012 and has since spread to numerous counties. The Ohio Department of Natural Resources

(ODNR) employs an Integrated Pest Management (IPM) strategy, using systemic pesticides to treat eastern hemlock trees where infestations are discovered and to protect trees in areas of high ecological or economic value. The predatory beetles *Laricobius nigrinus* and *L. osakensis* are also being released at some sites as a biological control (ODNR 2017). While treatment and prevention efforts may prevent or delay mortality in select hemlock stands, eastern hemlock mortality and a subsequent response in the forest community will almost surely occur in untreated stands eventually. The isolated nature of Ohio's hemlock stands, combined with a species composition which differs from elsewhere in its range, make Ohio's hemlock forests unique. Furthermore, the fact that HWA has only recently entered the state provides an opportunity to study conditions in these forests just prior to the likely loss of many eastern hemlock. Ohio's hemlock stands remain understudied and many questions about them remain unanswered. The goal of this study is to expand the current understanding of these forests in southeastern Ohio's Hocking Hills region, a deeply dissected part of the unglaciated Allegheny Plateau (Hall 1951), where much of the state's hemlock forests can be found. By resampling plots established roughly a decade ago and sampling new transects in the non-hemlock forests above them, this study seeks to evaluate forest dynamics in isolated hemlock stands of southeastern Ohio. A primary motivation for conducting this research is

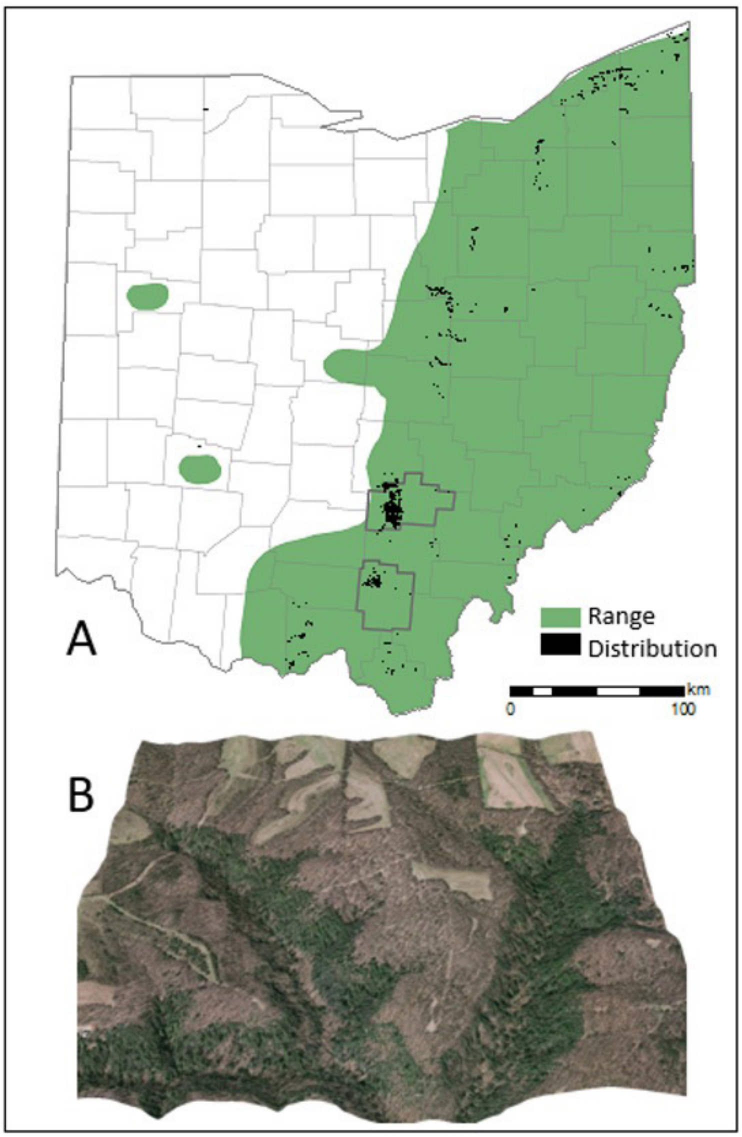

FIGURE 1. Eastern hemlock in Ohio. A: Range map within the state, and localized extent of the actual distribution. Boundaries of Hocking (north) and Jackson Counties, location of the study plots, are shown in heavy outline. B: Leaf-off image showing characteristic distribution of the evergreen hemlock in the Hocking Hills, situated in ravines and side slopes surrounded by a matrix of primarily deciduous mixed mesophytic forest. Distribution map and image from Stump (2008).

to provide references for restoration if long-term, sustainable control of HWA, such as biological control or host plant resistance, can be established in the future. Specifically, the study addresses the following research questions:

- What is the current composition and structure of hemlock forests throughout the Hocking Hills region of southeastern Ohio? Have these characteristics remained stable since initial surveys a decade prior?
- What are the growth rates and mortality rates within these hemlock stands over the past decade?
- What non-hemlock species currently dominate the canopy in and just outside of these hemlock stands? In other words, which species are in the best position to respond initially following HWA-induced mortality in the Hocking Hills, through growth release or through seed rain into canopy gaps?
- What invasive species are present that may potentially alter post-HWA succession in these forest communities?

METHODS AND MATERIALS

Study Area

Plots were established in the Hocking Hills region of Hocking and Jackson Counties in southeastern Ohio. The Black Hand Sandstone formation is a defining feature, resulting in high cliffs and narrow gorges; large boulders are often found beneath the sandstone cliffs. Hemlock stands occur in sheltered topographic positions, in ravines or on the sides of slopes (Fig. 1B). Numerous parks, preserves, and natural areas are located in the region, and study sites were located within these, or occasionally on adjacent public lands. Two or 3 plots were established in each sampled area. Sample plots were situated in hemlock-dominated stands, though the larger region falls within the Mesophytic forest region (Dyer 2006) characterized by high tree species diversity.

Vegetation Sampling

Thirty plots measuring 20 × 40 m (800 m^2) were initially established and surveyed from 2008 to 2011 to record baseline conditions in the hemlock stands of southeastern Ohio, before the arrival of HWA (Dyer unpublished; Stump 2008). Sampling occurred May to October. Candidate sites were first identified using GIS and located using GPS. The final plot locations were selected to be representative of the area, with mature hemlock dominating the canopy, and having uniform slope and aspect; plots were characteristically situated in ravines and adjacent slopes. To avoid edge effects, plots were established ≥100 m from roads or other canopy breaks. The initial corner was located randomly, and the plot established with the long axis parallel to slope. Plot corners were permanently marked with PVC pipe and rebar, and their GPS coordinates recorded. Trees and saplings in each of the 30 plots were resampled May to September 2020 in order to determine growth and mortality rates, as well as to assess the stability of composition and structure characteristics.

All trees ≥8 cm in diameter at breast height (DBH) (1.37 m) were identified by species and marked by nailing each with a numbered aluminum tag. During the initial survey and resurvey, DBH was recorded for each tree, as well as its canopy class (dominant, codominant, intermediate, suppressed). Eastern hemlock trees were assigned to 1 of 5 vigor classes based on percentage of remaining green foliage (1 to 5: >75%, 51 to 75%, 26 to 50%, 1 to 25%, dead). Additionally, all saplings (woody plants <8 cm in diameter and ≥1 m in height) were tallied by species in the initial survey and resurvey. Any saplings which had grown larger than this size category since the original surveys were tagged and measured as trees. Evidence of the presence of HWA was assessed in 2020 at all plots by inspecting the underside of hemlock lower branches for woolly ovisacs from the previous winter.

At the time of initial establishment, 8 seedling/herbaceous plots were censused within each of the 30 plots. Quadrats measuring 1 × 1 m were situated inside each corner of the 20 × 40 m plot, such that the permanently marked plot post served as a corner of the 1 × 1 m quadrats. Midpoints along each 20 × 40 m plot leg were marked out on the sampling date and served as the midpoint of the outside edge of the other four 1 × 1 m quadrats. In each quadrat, 1 of 7 cover classes (0 to 1%, 1 to 5%, 5 to 10%, 10 to 25%, 25 to 50%, 50 to 75%, >75%) was assigned to all vascular herbaceous species combined, as well as for individual herbaceous species and for bryophytes (which were not differentiated). Tree seedlings and other woody plants (<1 m) were tallied by species.

Also at the time of initial plot establishment, several measurements were taken to establish baseline environmental conditions, in addition to slope and aspect. These include estimates of stand age, soil conditions, and canopy cover. Two increment cores were extracted at a height of 1 m from 10 randomly selected trees on each plot and cross-dated in the lab after developing a list of marker years from inspecting several dozen cores (Speer 2010); this allowed an estimation of the minimum establishment age for each plot (no age adjustments were made to account for the 1 m coring height). Additionally, from 2 or 3 sites within each plot, composite soil samples were collected from the top 10 cm within a 0.5 m^2 area after removing the organic horizon. A minimum sample of 250 g was stored in a cooler, and analyzed for pH, percent carbon, percent nitrogen, and C:N ratio upon return from the field (Brookside Laboratories, New Bremen, Ohio). To quantify canopy cover, hemispheric photos were taken at 2 designated corners in each plot, and images were analyzed in the lab (WinSCANOPY™, Regent Instruments Inc., Quebec City, Quebec, Canada).

To capture microclimate and soil conditions beneath the dense hemlock canopy, data loggers were installed just outside of 6 plots when they were established, adjacent to an eastern hemlock tree; plot accessibility was a consideration in their selection. Relative humidity and temperature sensors were installed at a height of 0.5 m within a ventilated solar radiation shield (HOBO® Pro Series, Onset Computer Corporation®, Bourne, Massachusetts). Soil probes were inserted at 20 cm depth to record moisture (Decagon® ECH2O Soil Moisture Sensor EC-5) and temperature (Decagon ECT Soil Temperature Probe). Soil texture was determined by feel at the time of installation. Data loggers (Em50 or Em5b, Decagon Devices, Pullman, Washington) were mounted to the post of the solar radiation shield. Sensors recorded at 1-hour intervals for 2 to 4 years after installation.

Since hemlock stands are largely constrained to valley settings in this part of its range, 500 m^2 transects were established upslope of each plot in 2020 to identify species most likely to contribute to the seed rain following loss of eastern hemlock to HWA. Transects were placed at the boundary of the hemlock stand, where non-hemlock species outnumber hemlock. Transects measuring 10×50 m were demarcated with stakes and centered over the hemlock plots below, such that the long axes of the transect and plot were parallel. Within these transects, DBH and canopy class of all non-hemlock trees ≥8 cm in diameter were recorded. Since invasive species could play a role in shaping the post-HWA forest community, special attention was also given to their identification in or around both plots and transects, in addition to recording their percent cover within the herbaceous plots described previously. A supplemental material file is available online and includes raw data on tree and sapling data collected on both plots and transects, environmental data for the plots described above, as well as charts of air and soil temperatures within the hemlock stands.

Statistical Analysis

Descriptive statistics were calculated to establish baseline conditions in both plots and transects prior to HWA-induced mortality. A comparison of descriptive statistics from the 2020 survey with those from the survey a decade earlier provided an assessment of the stability of composition and structure over that time frame. For trees, relative density and dominance (basal area) were computed for each plot and transect; relative density was computed for saplings. These statistics were also computed across all sites combined during each sample period, as was relative frequency of occurrence for both trees and saplings. From these measurements, Importance Values (IV) for each species were computed by averaging relative density, dominance, and frequency for trees, and relative density and frequency for saplings. Additionally, these calculations were performed with a dataset in which hemlock had been removed, to more easily compare non-hemlock species in the plots versus the transects above. The Shannon diversity (H') index (Monk 1967) was also computed for each plot, for both survey periods.

To evaluate the degree of change within the plots, a t-test for dependent samples was performed (using Microsoft Excel® 2022) to determine if there was a difference in tree species richness, Shannon diversity (H'), or the number of individuals. This analysis was also performed on the number of hemlock trees and saplings between the 2 survey periods. The null hypothesis was no difference in these metrics in the initial survey vs. the 2020 survey. Cohen's d, which quantifies the magnitude of the standardized mean difference between the 2 surveys, was calculated as a measure of effect size (Cohen 1988).

G-tests (Sokal and Rohlf 1995) were performed to determine if individual non-hemlock species demonstrated an association with topography (slope, aspect) or soil properties (pH, percent carbon and nitrogen, C:N ratio) on a plot. Observed occurrences during the initial surveys were compared to expected values, based on the proportion of all trees occurring in a particular class. To minimize errors associated with small sample sizes, analysis was restricted to species that accounted for ≥2% of all trees.

Growth and mortality rates were calculated by comparing the 2020 resurvey data to that of the initial surveys in 2008 to 2011, and are included in the supplemental material file. Mortality rate was based on the number of individuals that died over the survey period, expressed as a percentage of the number of trees in the initial survey; this value was then annualized (using the average number of years between surveys for each species). Overall mortality rates were computed for each plot, as well as for each species across all 30 plots. For growth rates, basal area was computed from DBH measurements of the main stem recorded in both surveys, and basal area increment (BAI) for each tree calculated as a percent change since the initial survey. By dividing BAI by the number of years between surveys, growth rate for each tree was expressed as an average annual increment over the survey period. Pearson product-moment correlation was performed (using SAS® v. 9.4) to determine if growth rates on a plot were linked to mortality, which could open the canopy and result in a growth release for the remaining individuals. For each species, average growth rate on a plot was correlated with the overall mortality rate for the plot. Finally, size-class histograms were created for species representing ≥3% of total trees, to characterize forest structure and to infer age distributions.

RESULTS

Plot Characteristics

The hemlock stands of the Hocking Hills can be considered second-growth forests; the minimum establishment year for the oldest tree on each plot was between 1860 to 1900 for the majority of plots, with 1769 as the earliest year and 1923 as the latest. Average slope of the 30 plots was 20°, ranging from 7 to 31°. Just under half were located on northwest-facing slopes, with the fewest number (3 plots) on southeast-facing slopes. pH of the upper 10 cm of the soil averaged 4.5 across the 30 plots, ranging from 4.0 to 5.6. Soils had an average of 2.36% total carbon, 0.13% total nitrogen, and 19.33 C:N among plots. Average canopy cover based on hemispheric imagery was 91%. This dense canopy cover mediated temperatures throughout the day. Compared to temperature recorded at Zaleski, Ohio, the nearest weather station to the 6 data loggers, approximately 25 km southeast of the majority of plots (Menne et al. 2012), the average daily maximum temperature recorded in the hemlock stands was 3.4 °C cooler. Differences were more pronounced in the summer; from the March equinox to the September equinox maximum temperatures were 3.9 °C cooler compared to the Zaleski weather station. In the other half of the year ("winter") the average daily maximum temperature was 2.9 °C cooler under the hemlock canopy. Soil temperatures demonstrated a more muted oscillation throughout the year, lagging behind air temperature. Minimum temperatures occurred in March (about 4 °C), and reached a maximum in August to September (about 18 °C). Volumetric water content exhibited pronounced and consistent variation between the 6 logger sites, 4 of which had a sandy clay loam texture and 2 were clay loam. A characteristic "growing season" pattern emerged among all sites, with lowest values recorded in late summer into fall, and highest values in the early spring.

Tree seedlings were rare in the plots, based on tallies within the eight, 1 × 1 m quadrats c. 2010. Red maple was the most abundant and occurred on a majority of plots, averaging 44 seedlings within the 8 quadrats. Beech was the next most frequently encountered tree seedling, but occurred on less than a third of the plots averaging only 5 seedlings. The majority of sampled plots had

<5% cover of herbaceous vascular plants when they were established. Higher cover values were attributable to the presence of ferns (notably Christmas fern (*Polystichum acrostichoides*) and wood fern (*Dryopteris* spp.)). Aside from ferns, only a few vascular herbs were observed on multiple plots, notably partridgeberry (*Mitchella repens*), Solomon's seal (*Polygonatum biflorum*), Indian cucumber (*Medeola virginiana*), and Canada mayflower (*Maianthemum canadense*). Mosses were present on the majority of sites.

The majority of hemlock trees were in the suppressed canopy class in both surveys, with a mean vigor class value of around 2 (51 to 75% remaining green foliage cover). Mean vigor successively improved with the intermediate and dominant/codominant classes (Table 1). Table 2 presents density values for the other common species, by canopy class. In the 2020 survey, a decade after initial surveys, 2 hemlock saplings were recruited into the tree category, and 114 hemlock trees had died; the majority of these were in the suppressed class (Table 3). The number of hemlock trees decreased in 27 of 30 plots, resulting in a significant decrease per plot from c. 2010 ($\overline{x}$ = 29.2, s = 11.1) to 2020 ($\overline{x}$ = 25.5, s = 9.9); t(29) = -7.1, p < 0.001. The effect size, as measured by Cohen's d, was d = 1.29, indicating a large effect. Among all other species, there was no recruitment from the 2010 sapling category, and 48 trees died (31 were in the suppressed class). This mortality resulted in a significant decrease in the number of total trees per plot from c. 2010 ($\overline{x}$ = 42.2, s = 12.6) to 2020 ($\overline{x}$ = 36.8, s = 11.4); t(29) = -9.1, p < 0.001. The effect size, as measured by Cohen's d, was d = 0.44, indicating a small effect. Eight plots experienced mortality of the sole individual of a tree species on that plot (in one case, 2 individuals), such that mean plot richness declined significantly from c. 2010 ($\overline{x}$ = 5.8, s = 1.9) to 2020 ($\overline{x}$ = 5.4, s = 1.6); t(29) = -2.8, p = 0.008, though the effect was small: Cohen's d = 0.23.

Average Shannon diversity for trees was low for both time periods and did not change significantly between c. 2010 ($\overline{x}$ = 0.98, s = 0.32) and 2020 ($\overline{x}$ = 0.95, s = 0.31); t(29) = -1.5, p = 0.15.

Baseline Composition and Structure of Hemlock Stands

Despite some mortality, hemlock remains by far the dominant species in all plots as it was in the initial surveys (c. 2010 Importance Value = 47.4) (Table 4). Although no other species in the plots compares to it in terms of abundance or basal area, a small number of deciduous species stand out as common non-hemlock components of the community. These include tulip-poplar (IV = 7.2), chestnut oak (IV = 6.9), white oak (IV = 6.4), red maple (IV = 6.2), and sweet birch (IV = 5.7; all values from c. 2010). Sourwood (*Oxydendrum arboreum*) (IV = 4.0), although not particularly significant in terms of basal area, is a common sight in the understory across the study area (43% frequency of occurrence). This is the same frequency as beech (IV = 4.6), though beech occurs in lower densities. Total basal area per plot averaged 48.7 m^2/ha c. 2010, and 49.6 m^2/ha in 2020.

Size-class analysis reveals a reverse-J curve for eastern hemlock, indicating continuous recruitment as well as canopy dominance; a decrease in the smallest size class is evident between the 2 surveys (Fig. 2A). Size-class graphs for important deciduous species are displayed in Fig. 2B. To allow direct comparison with transect data, size-class graphs are based on 2020 surveys. Red maple and sweet birch are most numerous in the smaller size classes, while tulip-poplar, white oak, and chestnut oak are overrepresented in the larger size classes.

In the sapling size class (<8 cm DBH), eastern hemlock occurred on ≥90% of plots in both surveys (Table 5). In addition to its high frequency, hemlock also occurred in the highest density.

However, 21 of 28 plots experienced a decrease in the number of hemlock saplings, and their overall density decreased in 2020 (Table 5). The decrease in the number of hemlock saplings per plot was significant from c. 2010 ($\overline{x}$ = 26.0, s = 28.7) to 2020 ($\overline{x}$ = 14.5, s = 13.7); t(27) = -3.4, p = 0.002. The effect size, as measured by Cohen's d, was d = 0.65, indicating a moderate to large effect. Beech was the next most frequently occurring sapling, occurring on about a third of plots. Its great increase in density in 2020 was inflated by 50 saplings tallied on a single plot. Spicebush (*Lindera benzoin*)

Table 1
Density of hemlock trees (≥8 cm DBH) surveyed c. 2010 and 2020 across 30 plots, by canopy class. For each canopy class, mean vigor class is presented with standard error of the mean (SEM). Vigor class ranges from 1-5 and is based on percentage of remaining green foliage (see text for details).

	c. 2010			2020		
Canopy class	**t/ha**	**Mean vigor**	**SEM**	**t/ha**	**Mean vigor**	**SEM**
Dominant/codominant	10.4	1.36	0.13	32.5	1.42	0.08
Intermediate	91.7	1.41	0.04	106.3	1.68	0.05
Suppressed	263.3	2.07	0.04	180.0	2.21	0.05

Table 2
Absolute density (t/ha) by canopy class, for non-hemlock trees surveyed c. 2010 and 2020 across thirty, 20 x 40 m plots. Species represent ≥2% of total trees sampled, listed in order of 2010 Importance Value (see Table 4).

	c. 2010			2020		
Common name	**Dom/codom[a]**	**Interm[b]**	**Suppressed**	**Dom/codom[a]**	**Interm[b]**	**Suppressed**
Tulip-poplar	7.1	11.7	4.2	11.3	7.9	2.1
Chestnut oak	5.0	17.5	1.3	10.0	12.9	0.8
White oak	5.8	9.6	1.7	9.2	5.8	0.0
Red maple	1.3	7.1	11.7	2.9	5.8	7.9
Sweet birch	0.4	17.5	6.3	5.8	14.2	1.7
American beech	1.7	5.4	3.3	4.6	3.3	2.1
Sourwood	0.0	2.1	15.4	0.0	4.6	8.3

[a] Dom/codom = combined dominant/codominant classes; [b] Interm = intermediate.

Table 3
Changes in the number of hemlock by canopy class in the 2020 resurvey compared to initial survey c. 2010

	c. 2010	2020			
Canopy class	**n**	**Dom/codom**	**Intermediate**	**Suppressed[a]**	**Dead**
Dominant/codominant	**25**	**20**	0	1	4
Intermediate	**220**	48	**158**	2	12
Suppressed	**632**	10	97	**427**	98

[a] Two c. 2010 saplings entered the 2020 suppressed tree class.

Table 4
Summary statistics for trees (≥8 cm DBH) surveyed c. 2010 and 2020 across 30 plots, sorted by 2010 Importance Value

Scientific name	Common name	Absolute density (t/ha)		Relative density (%)		Relative dominance (%)		Relative frequency (%)		Importance Value	
		c. 2010	2020	c. 2010	2020	c. 2010	2020	c. 2010	2020	c. 2010	2020
Tsuga canadensis	Eastern hemlock	365.4	318.8	69.3	69.2	55.5	55.1	17.3	18.6	47.4	47.7
Liriodendron tulipifera	Tulip-poplar	22.9	21.3	4.3	4.6	9.1	9.8	8.1	8.1	7.2	7.5
Quercus montana	Chestnut oak	23.8	23.8	4.5	5.2	7.6	8.4	8.7	9.3	6.9	7.6
Quercus alba	White oak	16.7	15.0	3.2	3.3	7.8	7.9	8.1	8.7	6.4	6.6
Acer rubrum	Red maple	20.0	16.7	3.8	3.6	3.2	3.0	11.6	11.8	6.2	6.1
Betula lenta	Sweet birch	24.6	21.7	4.7	4.7	4.2	4.0	8.1	8.1	5.7	5.6
Fagus grandifolia	American beech	10.4	10.0	2.0	2.2	4.3	4.5	7.5	7.5	4.6	4.7
Oxydendrum arboreum	Sourwood	17.5	13.3	3.3	2.9	1.3	1.2	7.5	8.1	4.0	4.1
Quercus rubra	Northern red oak	4.2	4.2	0.8	0.9	2.4	2.6	4.6	5.0	2.6	2.8
Acer saccharum	Sugar maple	9.6	7.1	1.8	1.5	1.0	0.8	4.6	3.7	2.5	2.0
Nyssa sylvatica	Blackgum	2.5	1.7	0.5	0.4	0.5	0.3	3.5	2.5	1.5	1.1
Carya glabra	Pignut hickory	2.5	2.5	0.5	0.5	0.7	0.8	2.9	3.1	1.4	1.5
Quercus coccinea	Scarlet oak	2.5	2.1	0.5	0.5	1.0	0.7	1.7	1.9	1.1	1.0
Quercus velutina	Black oak	1.3	1.3	0.2	0.3	0.5	0.5	1.7	1.9	0.8	0.9
Fraxinus pennsylvanica	Green ash	0.8	0.4	0.2	0.1	0.4	0.3	1.2	0.6	0.6	0.3
Carya laciniosa	Shellbark hickory	1.3	0.8	0.2	0.2	0.1	0.1	1.2	1.2	0.5	0.5
Carya cordiformis	Bitternut hickory[a]	0.4	0	0.1	0	0.2	0	0.6	0	0.3	0
Prunus serotina	Black cherry[a]	0.4	0	0.1	0	0.0	0	0.6	0	0.2	0
Ostrya virginiana	Hophornbeam[a]	0.4	0	0.1	0	0.0	0	0.6	0	0.2	0
	TOTAL	527.1	460.4								

[a] Single trees surveyed c. 2010 which were no longer living in 2020: bitternut hickory, hophornbeam, black cherry.

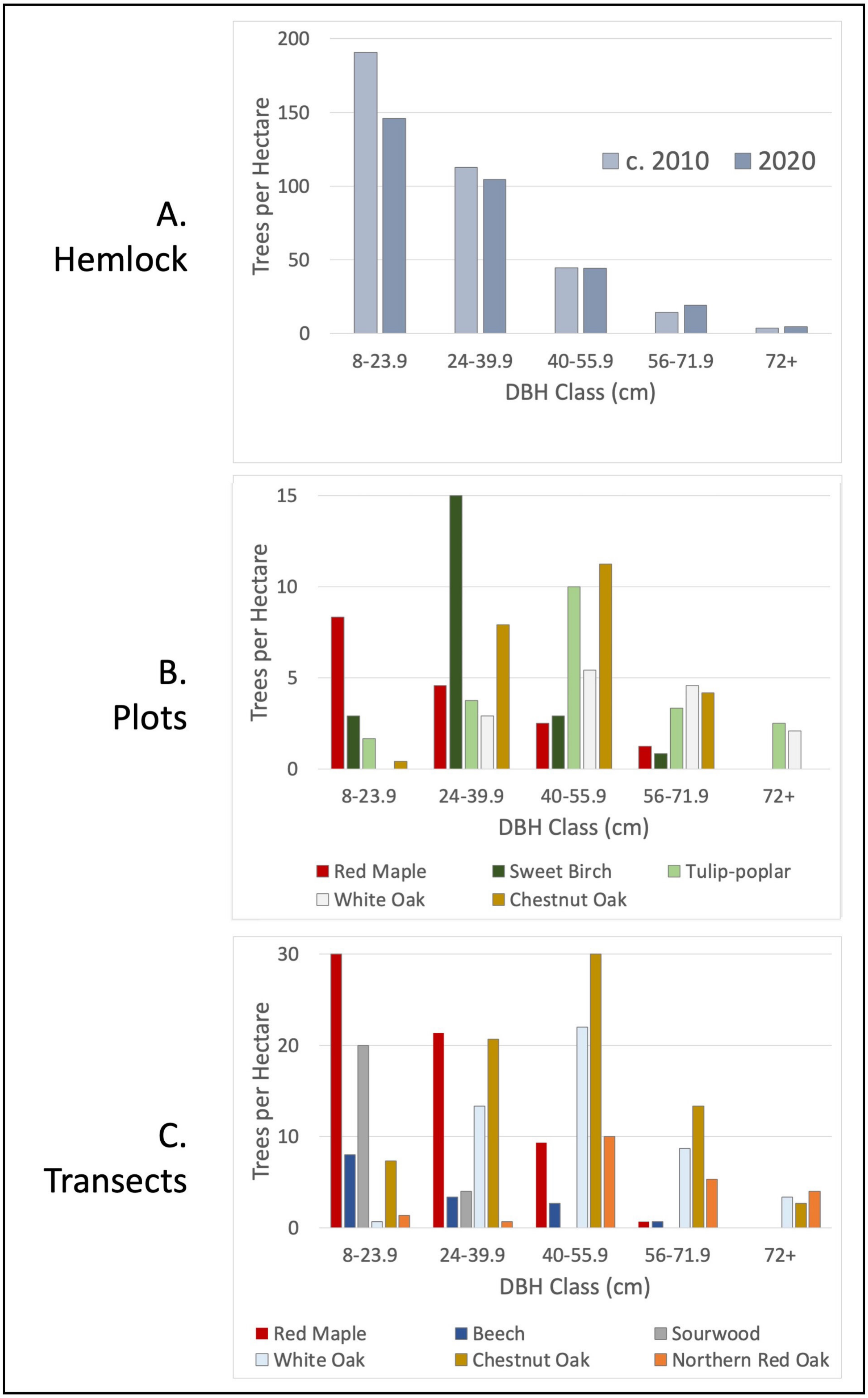

FIGURE 2. Size-class distributions. Note difference in scale of y-axes. A: Eastern hemlock sampled in 30 plots, c. 2010 and 2020. B: Non-hemlock species comprising ≥3% of all trees sampled in 30 plots in 2020. C: Non-hemlock species comprising ≥3% of all trees sampled in 30 transects in 2020. Higher density values in C compared to B reflect the lower abundance of eastern hemlock in transects compared to plots.

Table 5
Density and frequency of saplings (woody plants <8 cm in diameter and ≥1 m in height) surveyed c. 2010 and 2020 across thirty, 20 x 40 m plots. Relative frequency represents the percentage of plots with occurrence.

		Absolute density (t/ha)		Relative frequency (%)	
Scientific name	**Common name**	**c. 2010**	**2020**	**c. 2010**	**2020**
Acer rubrum	Red maple	0.8	1.3	3.3	3.3
Acer saccharum	Sugar maple	7.9	4.2	13.3	10.0
Betula lenta	Sweet birch	6.7	5.0	20.0	13.3
Carpinus caroliniana	American hornbeam	9.6	0.8	10.0	6.7
Carya glabra	Pignut hickory	0.4	0	3.3	0
Carya ovata	Shagbark hickory	2.1	0.8	3.3	3.3
Elaeagnus umbellata	Autumn olive (NNI)[a]	0	1.7	0	3.3
Fagus grandifolia	American beech	7.9	27.5	30.0	33.3
Fraxinus americana	White ash	4.6	0.4	3.3	3.3
Fraxinus pennsylvanica	Green ash	3.3	0	6.7	0
Fraxinus sp.	Ash sp.	0.4	0	3.3	0
Hamamelis virginiana	American witchhazel	4.2	1.7	13.3	3.3
Lindera benzoin	Spicebush	1.3	18.8	6.7	10.0
Liriodendron tulipifera	Tulip-poplar	1.7	1.7	3.3	6.7
Magnolia sp.	Magnolia sp.	2.9	2.1	3.3	3.3
Nyssa sylvatica	Blackgum	2.1	0.8	6.7	3.3
Ostrya virginiana	Hophornbeam	0.4	0	3.3	0
Oxydendrum arboreum	Sourwood	5.8	7.1	30.0	26.7
Quercus velutina	Black oak	0	0.4	0	3.3
Rosa multiflora	Multiflora rose (NNI)[a]	0.4	0	3.3	0
Tsuga canadensis	Eastern hemlock	302.9	169.6	93.3	90.0
Viburnum acerifolium	Mapleleaf viburnum	5.4	0.8	3.3	3.3
	TOTAL	370.8	244.6		

[a] NNI signifies non-native invasive.

also experienced a large increase on a single plot (Table 5). The supplemental material file includes a complete tally of saplings by plot. In addition to tree species, the tally includes 3 native shrubs (American witchhazel (*Hamamelis virginiana*), spicebush, and mapleleaf viburnum (*Viburnum acerifolium*)), and 2 non-native (and invasive) shrub species: autumn olive (*Elaeagnus umbellata*) and multiflora rose (*Rosa multiflora*). Four individuals of autumn olive were tallied on 1 plot in 2020, and a single multiflora rose was observed on 1 plot during the initial survey only.

G-tests indicated that 7 common non-hemlock tree species (≥2% of total) demonstrated a significant association ($\alpha = 0.05$) with topographic settings and edaphic properties of the plots (Table 6). Some of these associations should be interpreted with caution, since a large percentage of a few species occurred on just 1 or 2 plots, and conditions on those plots might overemphasize species-environment relationships: 36% of tulip-poplar occurred on 1 plot, 34% and 21% of sweet birch occurred on 2 plots, 23% of white oak was found on 1 plot, and 19% occurrence was observed for sourwood (on each of 2 plots) and chestnut oak (1 plot). When plots are divided along a NW-SE line, sourwood and white oak were associated with "warm" (SW-tending) aspects, whereas tulip-poplar and red maple were significantly associated with "cool" (NE-tending) aspects. (Aspect was the only association demonstrated by red maple.)

Sourwood and tulip-poplar were associated with steeper slopes (>20°), while sweet birch and white oak preferentially occurred on less-steep sites (≤20°). Soil properties seem to have a more widespread influence among the common non-hemlock species. Although pH was generally low across the plots, 2 species (sourwood, chestnut oak) were associated with lower pH (<4.5) sites, and 3 species (sweet birch, beech, tulip-poplar) preferentially occurred on higher pH plots (≥4.5). Some species demonstrated an association based on the plot's carbon (≥2%: white oak, <2%: sweet birch) or nitrogen (≥0.13%: tulip-poplar, <0.13%: sourwood), but it was the ratio of C:N that evinced a stronger response. Sweet birch, beech, and tulip-poplar were associated with a low C:N ratio (<20), while sourwood, white oak, and chestnut oak were associated with a high C:N ratio (≥20); only 1 common species (red maple) was not statistically associated with the ratio of C:N measured on the plots.

Table 6
Statistically significant associations between common non-hemlock species sampled c. 2010, and a plot's topography and soil properties (G-test, *p* ≤ 0.05)[a]

Common name	Aspect	Slope	pH	% C	% N	C:N
Tulip-poplar	NE-tending	>20°	≥4.5	--	≥0.13	<20
Chestnut oak	--	--	<4.5	--	--	≥20
White oak	SW-tending	≤20°	--	≥2	--	≥20
Red maple	NE-tending	--	--	--	--	--
Sweet birch	--	≤20°	≥4.5	<2	--	<20
American beech	--	--	≥4.5	--	--	<20
Sourwood	SW-tending	>20°	<4.5	--	<0.13	≥20

[a] All plots fell into 1 of 2 classes for each variable. Species are listed in the same order as in Table 4.

Mortality and Growth Rates

Although no HWA ovisacs were noted in the field, eastern hemlock experienced significant mortality in several plots. Plots with high mortality rates typically displayed clear evidence of storm damage, with clustered fallen or snapped trees of various sizes. However, at the 3 Cantwell Cliffs plots, half the dead trees were still standing. In plot C in particular, 8 of 19 trees, mostly in the suppressed canopy class, died over the course of the study period, resulting in an annual mortality rate of 3.5%. Compared to canopy trees, hemlock mortality was often much more pronounced in the sapling size class. There was a great deal of variation in initial sapling abundance, however, with some plots having few or no saplings and others having over one hundred. Hemlock recruitment was much less common than mortality, with only 2 new individuals growing into the ≥8 cm DBH size class, and only 4 of 30 plots displaying an increase in the number of hemlock saplings.

Annual hemlock mortality rate was highly variable between plots, ranging from 0 to 3.5%. The average annual hemlock mortality rate (1.28%) is comparable to other common species like red maple (1.52%), sweet birch (1.19%), and white oak (1.00%) (Table 7). Numerous species experienced low, or no mortality, including chestnut oak (0%).

Annual hemlock growth rates were variable between plots, ranging from 0.6% to 2.8% per year; the 3 plots at one site (Clear Creek) each exceeded 2% annual growth, averaging 2.6%. Across all plots, the average annual growth rate of eastern hemlock (1.13%) is comparable to a number of other species within the plots (Table 7). Beech had the highest average annual growth rate, at 2.18%. There was no statistically significant correlation ($\alpha = 0.05$) between growth rate for individual species and mortality rates across the 30 plots.

Composition and Structure of Upslope Transects

A transect was established in upper slope and ridge positions above each plot to characterize the potential seed source following hemlock mortality. Three new species appeared in the transects: pitch pine (*Pinus rigida*), sassafras (*Sassafras albidum*), and mockernut hickory (*Carya tomentosa*). For the species that also occurred in the plots, responses to the change in topographic setting and the reduced competitive influence with hemlock varied by species (Table 8). For example, red maple became more important, largely due to a major increase in abundance and frequency, increasing in density roughly twofold. Meanwhile, the opposite trend occurred in sugar maple (*Acer saccharum*), which became less abundant. Northern red oak, white oak, and especially chestnut oak all became significantly more important in the transects, with chestnut oak standing out as the dominant species in all respects (density, dominance, and frequency). Although tulip-poplar was the most important deciduous species in the plots, it became rare moving upslope to the transects. Though not as dramatic, a similar trend is seen in sweet birch and beech. Sourwood remained a common sight in the understory of both plots and transects, maintaining a relatively high frequency across the study area but always with a low basal area.

Size-class analysis of important species in the transects (Fig. 2C) reveals that oak species have a large number of intermediate to large-sized individuals, contributing to their dominance of transect basal area. Other major species like sourwood, beech, and especially red maple have numerous individuals, but those individuals are typically in the smaller size classes. The size-class distributions of red maple, sourwood, white oak, and chestnut oak in the transects are quite similar to their distributions in the plots (Fig. 2B), though the number of trees per hectare in the latter is significantly lower due to the abundance of hemlock on the plots.

Invasive Species

In the initial surveys, no non-native species were noted in the seedling/herbaceous plots. In the sapling layer (woody plants <8 cm in diameter and ≥1 m in height), a single multiflora rose was observed in one plot. This individual was no longer present in 2020, but 4 individual autumn olive were recorded in a different plot (Table 5). No non-native individuals ≥8 cm DBH were recorded in the tree layer in any survey. In the 2020 resurvey, observations were noted of invasive herbaceous species both in and around sample sites. Invasive species were observed in or near one-third of all sites (plot-transect pairs), though often in low abundance. Cantwell Cliffs, the site experiencing high hemlock mortality, was the exception; invasive plant species were found in higher abundance in and around plots there, including multiflora rose, autumn olive, and Japanese stiltgrass (*Microstegium vimineum*). Japanese stiltgrass was by far the most frequently encountered invasive species across all study areas. Populations of the species tended to be large and dense, especially along trails. Other invasive species, including garlic mustard (*Alliaria petiolata*) and Japanese barberry (*Berberis thunbergii*), were represented by no more than a few scattered individuals at the time of sampling.

DISCUSSION AND SUMMARY

Baseline Conditions of Hemlock Stands

Situated in ravines and gorges, hemlock stands in the Hocking Hills are steep and sheltered, with high C:N ratio soils owing to low-nitrogen litter and slow decomposition (Ignace 2019). Hemlock was abundant in all tree strata, dominating the suppressed and intermediate canopy positions. It was also by far the most abundant and frequently encountered species in the sapling size class, present at least in small numbers in the majority of plots. Given the deep shade of these hemlock-dominated stands and their relatively infertile soils, the low

Table 7
Average annual growth (with standard error) and mortality rates[a]. Average time between surveys for all trees combined is 10 years, but for individual species ranged between 9 to 11 years.

Common name	Average annual growth rate (%) (±SE)	Average annual mortality rate (%)
Eastern hemlock	1.13 (0.05)	1.28
Tulip-poplar	1.78 (0.20)	0.66
Chestnut oak	1.22 (0.10)	0.00
White oak	1.05 (0.11)	1.00
Red maple	1.05 (0.13)	1.52
Sweet birch	1.20 (0.14)	1.19
American beech	2.18 (0.73)	0.40
Sourwood	1.06 (0.27)	2.38
Northern red oak	0.94 (0.35)	0.00
Sugar maple	1.13 (0.34)	2.61
Blackgum	0.92 (0.30)	3.33
Pignut hickory	0.79 (0.09)	0.00
Scarlet oak	0.84 (0.36)	1.67
Black oak	1.22 (0.55)	0.00
Green ash	0.91 (---)	5.00
Shellbark hickory	0.18 (0.23)	3.03
Bitternut hickory	---	11.11
Black cherry	---	9.09
Hophornbeam	---	11.11

[a] Species are listed in the same order as in Table 4.

species diversity of these plots is unsurprising. With an average Shannon H' <1 for trees, these stands are less diverse than the broader Mixed Mesophytic forest region (average H' value of 2.73 for old-growth stands), and even Braun's Hemlock-White Pine-Northern Hardwood region (average 1.85) (Monk 1967).

Yet there are common co-occurring species with hemlock in the Hocking Hills. These non-hemlock species already in the canopy would be the first to respond to hemlock mortality, likely maintaining dominance in the ravine and slope positions. The most important non-hemlock species, tulip-poplar, is not equally distributed among the plots, and a

Table 8
Summary statistics for trees (≥8 cm DBH) surveyed in 2020 across thirty, 800 m^2 plots and their corresponding 500 m^2 transects[a], sorted by transect Importance Value. Table values exclude contributions of hemlock, to allow a direct comparison of non-hemlock trees.

		Relative density (%)		Relative dominance (%)		Relative frequency (%)		Importance Value	
Scientific name	Common name	Plots	Transects	Plots	Transects	Plots	Transects	Plots	Transects
Quercus montana	Chestnut oak	16.6	25.1	18.7	33.7	10.4	15.9	15.2	24.9
Quercus alba	White oak	10.5	16.3	17.5	24.0	9.6	15.2	12.5	18.5
Acer rubrum	Red maple	11.6	22.6	6.6	10.6	14.4	15.2	10.9	16.1
Quercus rubra	Northern red oak	2.9	7.2	5.8	14.6	4.8	11.0	4.5	10.9
Oxydendrum arboreum	Sourwood	9.3	8.1	2.6	1.5	9.6	10.3	7.2	6.7
Fagus grandifolia	American beech	7.0	5.0	10.0	2.4	9.6	8.3	8.8	5.2
Carya glabra	Pignut hickory	2.6	2.3	1.7	1.4	4.0	5.5	2.8	3.1
Pinus rigida	Pitch pine	---	2.5	---	1.7	---	4.1	---	2.8
Betula lenta	Sweet birch	15.1	2.3	9.0	1.8	10.4	4.1	11.5	2.7
Liriodendron tulipifera	Tulip-poplar	14.8	1.6	21.7	4.0	11.2	2.1	15.9	2.6
Nyssa sylvatica	Blackgum	1.2	2.5	0.8	1.1	3.2	2.1	1.7	1.9
Quercus velutina	Black oak	0.9	1.1	1.2	2.2	2.4	2.1	1.5	1.8
Acer saccharum	Sugar maple	5.2	2.3	1.9	0.6	6.4	2.1	4.5	1.6
Sassafras albidum	Sassafras	---	0.9	---	0.3	---	1.4	---	0.9
Carya tomentosa	Mockernut hickory	---	0.5	---	0.2	---	0.7	---	0.5

[a] Plot species not occurring in the transects include scarlet oak (Plot IV = 1.6), shellbark hickory (Plot IV = 0.8), and green ash (Plot IV = 0.6).

small number of plots account for much of its basal area. Chestnut oak and white oak commonly co-occur with hemlock, especially on less fertile sites (C:N ≥20), though they each account for less basal area than tulip-poplar. The prevalence of chestnut oak and white oak throughout the plot extent is similar to trends seen in the smaller hills of the Glaciated Allegheny Plateau of northeast Ohio (Macy 2012) and Connecticut (Orwig and Foster 1998). In Martin and Goebel's (2013) Hocking Hills sites, these species increased in importance upslope.

In smaller size classes, red maple, sweet birch, and sourwood are also relatively abundant across the plots. The generalist red maple had the highest frequency of occurrence of any non-hemlock species and among the highest densities as well. The prevalence of sweet birch is especially relevant, as studies of post-HWA forests often indicate birch species as being among the first trees to respond to hemlock mortality (Orwig and Foster 1998; Small et al. 2005; Stadler et al. 2005; Eschtruth et al. 2006), potentially coming to dominate in the long term at sites where they occur in large numbers (Jenkins et al. 2000).

Recruitment, Growth, and Mortality

Eastern hemlock produces good seed crops at 2 to 3-year intervals, but natural regeneration is often poor. This has been attributed to environmental factors such as light levels, low seed viability, soil moisture, soil pH, and the allelopathic effects of hemlock litter (Goerlich and Nyland 2000). In a literature review of hemlock regeneration, Goerlich and Nyland (2000) concluded that it depends especially on a good seed year followed by several years of favorable moisture conditions. The current study involved sampling from 2008 to 2011 with a 2020 resurvey, and it is possible that dry conditions contributed to the decrease in hemlock saplings (<8 cm DBH and ≥1 m in height) observed over that time span. May to July precipitation in 2012 was 35% below the 1991 to 2020 average for the area, following 2 years of above-average precipitation. Similarly, May to July precipitation in 2020 was 22% below normal values, following 3 years of above-average precipitation (PRISM Climate Group, https://prism.oregonstate.edu).

Though the majority of plots contained eastern hemlock saplings, only a small number of non-hemlock saplings were noted at most plots. Exceptions to this observation (abundant beech saplings in 1 plot, spicebush in another) suggest that site-specific differences could influence post-HWA communities, as saplings of other species could exhibit a growth release due to the increase in light availability following hemlock mortality (Eschtruth et al. 2006). The dense growth of shrubs and saplings in plots like these would likely have a negative effect on the ability of other species to seed in should hemlock experience significant mortality, similar to the rhododendron thickets of the central and southern Appalachians (Martin and Goebel 2012; Brantley et al. 2013).

Similarly, invasive species increased following hemlock decline in New England (Orwig and Foster 1998; Small et al. 2005). In the Delaware Water Gap, invasive plants which were previously absent or unnoticed had expanded their distribution considerably following hemlock mortality, after which they were observed in 35% of plots (Eschtruth et al. 2006). Although not observed in this study, one species of particular concern in the Hocking Hills would be tree-of-heaven (*Ailanthus altissima*). It is an early successional, aggressively invasive species that produces great quantities of wind-dispersed seeds, grows rapidly, and maintains dominance on open and disturbed sites through clonal spread and the production of allelopathic compounds. Although classified as shade intolerant, it can persist for many years under shaded conditions and is tolerant of both poor soil conditions and drought (Iverson et al. 2019); buried seeds can remain viable for many years (Rebbeck and Jolliff 2018). In Tar Hollow State Forest located in the Hocking Hills, tree-of-heaven seedlings in densities of >100 ha^{-1} were found on 42% of plots that experienced harvest within the previous 20 years (Rebbeck et al. 2017). Tree-of-heaven has the potential to appear in large canopy gaps created by hemlock mortality. In the current study, most invasive herbaceous plant and shrub species were represented by only a few scattered individuals. Japanese stiltgrass, however, was much more common and numerous across the study sites, growing thickly alongside trails and roads. Like tree-of-heaven, Japanese stiltgrass is capable of aggressive growth even in the shade (Leicht et al. 2005), so once colonization of the post-HWA forest occurs, these populations would likely persist.

The average growth rate (1.2%) among eastern hemlock trees was similar to that of other common species in the 30 plots. Its mortality rate ranged from 0% to 3.5% per year (Table 7). Snapping and uprooting by wind appeared to be the leading cause of mortality for adult hemlock trees, as "multiple wind events" had recently contributed to an increase in downed trees across the state forest (Dave Glass, Forest Manager, Ohio Department of Natural Resources, pers. comm. via email, December 2020). In contrast, on the one site with the highest hemlock mortality rate (Cantwell Cliffs Plot C), over half of the dead eastern hemlock were still standing and, defoliation aside, appeared relatively undamaged, with little snapping of branches or splitting or peeling of bark. This would seem to indicate relatively recent mortality that cannot be attributed to wind or storm damage. Although no direct evidence of the presence of HWA was discovered on the plot, these standing dead trees may represent HWA-induced mortality since "extensive HWA infestation" has been discovered in the Cantwell Cliffs area (Tom Macy, Forest Health Program Manager, Ohio Department of Natural Resources, pers. comm. via email, October 2020). Larger mature hemlock trees on Hocking State Forest land have been treated with systemic pesticides to guard against such infestation and subsequently marked with orange blazes. These orange markings were noted at nearby Cantwell Cliffs plots A and B, which experienced significantly less mortality. Orange markings were not noted at plot C, giving further evidence to the possibility that the standing dead trees at plot C represent early victims of HWA in Hocking County. However, it is possible that this mortality was caused by Rosellinia needle blight, which has been on the increase in southeastern Ohio's hemlock stands since 2020 (USFS 2022). This fungal infection eventually leads to branch dieback, and has resulted in the death of understory hemlock saplings (Tom Macy, Forest Health Program Manager, Ohio Department of Natural Resources, pers. comm. via email, June 2022).

In these c. 140-year-old stands, competitive thinning appears to be another major source of mortality among hemlock trees in the smallest size class. This was especially apparent in sites with a high density of trees in the initial surveys, where mortality was seen almost exclusively among small, suppressed hemlock trees. At other plots, mortality of hemlock saplings was much more severe than in suppressed trees. Plots with the highest number of saplings (>50) c. 2010 all experienced high mortality, losing between 3.6% to 7.9% of their saplings per year. Overall, sapling mortality is more prevalent than growth into the larger size class in these plots in the decade since the initial surveys. Elsewhere in its range, little published research is available documenting eastern hemlock mortality or growth rates outside of an HWA infestation context (but see Thomas et al. 2021).

Topographic Variation within Hemlock Stands

Eastern hemlock in Ohio is primarily found in gorges and on steep slopes, which Black and Mack (1976) attribute to a combination of low light, cooler temperatures, and readily available soil moisture. Moving upslope toward the drier and more exposed upper slopes and ridgetops resulted in a decrease in hemlock (Fig. 1B), and a corresponding increase in the density of non-hemlock species. These non-hemlock (primarily deciduous) species are therefore in a good position to disperse seeds to the slopes and valleys below in the event of HWA-induced mortality.

In southeastern Ohio, as elsewhere in the eastern United States, a topographic pattern is evident with oak species more prominent on upper slopes and ridges, and more mesophytic species such as sugar maple and tulip-poplar occurring in greater abundance on lower slopes and valleys (Dyer and Hutchinson 2019). This pattern emerges within the hemlock-dominated stands as well. Sugar maple, sweet birch, and tulip-poplar all grew in significantly fewer numbers in the upslope transects compared to the plots. Oak species were well-represented in the upslope transects, with white oak, chestnut oak, and northern red oak all growing in significantly higher number than in the plots. In contrast, red maple abundance more than doubled in the upslope transects compared to the plots. The shift from hemlock-mixed hardwood to oak-red maple stands moving upslope has been observed from other unglaciated Allegheny Plateau sites (Martin and Goebel 2013) to Connecticut (Small et al. 2005). The pattern suggests that with hemlock mortality, mesophytic species are likely to maintain their positions in the sheltered lower topographic settings. Due to their abundance in both the plots and the upslope transects, however, oak species could relatively quickly become dominant components of the post-HWA canopy regardless of slope position. Previous studies have also documented the potential for oak species to grow rapidly in response to hemlock mortality (Orwig and Foster 1998; Small et al. 2005). The role of red maple, a prominent representative of both plots and transects in smaller size classes, may disrupt the mesic-to-xeric topographic pattern of post-HWA communities.

A broader pattern of mesophication likely accounts for the abundance of recently established red maple in the upslope transects. This increased competitiveness of red maple makes them especially capable of expanding their populations in the future absence of eastern hemlock, just as they did in HWA-impacted Connecticut forests (Orwig and Foster 1998), as well as in sites previously impacted by chestnut blight (*Cryphonectria parasitica*) (Keever 1953; Woods and Shanks 1959; Good 1968). Concomitantly with the increase in red maple, a decrease in the formerly dominant white oak is being observed in much of the eastern United States, including southeastern Ohio (Dyer 2001). Although white oak is still a dominant species in the transects (attaining the second highest Importance Value overall by virtue of its typical large size), the near-complete lack of individuals in the smallest size class in both plots and transects—and the absence of white oak saplings—suggest a possible decline in these hemlock stands.

In contrast to white oak, populations of northern red oak and chestnut oak have been observed to increase in the eastern United States. Abrams (2003) attributes this change to the rapid growth of northern red oak and chestnut oak compared to white oak, allowing them to more easily colonize new sites following disturbances even in mesic conditions. Chestnut oak was the second most important non-hemlock species in the plots and by far the most important in the transects, where it attained the highest density, basal area, and frequency of occurrence. Northern red oak, while not as numerous, is also found in greater numbers in the transects away from competition with eastern hemlock. In the short term, it appears that chestnut oak and northern red oak are in an especially good position, along with the aggressively expanding red maple, to disperse into the large gaps left below following future HWA-induced mortality. Expanding the timeline, however, drought stress associated with a warming climate could alter these dynamics, possibly favoring white oak over red maple (Vose and Elliott 2016).

Conclusions

As a foundation species, eastern hemlock acts as the pillar of a unique ecosystem. To maintain the ecological integrity of these unique ecosystems, as well as to preserve the tourism-dependent economy of the Hocking Hills region, protecting as much hemlock forest as possible from HWA is the best course of action. The Ohio Department of Natural Resources is implementing an Integrated Pest Management (IPM) strategy in the Hocking Hills region, using a combination of targeted neonicotinoid insecticide application and the release of adelgid-specialist *Laricobius* beetles. Management areas were targeted based on stand size, land ownership, and conservation value (ODNR 2017). The current study has confirmed other benefits of this area regarding the establishment of predatory beetles: hemlock dominates these stands (55% relative basal area), and their spacing (69% relative density) enables the beetles to find each other and their prey (Mayfield et al. 2020). With large areas under state ownership, silvicultural practices may also be implemented, should treatments such as thinning (Brantley et al. 2017) or gap creation (Miniat et al. 2020) prove detrimental to HWA and beneficial to infested hemlock. However, it seems probable that HWA will eventually lead to the loss of hemlock where protection strategies are not implemented throughout its range in Ohio. Resampling these plots in the future is recommended, after HWA has had more of an impact on hemlock health. Understanding the transition from hemlock forest to deciduous forest in southeast Ohio is important from both ecological and economic perspectives, potentially guiding conservation and land management efforts. Furthermore, an understanding of pre-HWA composition, structure, and forest dynamics can inform restoration efforts if, in the long-term future, sustainable HWA control or host tree resistance or tolerance is developed.

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SUPPLEMENTAL MATERIAL

Supplemental material (an Excel® data file) to accompany this report is available at: https://kb.osu.edu/handle/1811/105365