Eastern Hemlock (*Tsuga canadensis*) Forests of the Hocking Hills Prior to Hemlock Woolly Adelgid (*Adelges tsugae*) Infestation

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Table of Contents

Abstract 5
1 Introduction 7
1.1 Eastern Hemlock & its Role as a Foundation Species 7
1.2 Hemlock Woolly Adelgid 10
1.3 Hemlock Forests in Transition 12
1.4 Multiple Paths to Succession 16
1.5 Hemlock & HWA in Ohio 17
2 Methods 21
2.1 Study Area 21
2.2 Field Sampling of Hemlock Forests 22
2.3 Field Sampling of Surrounding Deciduous Stands 24
2.4 Data Analysis 25
3 Results 27
3.1 Baseline Conditions of Hemlock Stands 27
3.2 Change Over Time: Mortality & Growth Rates 32
3.3 Composition of Transects & Comparison with Hemlock Stands 35
3.4 Invasive Species 39
4 Discussion 40
4.1 Characterization of Hemlock Plots 40
4.2 Change in Plots Over Time: Recruitment & Growth 42
4.3 Change in Plots Over Time: Mortality 44
4.4 Composition of Transects & Comparison to Plots 48
4.5 Invasive Species 52
5 Conclusion 55
6 References 59
7 Appendices 63
7.1 Coordinates 63
7.2 Plot Characteristics 64
7.3 Plot Age 65
7.4 Calculations & Analysis 66

Abstract

Eastern hemlock (*Tsuga canadensis*) is an important foundation species, altering its environment and supporting a variety of organisms not generally found in deciduous forests. The hemlock forests of the Hocking Hills region in southeast Ohio are particularly unique, occurring in isolated pockets in ravines and on steep slopes on the western edge of the range of the species. However, this unique ecosystem is under threat from hemlock woolly adelgid (HWA, *Adelges tsugae*), an invasive insect pest which entered the state in 2012.

The goal of this study is to characterize the hemlock stands of the Hocking Hills just prior to HWA infestation and describe how these forests have changed in the past decade in terms of growth and mortality. An additional goal is to record non-hemlock species growing alongside these hemlock stands which could become dominant following HWA-induced mortality, as well as any invasive plants present which could pose a threat to native diversity following such a disturbance. In order to accomplish these goals, thirty 20 x 40 m plots established roughly a decade ago were resampled. Within these plots, the diameter of tagged trees was measured and their health and canopy position assessed, and saplings counted as well. Transects measuring 10 x 50 m were established on the upper slopes or ridges above each plot to record non-hemlock species that have the potential to seed into the hemlock stands below. The existence of any invasive plants was also recorded in both plots and transects.

It was found that hemlock, for the most part not yet impacted by HWA, was still the dominant species in all plots, with an average importance value of 47.78. Storm damage and competitive thinning rather than HWA infestation appeared to account for the majority of mortality. Growth and mortality rates among hemlocks (on average, 1.18% annual growth and

13.24% total mortality) were both comparable to those seen in deciduous species on the plots. A mixture of hardwood species such as tulip poplar (*Liriodendron tulipifera*), chestnut oak (*Quercus montana)*, white oak (*Quercus alba*), sweet birch (*Betula lenta*) and red maple (*Acer rubrum*) were common components of hemlock stands. Therefore, these trees can be expected to be among the first species to dominate the canopy following future hemlock mortality. Chestnut oak dominates the deciduous stands above the hemlock plots, with red maple, white oak, and red oak (*Quercus rubra*) also commonly recorded. Each of these species could contribute to the composition of post-HWA forests by dispersing to the slopes and valleys below. Invasive plant species were found at one-third of sampling sites, with Japanese stiltgrass (*Microstegium vimineum*) being by far the most numerous. This is worrying, as the expansion of invasive species following hemlock mortality could potentially inhibit the regeneration of native species. In short, a variety of deciduous species appear poised to take advantage of increased resource availability in the absence of hemlock, but unfortunately the same can also be said for invasive plants. The results of this study can inform forest management and conservation efforts in the isolated and unique hemlock stands of southeast Ohio.

1. Introduction

1.1: Eastern Hemlock and its Role as a Foundation Species

Eastern hemlock is an evergreen coniferous tree with a wide range, occurring from eastern Canada down to the southern Appalachians and west into the Great Lakes region (Fig. 1.1). Within this range it occurs in cool, moist locations in a variety of habitats and elevations, from the sheltered slopes and valleys of the Appalachian Mountains and their foothills to flats and the edges of wetlands to the northeast (Godman & Lancaster 1990). In Ohio, hemlock forests exist primarily in isolated pockets geographically disconnected from the rest of this range (Fig. 1.2). These pockets, particularly in the unglaciated southeastern part of the state, often occur in steep ravines and gorges with shallow soils rather than the flats or mountain habitats seen elsewhere in hemlock's range (Black & Mack 1976). Among the longest-lived and most shade-tolerant of trees in eastern North America, it is capable of growing in dense stands in which it dominates the canopy. The combination of dense growth, a high leaf area index, and an overall low transpiration rate (Catovsky et al. 2002) creates cool, shaded, and moist conditions which perpetuate further hemlock growth. Furthermore, when hemlocks grow in riparian habitats, the shade they provide as well as their steady, low transpiration rates throughout the year help stabilize stream levels no matter the season (Brantley et al. 2013).

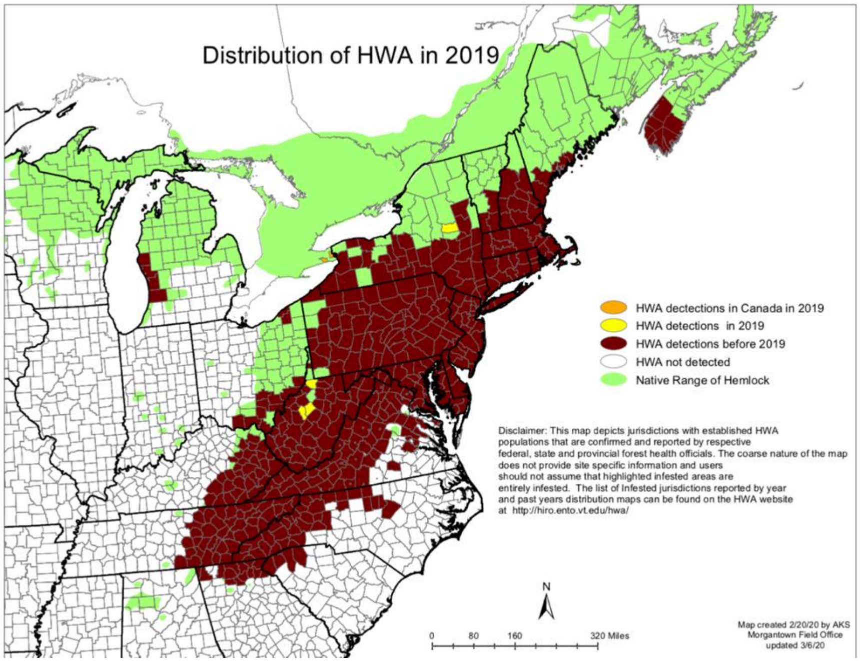

Figure 1.1: Range of eastern hemlock and known HWA infestation as of 2019 (created by the U.S. Forest Service's Morgantown, WV Field Office, updated March 6, 2020).

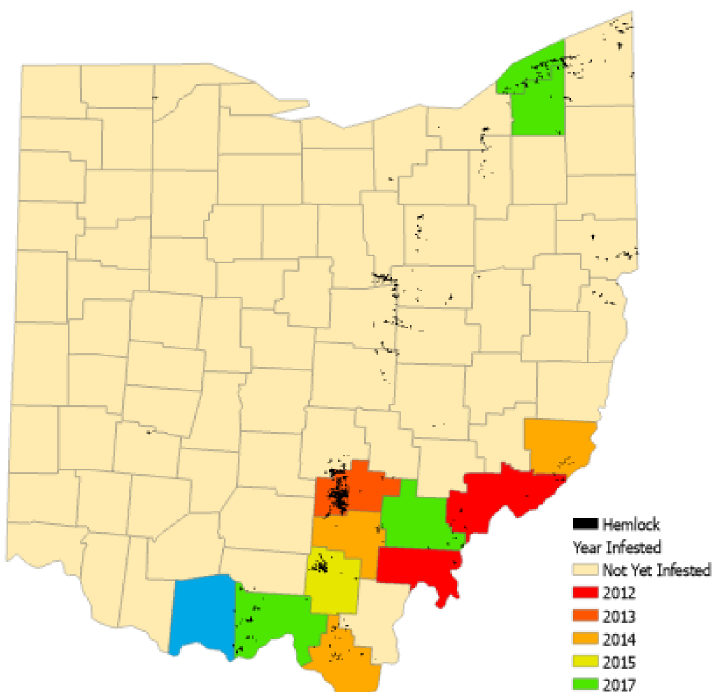

Figure 1.2: Location of hemlock populations and HWA infested counties in Ohio (map by author with hemlock data from Stump 2008 and infestation discovery dates from Apsley 2018). No new infestations have been discovered 2019-2020.

Due to its dominant influence on habitat, eastern hemlock is considered a foundation species, a plentiful species which changes or stabilizes local conditions, often providing habitat for other species in the process (Ellison et al. 2005). The cool, dark conditions that hemlock forests create tend to inhibit the growth of other plant species, lowering the density and diversity of understory herbs and shrubs in particular (Ellison et al. 2015). However, this is certainly not the case for fungal and animal species, many of which thrive in hemlock forests or even depend upon them for their survival. An analysis of soils in western Massachusetts found that rare fungi are strongly associated with eastern hemlock as opposed to nearby birch forests, indicating that fungal diversity may be higher in hemlock forests than their deciduous counterparts, at least in New England (Fassler et al. 2019). Equally as important (and better established) is the role of eastern hemlock in the lives of numerous aquatic and amphibious species as a result of the cooling and stream-stabilizing effect of their low transpiration and the shade they provide. For example, 10% of aquatic macroinvertebrates in the Delaware Water Gap National Recreation Area in Pennsylvania and New Jersey were found in association with hemlock stands (Snyder et al. 2002). Another Delaware Water Gap study found that cold water fish such as brook trout (*Salvelinus frontinalis*) and brown trout (*Salom trutta*) were two to three times more likely to be found in streams flowing through hemlock stands than deciduous forest stands (Ross et al. 2003). A number of birds are also strongly associated with the hemlock forests on which they rely for shelter, including the black-throated green warbler (*Dendroica virens*), Blackburnian warbler (*D. fusca*), hermit thrush (*Catharus guttatus*), and Acadian flycatcher (*Empidonax virescens*; Tingley et al. 2002). Eastern hemlock exerts strong control on the abundance and diversity of numerous organisms.

1.2: Hemlock Woolly Adelgid

Unfortunately, hemlock forests and the organisms which depend upon them are under threat from an invasive pest. Hemlock woolly adelgid (HWA; *Adelges tsugae*) is a tiny, aphid-like insect (Fig. 1.3) which feeds on the parenchyma cells of young shoots of hemlock trees. In doing so, it has been shown to be capable of killing eastern hemlock in as little as four years (McClure 1991).

Figure 1.3: An example of HWA infestation, with woolly ovisacs clearly visible, at Canter's Cave in Jackson, Ohio. These woolly sacs are the primary means of identifying HWA infestation. (Photo by author).

Accidentally introduced in eastern Virginia in the 1950s, it has since spread throughout much of the range of eastern hemlock (Fig. 1.1) and Carolina hemlock (*Tsuga caroliniana*), resulting in widespread mortality. In south-central Connecticut, where hemlock woolly adelgid arrived in 1985, mortality rates exceeding 90% were observed in some stands. Of the hemlock trees that remained, 90% displayed major loss of foliage (Orwig & Foster 1998). At the nearby Connecticut College Arboretum, a 70% decline in hemlock basal area was observed over the course of 20 years (Small et al. 2005). Twelve years after the arrival of HWA in the Delaware Water Gap in Pennsylvania and New Jersey, it was estimated that 20% of hemlock trees had died, with another 60% in decline (Evans 2004). In the Central Appalachians of Virginia and West Virginia, Martin & Goebel (2012) found hemlock forests in various stages of severe decline. These Central Appalachian stands had experienced infestations lasting anywhere from nine to 32 years, much longer than the four-year timeframe of decline and mortality of hemlocks suggested by McClure (1991). However, this is consistent with a view of HWA-induced mortality in which especially vulnerable individuals experience rapid die-offs, followed by a slow decline of less susceptible trees. For example, trees growing on dry sites have been found to die rapidly, while nearby trees in moister environments generally take longer to succumb (Orwig et al. 2003). Hemlock mortality has also been suggested to be a density-dependent process at the stand level. The greater the density of hemlock trees in a stand, the higher the likelihood of HWA spreading from tree to tree, so less dense stands may take longer to decline (Macy 2012). Models have also been used to predict hemlock mortality where HWA infestation had not yet occurred. For example, in eastern Kentucky, models created with the USDA Forest Service's Forest Vegetation Simulator (FVS) predict near-complete mortality within twenty years of HWA infestation (Spaulding & Rieske 2010). In northeast Ohio, FVS modeling of HWA-induced mortality also predicted a wide range of potential mortality rates between sites, ranging from 44.5% to 85.9%, likely due to differences in the initial density of hemlock (Macy 2012). In short, the time between infestation and mortality, as well as overall mortality rate, varies from stand to stand, but high levels of mortality will eventually result without human intervention.

1.3: Hemlock Forests in Transition

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 the post-HWA stands. For example, twelve years after the arrival of HWA in Connecticut, Orwig and Foster (1998) noted that hemlock mortality at their study sites had already resulted in a shift toward canopy dominance by birch, oak, and maple. Of these, birch and oak were already important in the overstory, with maple increasing in importance in the understory as a result of gaps left by dead hemlocks. Though birches are often considered early successional species, modeling has suggested that they may persist as canopy dominants for long periods of time where they attain a high density following hemlock mortality. Jenkins et al. (2000) used SORTIE to model forest dynamics following hemlock decline in northwestern Connecticut. Similar to the observations of Orwig and Foster (1998), the simulation suggested a rapid transition toward dominance by yellow birch (*Betula alleghaniensis*) and American beech (*Fagus grandifolia*). An increase in birch growth was also seen in the Delaware Water Gap, but despite 25% of adult hemlocks either dead or dying at the time, little change in the composition of the canopy was yet observed (Eschtruth et al. 2006). Results like these suggest that early successional species like birches may be among the first trees in the canopy to exhibit a significant growth response to hemlock mortality, with some potential for long-term dominance where they grow in abundance.

Which species become dominant in the absence of hemlock also depends upon topographic variation within a forest, or upon variations in habitat settings between forest stands in relatively close proximity. Twenty years after the arrival of HWA at Connecticut College Arboretum, an increase in the basal area of oak species including black oak (*Q. velutina*), scarlet oak (*Q. coccinea*), and red oak was observed along dry ridge environments. Oaks came to account for 41% of basal area overall at the ridge tops. In the more mesic valleys below, a mixture of hardwoods came to dominate the canopy. Basal area of these same oak species also increased significantly in the valleys, but here they faced competition with sweet birch and American beech (Small et al. 2005). Variation in non-hemlock species was also observed in two adjacent physiographic regions, among forest stands situated along a 200 km transect in northeastern Ohio. In these stands not yet invaded by HWA at the time, differences were noted in forest composition between swampy hemlock stands of the Huron-Erie Lake Plains (ELP) region and riparian forests of the Glaciated Allegheny Plateau (GAP) region (Macy 2012). The most abundant non-hemlock canopy trees in the ELP were red oak and red maple. In the GAP, red maple was still a major non-hemlock component of the canopy, but white oak rather than red oak was abundant. Furthermore, modeling using the Forest Vegetation Simulator, Hemlock Woolly Adelgid Event Monitor predicted a wide range of potential HWA-induced mortality rates between sites, from 44.5% in the ELP to 85.9% in the GAP. This was likely a result of the greater initial density of hemlock in the latter. Although the model makes no attempt to predict the future composition of these stands, the differences both in hemlock mortality and in deciduous components of the forest suggest that post-HWA communities may look significantly different across a relatively short distance.

In the central Appalachian Mountains of Virginia and West Virginia, the slow decline of hemlock has led to shifts in forest composition which display perhaps the clearest example of post-HWA forest communities diverging as a result of differences in topography. This is largely due to the elevational gradient present at these mountain sites and the related climate gradient, which create elevational zones of vegetation. These gradients are much more pronounced than at other cited studies. At lower elevations, a post-HWA transition to deciduous trees, particularly birches and American beech, was observed in the canopy. In riparian habitats, rhododendron (*Rhododendron maximum*) also increased in number in the understory. Toward the mountaintops, deciduous species begin to disappear, resulting in evergreen species such as red spruce (*Picea rubens*) and eastern white pine (*Pinus strobus*) beginning to dominate the canopy after hemlock mortality (Martin & Goebel 2012). A similar trend regarding riparian rhododendron populations has been noted in the southern Appalachians. In the US Forest Service's Coweeta Hydrological Laboratory in North Carolina, a shift toward a mixed deciduous forest dominated by sweet birch, tulip poplar, and red maple is already being observed on the lower slopes. In Coweeta's riparian habitats, however, rhododendron grows so thickly in the gaps created by dead hemlocks that few trees are able to grow (Brantley et al. 2013).

A similar pattern of geographic variation can be seen in the sapling and seedling layers, which may differ significantly in composition from the canopy above. In the Huron-Erie Lake Plains of northeastern Ohio, hemlock and beech were the only species found as saplings despite the prevalence of red maple and red oak in the canopy. Red maple and black cherry dominated the seedling layer. In the adjacent Glaciated Allegheny Plateau, red maple was still a major non-hemlock component of all three layers, but white ash (*Fraxinus americana*) rather than black cherry was a major component of the seedling layer. Hemlock was not found to be present in the seedling layer in either region, possibly a result of soil pathogens or increased deer browse (Macy 2012).

Regardless of composition, these lower layers experience increased growth and establishment following hemlock mortality and an opening of the canopy. Small et al. (2005) noted an increase in the abundance of sassafras (*Sassafras albidum*) saplings on ridges, while black cherry (*Prunus serotina*) and red maple experienced a similar increase in the valleys. Similar increases in the abundance of saplings, as well as growth in understory trees, should be expected as a result of the increased light availability in the gaps left behind by dead hemlocks. It also appears that hemlock mortality does not need to be as severe as that seen in Connecticut for a response in the sapling layer to occur. Despite a relative lack of change in canopy composition in the Delaware Water Gap, there was a significant increase in the abundance of saplings of tulip poplar, blackgum (*Nyssa sylvatica*), sassafras and, oddly enough, eastern hemlock (Eschtruth et al. 2006). However, this increase in hemlock likely only represents a response in hemlock seedlings to increased light rather than continuing reproduction of declining adult hemlocks. The geographic variation in post-HWA communities is seen again and again throughout hemlock's range in each layer of the forest. It demonstrates a need for further study of stands at the edge of the range if we are to understand the future transition of hemlock forests to deciduous forests at a local level.

1.4: Multiple Paths of Succession: Impact of Other Environmental Factors on Post-HWA Forest Composition

There are a variety of climatic and ecological processes and factors which complicate predictions of future forest conditions in the aftermath of HWA, particularly in the long term. The majority of studies which attempt to predict post-HWA forest composition are based on the current composition of those forests and thus neglect these evolving issues. One such issue is mesophication, which refers to the change in forest composition in eastern North America toward species which thrive in cooler, wetter conditions as a result of fire suppression (Nowacki & Abrams 2008), increased precipitation, decreased temperature, changes in land use, and other factors (McEwan et al. 2011). Mesophytic species like sugar maple (*Acer saccharum*) and red maple are already beginning to replace drought-tolerant, fire-resistant trees such as oaks (Abrams 1992). This trend could have a significant impact on post-HWA forest composition, as oaks are frequently identified as, or predicted to become dominants following hemlock mortality (Orwig & Foster 1998, Small et al. 2005, Spaulding & Rieske 2010). Yet the process of mesophication could very well be reversed. Climate change threatens to create hotter, drier conditions even in the currently mesic eastern U.S., potentially creating an environment more suitable for oaks once more. In fact, Vose and Elliot (2016) predict that climate change will result in a transition back toward oak dominance whether human management is involved or not, though when or even if this change will occur is impossible to predict with certainty. After all, heat or drought may be extreme enough in some areas to slow the growth of even drought-tolerant oaks, and other factors such as invasive pests and pathogens or the rapidly increasing white-tailed deer

(*Odocoileus virginianus*) population introduce a great deal of uncertainty to any such long-term predictions (Dey 2014).

In addition, hemlock woolly adelgid is but one example of an invasive pest threatening native trees. Numerous other tree species are threatened by a suite of other exotic pests and pathogens. To make matters worse, some of these invasive species (HWA included) are likely to expand their ranges as the climate warms (Dukes et al. 2008). Invasive plants also have the potential to grow in dense thickets that can outcompete and push out native plants (D'Antonio & Meyerson 2002). This threat is especially relevant in forests impacted by HWA, since the many gaps in the canopy created by fallen hemlock trees create prime conditions for rapid spread of invasive plants. This has already been observed in a number of hemlock stands affected by HWA. A long list of invasive species including tree of heaven (*Ailanthus altissima*), Japanese stiltgrass, Japanese barberry (*Berberis thunbergii*), Japanese honeysuckle (*Lonicera japonica*), oriental bittersweet (*Celastrus orbiculatus*), garlic mustard (*Alliaria petiolata*), and multiflora rose (*Rosa multiflora*) have all expanded in HWA-affected forests (Orwig & Foster 1998; Small et al. 2005; Eschtruth et al. 2006). These factors that have the potential to alter future forest composition should be considered in post-HWA projections in Ohio and elsewhere.

1.5: Hemlock & HWA in Southeast Ohio

Black and Mack (1976) were among the first to attempt to characterize Ohio's isolated hemlock forests, classifying them into four habitat types based on composition of both woody and herbaceous species. All four types are described as "floristically distinct" compared to more northern (Canadian and New England) populations. They also differ considerably from stands in the central and southern Appalachian Mountains, both in elevation and in species composition. The rhododendron thickets observed in central and southern Appalachia (Martin & Goebel 2012, Brantley et al. 2013) are mostly absent from Ohio's hemlock forests. The pines and spruce noted by Martin at high elevations are also uncommon, given the lack of mountains in the state.

Like hemlock forests throughout the Appalachian region, though, Ohio's hemlocks are now also dealing with the threat of hemlock woolly adelgid. HWA was first spotted in southeast Ohio in 2012 and has since spread to several counties (Fig. 1.2). Since then, the Ohio Department of Natural Resources (ODNR) has used systemic pesticides to treat hemlock trees where infestations are discovered and protect trees in areas of high ecological or economic value. Pesticides are one component of an integrated pest management system, with *Laricobius nigrinus* and *L.osakensis* beetles also being released at some sites to establish a biocontrol species (ODNR 2017).

While treatment and prevention efforts like these may prevent or delay mortality in select hemlock stands, the ODNR and other land-owning groups simply cannot afford to treat every hemlock. Hemlock mortality and a subsequent response in the forest community will surely occur in untreated stands eventually, just as these processes have occurred throughout the Appalachians. Some recent studies have begun to establish baseline conditions in Ohio's hemlock forests prior to this transition.

In the hemlock forests of the Unglaciated Allegheny Plateau region of southeastern Ohio, Martin & Goebel (2013) found that hemlock dominated all layers, not demonstrating the curious lack of seedlings found in the northeastern part of the state. Hemlock was at its most dominant at the bottom of slopes, particularly near streams, where it was often accompanied by American beech, sweet birch, and tulip poplar. Of these, only tulip poplar and American beech represented more than 10% of the basal area. These species decreased upslope, with oaks and maples occurring in greater numbers on the upper slopes and ridge tops. Here we see another example of potential diverging communities in a post-HWA future at a fine scale related to slope position.

In short, the isolated nature of Ohio's hemlock stands, combined with a species composition which differs from what one might find elsewhere in the range of the species, make Ohio's hemlock forests unique compared to stands in adjacent states. 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 hemlock. While studies like Martin and Goebel's help to establish baseline conditions in southern Ohio's hemlock stands, these forests remain understudied and many questions about them unanswered. As such, the goal of this thesis is to expand our current understanding of these understudied forests in southeast Ohio's Hocking Hills region, a deeply dissected part of the larger 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. Specifically, the study addresses the following research questions:

- What is the current composition and structure of hemlock forests throughout the Hocking Hills region?
- How have these hemlock stands changed in the past decade in terms of growth, mortality, composition, and structure?
- 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 replace hemlock following HWA-induced mortality in the Hocking Hills, either by growing in response to hemlock loss or seeding in from above?

- What invasive species are present and may potentially alter post-HWA succession in these forest communities?

2. Methods

2.1: Study Area

Thirty plots measuring 20 x 40 m (800 m^2) were initially established and surveyed by Dr. James Dyer (unpublished) and Nicole Stump (Stump 2008) from 2008-2011 in order to record baseline conditions in the hemlock stands of southeastern Ohio, before the arrival of HWA. These sites are located within and around the Hocking Hills region in Hocking and Jackson Counties. Included in these sampling locations are Clear Creek Metro Park, Crane Hollow Preserve, two Hocking Hills State Parks (Ash Cave and Old Man's Cave), two State Nature Preserves (Lake Katharine and Sheick Hollow) and Hocking State Forest lands located just outside Cantwell Cliffs State Park as well as in Hamilton and Red Rock Hollows, Long Hollow, Rocky Branch, and Spruce Run (Figure 2.1). Two to three plots were established at each site.

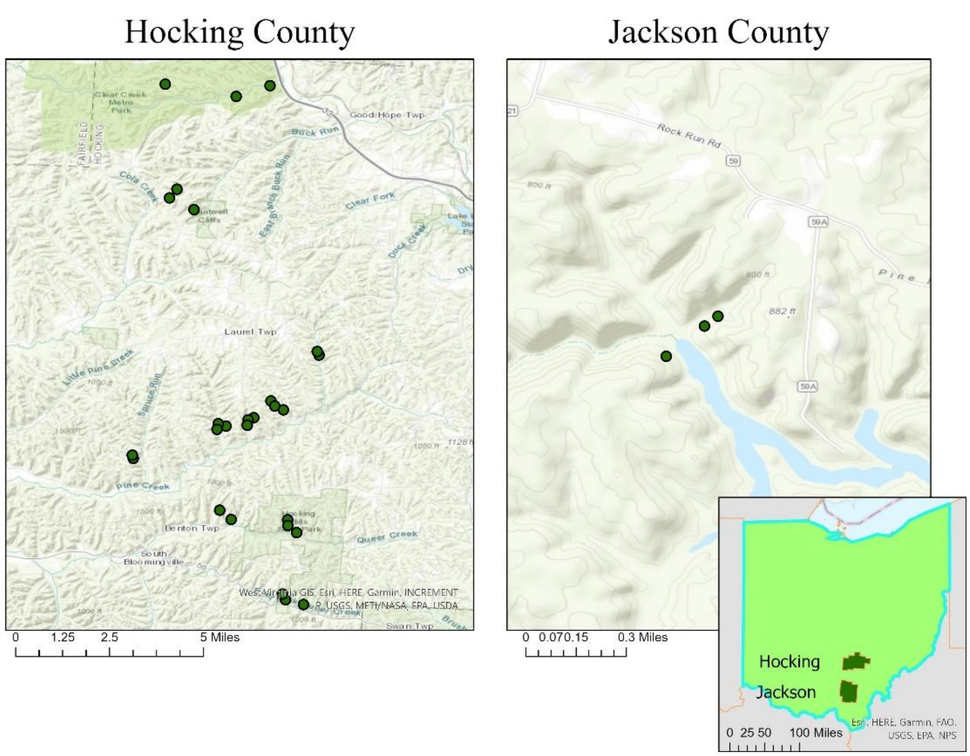

Figure 2.1: Locations of plots

All plots were purposefully located in hemlock-dominated forest stands. They were situated to avoid edge effects (≥100m from roads), though Cantwell Cliffs plot C was situated approximately 80m from a field and access road maintained by a natural gas company. These stands are best described as secondary growth forests, with tree cores (see Appendix 7.3) indicating establishment of a majority of adult trees in the late 1800s or early 1900s. The soil is shallow and acidic (pH ranges from 4.0 to 5.6), and often strewn with boulders. Generally, they occur in lower positions within ravines or on the sides of slopes, as is typical of hemlock stands in southeast Ohio.

2.2: Field Sampling of Hemlock Forests

Plots are permanently marked at the corners with rebar and PVC pipe, established with the long (40 m) axis parallel to the contour of the slope. All trees ≥8 cm in diameter at breast height (DBH) are tagged with aluminum tree tags. GPS coordinates allowed me to locate the plots and replicate past sampling of tagged trees. This included measurement of DBH (Fig. 2.2), the crown class of trees (Table 2.1), and hemlock vigor (a measure of health based on percentage of remaining green foliage; Table 2.2).

Figure 2.2: The author in the process of measuring the DBH of a hemlock in Cantwell Cliffs in September 2020.

Table 2.1: Crown classes assigned to each tree during field measurement

Crown Class	**Definition**
Dominant (D)	Canopy is well above its neighbors with no competition for light
Codominant (C)	Canopy is competing with only one other neighbor for light
Intermediate (I)	Canopy is on roughly the same level as the surrounding forest, competing with two or more neighbors for light.
Suppressed (S)	Tree is overtopped by the rest of the forest, existing in a light-limited environment

Table 2.2: Hemlock vigor classes assigned during field measurement

Hemlock Vigor Class	Percentage of Remaining Foliage
1	76-100
2	51-75
3	26-50
4	1-25
5	Dead

Additionally, all saplings, defined as woody plants < 8 cm in diameter and ≥ 1 m in height, were tallied by species. Any former saplings which had grown larger than this size category since the original surveys were tagged and measured. Evidence of the presence of HWA was also assessed at all plots by inspecting the underside of hemlock branches for woolly ovisacs from the previous winter.

A range of environmental data also exists for these plots from previous samplings, including slope and aspect measurements, tree core age estimates, and a combination of soil sample data (including carbon and nitrogen, pH, temperature and moisture) and climate data (temperature and humidity) collected by data loggers. Panoramic photos were also taken during the initial surveys, as well as hemispheric photos for assessing canopy cover.

2.3: Field Sampling of Surrounding Deciduous Stands

Since hemlock stands are largely constrained to valley settings in this part of its range, 500 m^2 transects were established above each plot in order to identify species most likely to seed in following loss of hemlock to HWA. Transects were placed at the boundary of the hemlock stand, or if there was no clear boundary (which was often the case) then the nearest point at which non-hemlock species outnumber the hemlocks. Transects measuring 10 x 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 crown class of all non-hemlock trees ≥8 cm in diameter were recorded. Special attention was also given to identifying and recording any invasive plant species in or around both plots and transects. These species could certainly play a role in shaping the post-HWA forest community, growing in number in response to the disturbance and subsequent availability of resources such as light. As such, the potential for these species to outcompete native plants was considered while sampling.

2.4: Data Analysis

Descriptive statistics were calculated to establish baseline conditions in both plots and transects prior to HWA-induced mortality and evaluate how the composition and structure of plots have changed since they were initially surveyed roughly a decade ago. Relative density and dominance (basal area) were computed for individual plots and transects. These metrics, along with relative frequency of occurrence, were also calculated for individual species across the combined study area. These metrics allow for the importance value of individual species ($\frac{RD+RBA+RF}{3}$) within the sampled community to be determined for trees ≥8 cm DBH. Only density and frequency metrics were computed for saplings since DBH was not recorded for this size class. Furthermore, dead trees, although they were recorded, were not included in calculations because they were no longer utilizing resources and thus were not contributing to competition. Additionally, these calculations were also performed with a dataset in which hemlock had been removed to more easily compare non-hemlock species in the plots versus the transects above.

Growth and mortality rates were calculated by comparing the 2020 resurvey data to that of the initial surveys in 2008-2011. Finally, size class histograms were created for species with greater than ten individuals present to infer age distributions. A more in-depth description of these equations and methods can be found in the appendix (section 7.4).

3. Results

3.1: Characterization of Baseline Conditions of Hemlock Stands

Eastern hemlock remains by far the dominant species in all plots (obvious in the canopy and ground views in Fig. 3.1), despite some mortality (section 3.2). With an overall importance value of 47.78 (Table 3.1) across the study area, no other species in the plots compare to it in terms of abundance or basal area. However, a small number of deciduous species stand out as common non-hemlock components of the community. These include tulip poplar (IV=7.80), chestnut oak (IV=7.31), white oak (IV=6.28), red maple (IV=6.07), and sweet birch (IV=5.71). Sourwood (*Oxydendrum arboreum*; IV=3.94), although not particularly significant in terms of basal area, is also a common sight in the understory across the study area (40% frequency of occurrence). This is similar in frequency to American beech, though beech occurs in lower densities.

Figure 3.1: Examples of hemlock forest typical for the study area, including a canopy view of the area surrounding Old Man’s Cave plot C and ground view of the hemlock forest just beyond Sheick Hollow plot B.

Table 3.1: Descriptive metrics for each species across all 30 plots, including absolute and relative density, absolute and relative basal area, percent frequency and relative frequency, and importance value. Initial (c. 2010) sampling data as well as current (2020) data are displayed side-by-side.

Common Name	Spp	Number c. 2010	Number 2020	Abs Dens (t/ha) c.2010	Abs Dens (t/ha) 2020	Rel Dens (%) c. 2010	Rel Dens (%) 2020	Abs BA (m2/ha) c. 2010	Abs BA (m2/ha) 2020	Rel Dom (%) c.2010	Rel Dom (%) 2020	Percent Freq c. 2010	Percent Freq 2020	Rel Freq (%) c.2010	Rel Freq (%) 2020	Importance Value c.2010	Importance Value 2020
Red maple	ACRU	48	40	20.00	16.67	3.79	3.62	1.54	1.47	3.17	2.97	63.33	60.00	11.59	11.61	6.18	6.07
Sugar maple	ACSA	23	18	9.58	7.50	1.82	1.63	0.50	0.42	1.03	0.84	26.67	26.67	4.88	5.16	2.57	2.54
Sweet birch	BELE	59	52	24.58	21.67	4.66	4.70	2.06	2.00	4.22	4.03	46.67	43.33	8.54	8.39	5.81	5.71
Bitternut hickory	CACO	1	0	0.42	0.00	0.08	0.00	0.09	0.00	0.19	0.00	3.33	0.00	0.61	0.00	0.29	0.00
Pignut hickory	CAGL	9	9	3.75	3.75	0.71	0.81	0.35	0.38	0.72	0.76	16.67	16.67	3.05	3.23	1.49	1.60
Shellbark hickory	CALA	3	2	1.25	0.83	0.24	0.18	0.07	0.06	0.15	0.12	6.67	6.67	1.22	1.29	0.54	0.53
American beech	FAGR	25	24	10.42	10.00	1.97	2.17	2.10	2.22	4.31	4.47	43.33	40.00	7.93	7.74	4.74	4.80
Green ash	FRPE	2	1	0.83	0.42	0.16	0.09	0.18	0.14	0.38	0.28	6.67	3.33	1.22	0.65	0.59	0.34
Tulip poplar	LITU	55	51	22.92	21.25	4.34	4.61	4.42	4.85	9.07	9.76	46.67	46.67	8.54	9.03	7.32	7.80
Black gum	NYSY	6	4	2.50	1.67	0.47	0.36	0.25	0.17	0.51	0.35	20.00	13.33	3.66	2.58	1.55	1.10
Ironwood	OSVI	1	0	0.42	0.00	0.08	0.00	0.00	0.00	0.01	0.00	3.33	0.00	0.61	0.00	0.23	0.00
Sourwood	OXAR	42	32	17.50	13.33	3.31	2.89	0.63	0.59	1.30	1.18	40.00	40.00	7.32	7.74	3.98	3.94
Black cherry	PRSE	1	0	0.42	0.00	0.08	0.00	0.02	0.00	0.05	0.00	3.33	0.00	0.61	0.00	0.24	0.00
White oak	QUAL	40	36	16.67	15.00	3.16	3.25	3.80	3.90	7.81	7.85	40.00	40.00	7.32	7.74	6.09	6.28
Scarlet oak	QUCO	6	5	2.50	2.08	0.47	0.45	0.50	0.37	1.04	0.75	6.67	6.67	1.22	1.29	0.91	0.83
Chestnut oak	QUMO	57	57	23.75	23.75	4.50	5.15	3.70	4.17	7.61	8.39	43.33	43.33	7.93	8.39	6.68	7.31
Red oak	QURU	10	10	4.17	4.17	0.79	0.90	1.17	1.29	2.40	2.59	20.00	20.00	3.66	3.87	2.28	2.46
Black oak	QUVE	3	3	1.25	1.25	0.24	0.27	0.24	0.27	0.50	0.54	10.00	10.00	1.83	1.94	0.86	0.92
Eastern hemlock	TSCA	876	762	365.00	317.50	69.14	68.90	27.06	27.36	55.55	55.09	100.00	100.00	18.29	19.35	47.66	47.78

In addition to their high number in the plots, the reverse-J curve displayed in the size class analysis of eastern hemlock (Fig. 3.2) clearly shows recruitment, with smaller and presumably younger individuals in the greatest abundance. Size class distribution graphs for important deciduous species are displayed in Figure 3.3, in which it can be seen that red maple and sourwood are most numerous in the smaller size classes, while tulip poplar, white oak and chestnut oak display a unimodal distribution, indicating overrepresentation in the larger size classes and a decrease in recruitment.

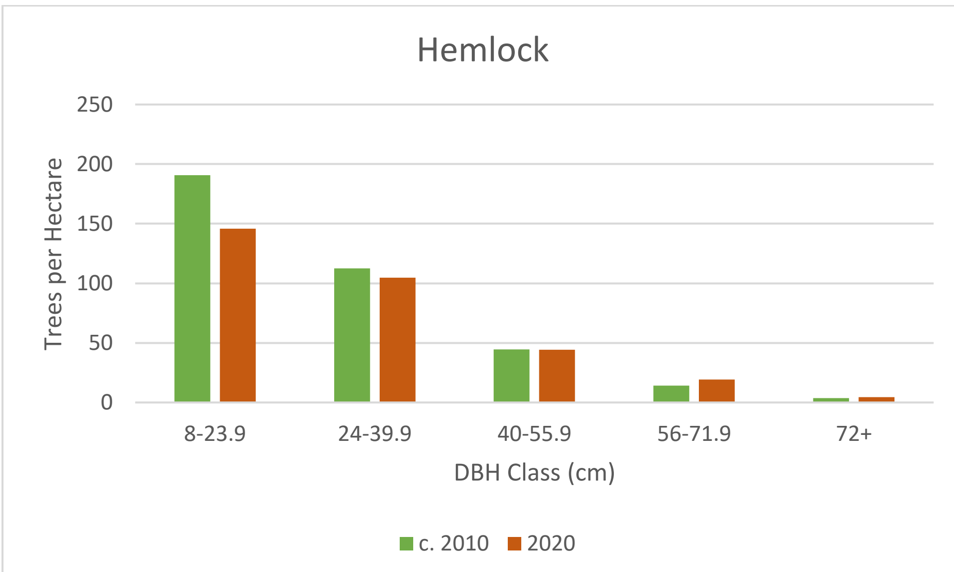

Figure 3.2: Eastern hemlock size distribution (c. 2010 and 2020) across all 30 plots.

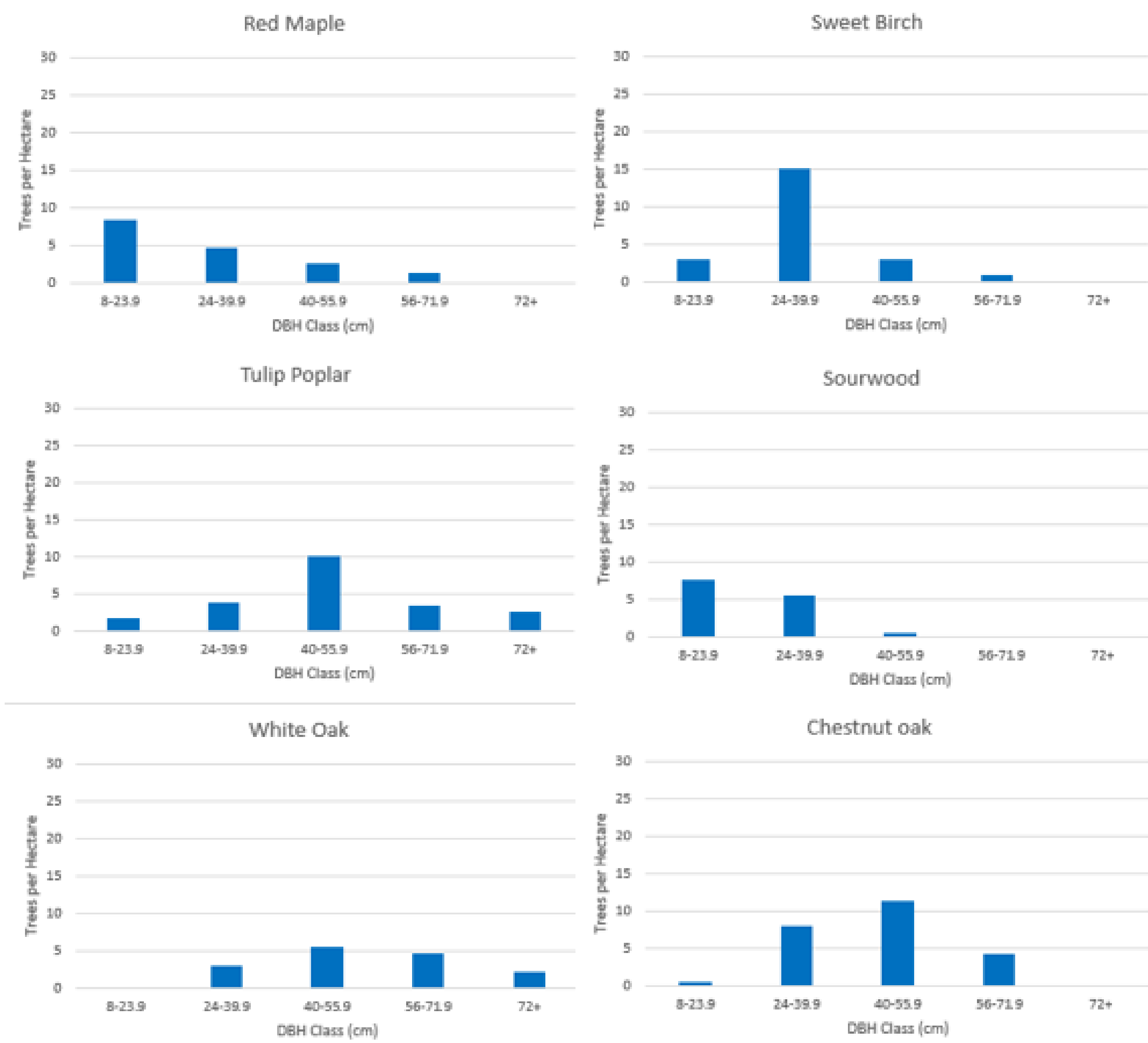

Figure 3.3: Size class distribution graphs of other major (non-hemlock) species across the 30 plots, as measured in 2020.

3.2: Change Over Time: Mortality and Growth Rates

Hemlock remains the dominant species in all plots since initial sampling. However, it is clear from the decline in individuals of smaller size classes (Fig. 3.2), as well as in overall mortality rates (Table 3.2), that hemlock as a whole has experienced significant mortality in several plots. Cantwell Cliffs plot C in particular stands out as having especially high mortality. Eight of 19 trees, mostly intermediate in crown class, died over the course of the study period, a mortality rate of greater than 42%. Other plots with high mortality rates displayed clear evidence of storm damage, usually in the form of clustered fallen or snapped trees of various sizes, such as in Old Man's Cave plots A and B or both plots at Rocky Branch. However, this was not the case for all plots which had experienced high mortality, such as in Cantwell Cliffs where half the dead trees were still standing. No direct evidence of the presence of hemlock woolly adelgid was discovered, but according to Tom Macy, a forestry program administrator with the Ohio Department of Natural Resources Division of Forestry, the Cantwell Cliffs area is believed to be "infested" with HWA based on prior observations (personal communication via email, October 2020). Hemlock mortality was often much more pronounced in the sapling size class (Table 3.2), though there was a great deal of variance in initial sapling abundance, with some plots having few or no saplings and others having over one hundred. In addition, recruitment of hemlocks was much less common than mortality, with only two new individuals (both at Cantwell Cliffs plot B) growing into the 8+ cm size range, and only four of thirty plots displaying an increase in the number of saplings of any species.

Table 3.2: Mortality rates of adult hemlock trees (≥8 cm DBH) and hemlock saplings (<8 cm DBH, ≥1 m in height) at each plot sampled.

	Adults			Saplings		
Plot	Number c. 2010	Number 2020	Mortality (%)	Number c. 2010	Number 2020	Mortality (%)
Ash Cave A	54	51	5.56	59	26	55.93
Ash Cave B	29	23	20.69	12	8	33.33
Ash Cave C	37	36	2.70	27	21	22.22
Cantwell Cliffs A	21	17	19.05	19	16	15.79
Cantwell Cliffs B	12	10	16.67	0	0	NA
Cantwell Cliffs C	19	11	42.11	3	1	33.33
Clear Creek A	18	17	5.56	0	0	NA
Clear Creek B	16	16	0.00	1	1	0.00
Clear Creek C	23	23	0.00	3	3	0.00
Crane Hollow A	19	17	10.53	108	62	42.59
Crane Hollow B	37	33	8.11	7	2	71.43
Crane Hollow C	39	34	2.56	3	1	66.67
Hamilton-Red Rock B	43	31	27.91	15	19	0.00
Hamilton-Red Rock C	43	37	13.95	12	14	0.00
Lake Katharine A	22	22	0.00	9	7	22.22
Lake Katharine B	30	28	3.33	11	6	45.45
Lake Katharine C	26	25	4.00	26	19	26.92
Long Hollow A	31	26	16.13	8	17	0.00
Long Hollow B	25	23	8.00	84	24	71.43
Long Hollow C	29	27	6.90	75	32	57.33
Old Man's Cave A	18	14	22.22	11	2	81.82
Old Man's Cave B	44	33	25.00	8	3	62.50
Old Man's Cave C	28	27	3.57	11	11	0.00
Rocky Branch B	55	48	12.73	34	15	55.88
Rocky Branch C	37	31	16.22	65	39	40.00
Sheick Hollow A	25	21	16.00	15	10	33.33
Sheick Hollow B	24	20	16.67	62	22	35.48
Sheick Hollow C	34	29	14.71	8	13	0.00
Spruce Run A	13	10	23.08	2	0	100.00
Spruce Run B	25	22	12.00	29	13	55.17
Average	29.20	25.40	12.53	24.23	13.57	36.74

Though hemlock mortality was highly variable between plots (Table 3.3), the overall mortality rate (13.24%) is similar to other common species like red maple (16.67%), sweet birch (11.86%), and white oak (10.00%, Table 3.3). Multiple oak species (*Q. montana, Q. rubra, and Q. velutina*) as well as pignut hickory (*Carya glabra*) stand out as having experienced no mortality. By contrast, three species were lost entirely between initial surveys and the 2020 resampling, including bitternut hickory (*Carya cordiformis*), ironwood (*Ostrya virginiana*), and black cherry, though each of these species only had one initial representative.

Annual hemlock growth rate in each individual plot, calculated by change in DBH averaged over the sampling period, can be found in Figure 3.4. There exists some variation from plot to plot, with Clear Creek Metro Park standing out as an outlier. The trees at this location grew noticeably more than hemlocks in all other plots, becoming the only hemlocks to achieve greater than 2% annual growth. Overall, the average annual growth rate of hemlock (1.18%) is comparable to a number of other species within the plots (Table 3.3). Tulip poplar stands out as a clear leader in terms of growth wherever it occurs, with an average annual growth rate of 3.08%, compared with growth rates of less than 1% for most other species. Across the 30 plots, high mortality rate was not related to increased growth rate in the surviving trees.

Table 3.3: Average annual growth rates and total mortality rates for all species recorded in plots

Scientific Name	Common Name	Spp	Number c. 2010	Number 2020	Mortality Rate (%)	Annual Growth Rate (%)
Acer rubrum	Red maple	ACRU	48	40	16.67	1.01
Acer saccharum	Sugar maple	ACSA	23	18	21.74	0.76
Betula lenta	Sweet birch	BELE	59	52	11.86	1.36
Carya cordiformis	Bitternut hickory	CACO	1	0	100.00	NA
Carya glabra	Pignut hickory	CAGL	9	9	0.00	0.89
Carya laciniosa	Shellbark hickory	CALA	3	2	33.33	0.17
Fagus grandifolia	American beech	FAGR	25	24	4.00	1.97
Fraxinus pennsylvanica	Green ash	FRPE	2	1	50.00	0.45
Liriodendron tulipifera	Tulip poplar	LITU	55	51	7.27	3.08
Nyssa sylvatica	Black gum	NYSY	6	4	33.33	0.61
Ostrya virginiana	Ironwood	OSVI	1	0	100.00	NA
Oxydendrum arboreum	Sourwood	OXAR	42	32	23.81	1.26
Prunus serotina	Black cherry	PRSE	1	0	100.00	NA
Quercus alba	White oak	QUAL	40	36	10.00	1.20
Quercus coccinea	Scarlet oak	QUCO	6	5	16.67	0.80
Quercus montana	Chestnut oak	QUMO	57	57	0.00	1.26
Quercus rubra	Red oak	QURU	10	10	0.00	0.85
Quercus velutina	Black oak	QUVE	3	3	0.00	1.23
Tsuga canadensis	Eastern hemlock	TSCA	876	762	13.24	1.18

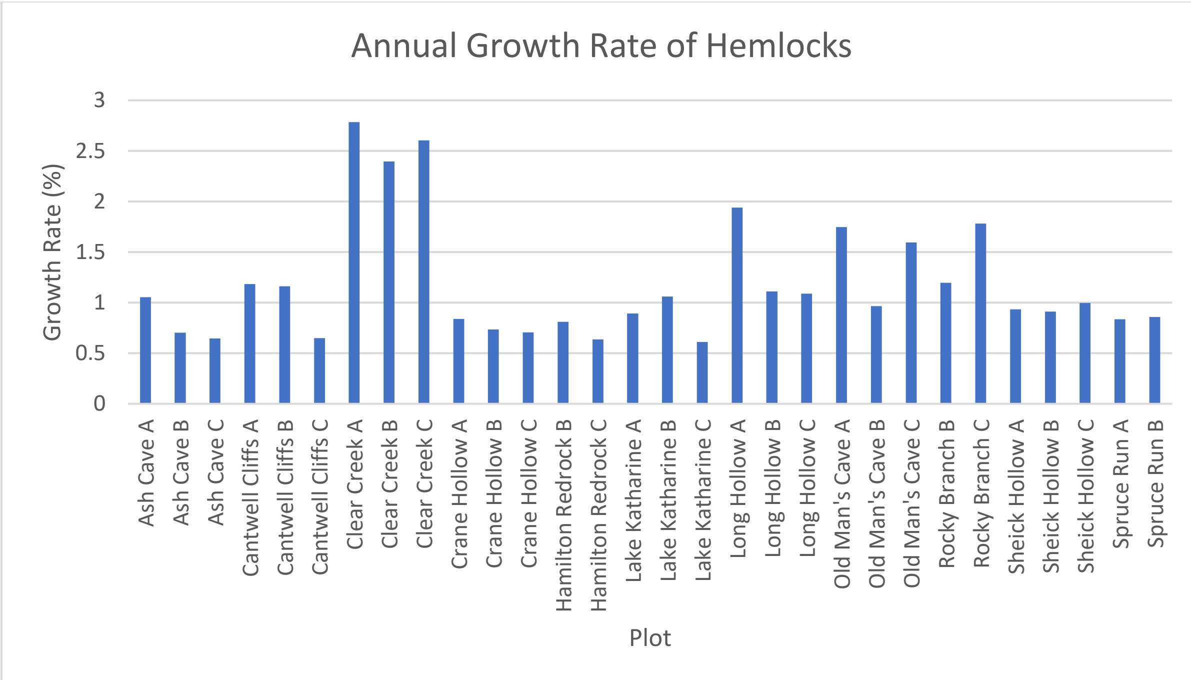

Figure 3.4: Average annual growth rates of hemlocks in each sampled plot.

3.3: Composition of Transects and Comparison with Hemlock Plots

A transect was established above each plot to characterize the potential seed source following hemlock mortality. Since hemlock was not measured in the transects, the descriptive metrics in Table 3.1 were recalculated after removing hemlock to allow direct comparison between plots and transects (Table 3.4).

Table 3.4: Number of trees ≥8 cm DBH and descriptive metrics (relative density, dominance, frequency, and importance value) for thirty 800 m^2 plots and 500 m^2 transects sampled in 2020. Calculations exclude hemlock occurring in the sampled areas.

Common Name	Spp	Number in Plots	Number in Transects	Plot Rel Dens (%)	Transect Rel Dens (%)	Plot Rel Dom (%)	Transect Rel Dom (%)	Plot Rel Freq (%)	Transect Rel Freq (%)	Plot Importance Value	Transect Importance Value
Red maple	ACRU	40	100	11.63	22.57	6.61	10.60	14.40	15.17	10.88	16.12
Sugar maple	ACSA	18	10	5.23	2.26	1.88	0.57	6.40	2.07	4.50	1.63
Sweet birch	BELE	52	10	15.12	2.26	8.98	1.78	10.40	4.14	11.50	2.72
Pignut hickory	CAGL	9	10	2.62	2.26	1.70	1.41	4.00	5.52	2.77	3.06
Shellbark hickory	CALA	2	0	0.58	0.00	0.26	0.00	1.60	0.00	0.81	0.00
Mockernut hickory	CATO	0	2	0.00	0.45	0.00	0.24	0.00	0.69	0.00	0.46
American beech	FAGR	24	22	6.98	4.97	9.97	2.37	9.60	8.28	8.85	5.20
Green ash	FRPE	1	0	0.29	0.00	0.62	0.00	0.80	0.00	0.57	0.00
Tulip poplar	LITU	51	7	14.83	1.58	21.74	4.01	11.20	2.07	15.92	2.55
Black gum	NYSY	4	11	1.16	2.48	0.78	1.11	3.20	2.07	1.71	1.89
Sourwood	OXAR	32	36	9.30	8.13	2.64	1.54	9.60	10.34	7.18	6.67
Pitch Pine	PIRI	0	11	0.00	2.48	0.00	1.67	0.00	4.14	0.00	2.76
White oak	QUAL	36	72	10.47	16.25	17.49	23.96	9.60	15.17	12.52	18.46
Scarlet oak	QUCO	5	0	1.45	0.00	1.66	0.00	1.60	0.00	1.57	0.00
Chestnut oak	QUMO	57	111	16.57	25.06	18.69	33.70	10.40	15.86	15.22	24.87
Red oak	QURU	10	32	2.91	7.22	5.78	14.55	4.80	11.03	4.50	10.94
Black oak	QUVE	3	5	0.87	1.13	1.21	2.16	2.40	2.07	1.49	1.79
Sassafras	SAAL	0	4	0.00	0.90	0.00	0.34	0.00	1.38	0.00	0.88

Three new species appeared in the transects: mockernut hickory (*Carya tomentosa*), pitch pine (*Pinus rigida*), and sassafras. 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. For example, red maple became more important (with its IV increasing from 10.88 to 16.12), largely due to a major increase in abundance and frequency, increasing in density roughly twofold. Meanwhile, the opposite trend occurred in sugar maple, which became less abundant, resulting in a decrease in IV from 4.50 to 1.63. 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).

In the plots, chestnut oak was also among the most important deciduous species, with the second highest importance value (15.22). Tulip poplar was the most important deciduous species in the plots (IV= 15.92), as it has the highest basal area (relative dominance= 21.74%) and among the highest density and frequency. However, tulip poplar became rare moving upslope to the transects (with only seven individuals and an IV of 2.55). Though not as dramatic, a similar trend is seen in sweet birch and American 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. 3.5) 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 may have numerous individuals, but those individuals are more often than not found in the smaller size classes. The size class distributions of red maple, sourwood, and white and chestnut oak in the transects are quite similar to their distributions in the plots (Fig. 3.3), though the number of trees per hectare in the latter is significantly lower due to the sheer abundance of hemlocks there.

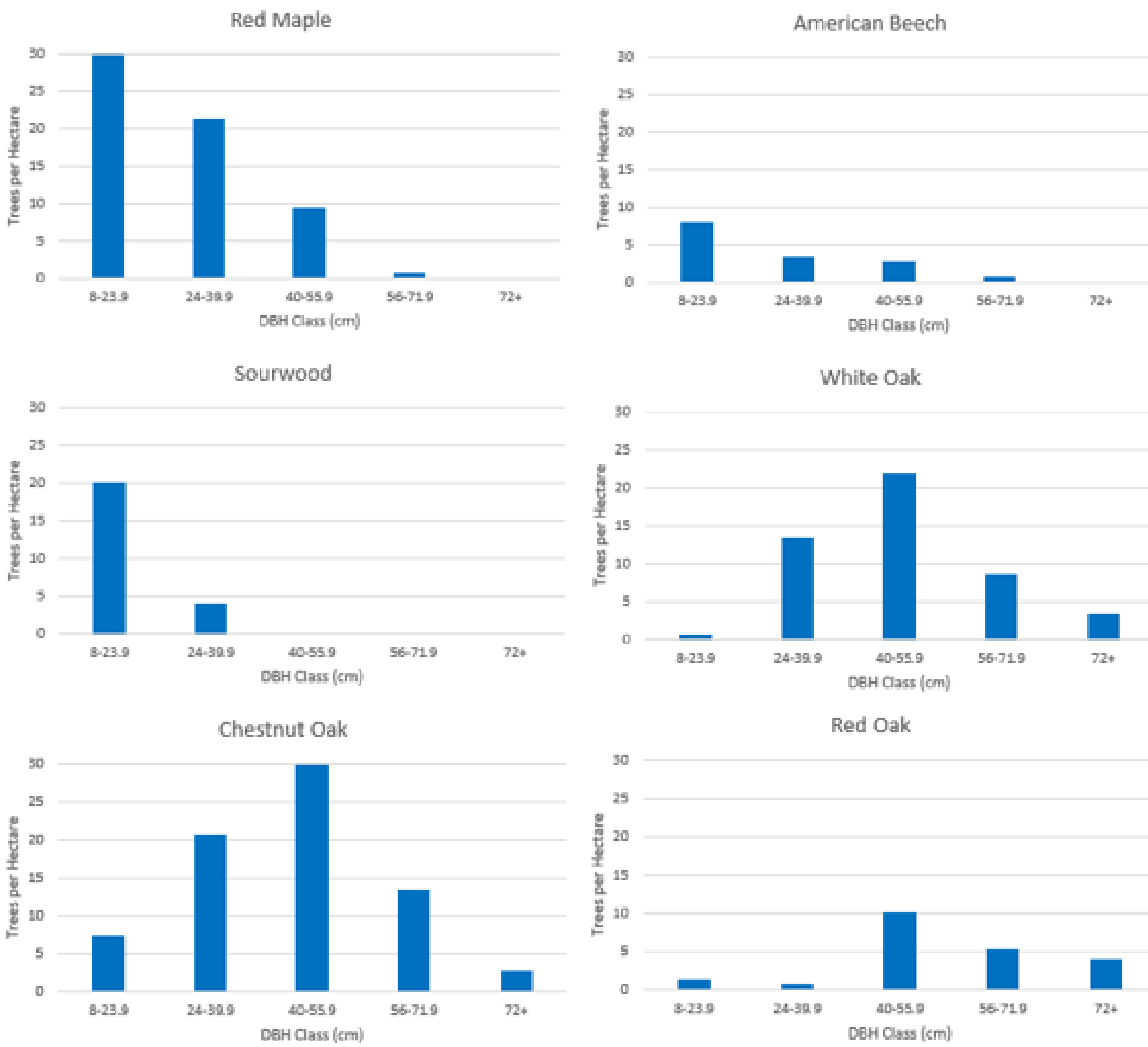

Figure 3.5: Size class distributions of major species in sampled transects.

In short, moving upslope has a negative effect on the competitive ability of hemlock, resulting in a greater abundance of certain deciduous species. Red maple, white oak, and chestnut oak are dominant non-hemlock species in the plots which become more dominant in the transects upslope and on ridgetops (and thus away from the dominance of hemlock). In contrast, tulip poplar, sweet birch, and American beech, which also are important non-hemlock species in the plots, become significantly less so in the transects.

3.4: Invasive Species

Invasive species were observed in or near one-third of all sites (plot-transect pairs). Garlic mustard (*Alliaria petiolata*) was found between Clear Creek plot B and transect B, and Japanese barberry (*Berberis thunbergii*) was found a mere few meters from Ash Cave plot B. The Cantwell Cliffs plots appeared to be especially plagued with invasive plants. Multiflora rose (*Rosa multiflora*) was discovered near Cantwell Cliffs plot B and autumn olive (*Elaeagnus umbellata*) was found within the same plot, while Japanese stiltgrass (*Microstegium vimineum*) lined the service road just above plot C. Stiltgrass was by far the most frequently encountered invasive species in the study area, as it was also noted along the roadside just below Ash Cave plot C, on the cliffside at Sheick Hollow transect A, and along the bridle trail just below all three plots at Long Hollow. Though only a small patch of stiltgrass was discovered at Sheick Hollow, populations of the species found at the other locations mentioned tended to be large and dense, especially along trails and roads. No other invasive species was represented by more than a few scattered individuals at the time of sampling.

4. Discussion

4.1: Characterization of Baseline Conditions of Hemlock Stands

Given that the plots were purposefully placed in these hemlock-dominated stands, and that hemlock woolly adelgid has arrived in Ohio only recently, it is unsurprising that eastern hemlock remains the dominant tree species in all plots. The abundance of hemlock trees among smaller DBH size classes also shows recent recruitment, as these smaller trees are presumed to represent younger individuals. Hemlock also represents by far the most abundant and frequently encountered species in the sapling size class, present at least in small numbers in the majority of sites. This was also the case in Martin & Goebel's 2013 study of nearby Unglaciated Allegheny Plateau plots.

Hemlock may represent a large majority of the trees in the sampling plots, but there are a number of deciduous species growing among them. Tulip poplar stands out as the most important non-hemlock species, accounting for the greatest portion of the basal area aside from hemlock itself. While tulip poplar has a high frequency of occurrence across the plots, the density of this distribution is far from even, with a small number of plots accounting for much of its basal area. Clear Creek plot A, Crane Hollow plot A, and all three Cantwell Cliffs plots supported large numbers of tulip poplar, often attaining large sizes in each of those locations. Additionally, Cantwell Cliffs plot B is exceptional in that tulip poplar is the only deciduous species in the adult size class. None of these plots are distinguished from other plots in the study in terms of slope, aspect, soil, or age, nor do they even appear to be especially similar to one another. Therefore, as a pioneer species (Beck 1990), perhaps tulip poplar simply dominates in plots where it was able to successfully colonize past gaps in the canopy, rather than sites currently exhibiting particular characteristics. Two oak species- chestnut oak and white oak- also commonly occur throughout the plots. Though there are more chestnut oaks than tulip poplars overall, it is not as dominant largely due to its smaller size on average. Still, both chestnut oak and white oak are among the non-hemlock species which attain the highest diameters overall.

Red maple, sweet birch, and sourwood are also relatively abundant but are generally smaller than tulip poplar or oak, occurring primarily in smaller size classes (<40 cm DBH). Red maple had the highest frequency of occurrence of any non-hemlock species and among the highest densities as well, indicating a high number of these smaller trees across the plots. While the frequency of occurrence of sweet birch was also relatively high, it was found in large numbers in only a few select plots, similar to tulip poplar. Sourwood, meanwhile, had among the highest densities but remained at such small diameters that it accounts for only a small portion of the basal area. American beech offers a good comparison in this case, as its relative frequency was equal to that of sourwood. While sourwood was more numerous, the relative dominance of American beech was over three times greater, demonstrating sourwood's overall low basal area despite its commonness.

In short, hemlock is still the dominant species across the plots by far, but several deciduous species occur alongside it in significant numbers. Non-hemlock species which are already in the canopy would be the first to grow and dominate in response to hemlock mortality, likely maintaining dominance in the formerly hemlock-dominated ravine and slope positions. These deciduous species vary in terms of density, dominance, frequency, and size class distribution.

The importance of tulip poplar and sweet birch is similar to observations made elsewhere in southeast Ohio by Martin and Goebel (2013). The prevalence of sweet birch is perhaps especially important, as studies of post-HWA forests often indicate birches as being among the first trees to respond to hemlock mortality (Orwig & Foster 1998, Small 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). However, the prevalence of chestnut oak and white oak in this study's plots stands out, as oaks only became important species at the ridge top positions of Martin and Goebel's Hocking Hills sites. The relative abundance of oak below the ridge tops is actually more similar to trends seen in the smaller hills of the Glaciated Allegheny Plateau of northeast Ohio (Macy 2012) or even Connecticut (Orwig & Foster 1998). This suggests that, in the event of HWA-induced hemlock mortality, a mixture of deciduous trees including both mesophytic species and typically xerophytic oaks would likely come to dominate these plots.

4.2: Change in Plots Over Time: Recruitment & Growth

Though the majority of plots contained hemlock saplings, only a small number of non-hemlock saplings were noted at most plots, but in this regard there are also a few exceptions. Cantwell Cliffs plot B was the site of a large number of spicebush (*Lindera benzoin*) stems, and Spruce Run plot A had experienced an incredible increase in American beech saplings (Fig. 4.4) since initial sampling. 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 & Goebel 2012, Brantley 2013). Furthermore, although spicebush will remain confined to the shrub layer by its small size, the beech saplings seen at Spruce Run could very well represent the post-HWA generation of canopy trees at this site. After all, these already abundant saplings would likely experience a growth response similar to that seen in the sapling layer of the Delaware Water Gap (Eschtruth et al. 2006) due to the increase in light availability following hemlock mortality. In this way these beech and other deciduous saplings differ from the much more commonly seen hemlock saplings in the study area, the majority of which would eventually also succumb to HWA without human intervention.

Figure 4.1: Dense growth of American beech saplings in Spruce Run plot A, likely as a result of the sparse growth of adult trees in this plot (photo by author).

The average growth rate among adult hemlocks was similar to that of other common species in the plots, with the exception of tulip poplar, which is known to exhibit rapid growth (Beck 1990). However, as noted in the Results, the Clear Creek plots represented a deviation from the average, attaining annual growth rates ≥2% compared to typical growth rates of around 1% or less. Examination of tree core data (see Appendix 7.3) revealed that the trees of Clear Creek were not significantly younger than those of other plots, nor did these plots differ significantly in density. This relatively rapid growth was also seen regardless of the size or crown class of the trees, with the largest trees experiencing growth rates similar to their smaller neighbors. As such, the high growth rate of hemlocks in the Clear Creek plots remains unexplained. Also somewhat mysterious is the fact that one would expect a high rate of mortality to result in a high rate of growth in surviving trees due to the decrease in competition for resources, but no such pattern was observed across the study area.

4.3: Change in Plots Over Time: Mortality

Although hemlock clearly remains dominant throughout all plots, a varying degree of hemlock mortality has occurred over the decade since initial sampling. The study area includes plots which have experienced a wide range of mortality, from no hemlock mortality whatsoever in some plots all the way up to 42% mortality seen at Cantwell Cliffs plot C.

Cantwell Cliffs plot C is located below a state forest road just outside the northernmost portion of Hocking Hills State Park. It contains some fallen trees toward the bottom of the slope (Fig. 4.2). However, over half of the dead hemlocks noted 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 (which was seen in a number of other plots). Although no direct evidence of the presence of hemlock woolly adelgid was discovered in plot C, these standing dead trees may represent HWA-induced mortality. Indeed, forestry program administrator Tom Macy confirmed that “extensive HWA infestation” has been discovered in the Cantwell Cliffs area. Larger adult 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, but not 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.

Figure 4.2: Fallen hemlock trees at Cantwell Cliffs plot C (photo by author).

Elsewhere in the study area, increased mortality was associated with apparent wind and storm damage. Snapped and fallen trees were found in clusters including multiple species and size classes across a number of plots. Ash Cave plot B was the site of multiple snapped and uprooted trees as well as a single burnt stump, likely the result of a lightning strike. At Long Hollow plot A, a cluster of fallen trees included not only hemlock but also the only bitternut hickory and ironwood individuals in the plots. Old Man's Cave plots A and B and Rocky Branch plots B and C also experienced significant mortality (examples in Fig. 4.3 below). According to email communications with ODNR Forest Manager David Glass (December 2020), “multiple wind events” have recently contributed to an increase in downed trees across the state forest. Furthermore, the rate of hemlock mortality for all 30 plots combined was similar to that of other common species (Table 3.3), meaning mortality was not species-specific. As such, it seems that snapping and uprooting by wind were the leading cause of mortality for adult trees across much of the study area.

Figure 4.3: Examples of downed debris in Old Man’s Cave plot B (left) and Rocky Branch plot B (right), likely the result of wind and storms (photos by author).

Competitive thinning appears to be another major source of mortality among individuals in the smallest size class. This was especially apparent in both Hamilton-Red Rock plots, where mortality (particularly in plot B) was seen almost exclusively among small, suppressed hemlock individuals. The density of trees in these plots was especially high in the initial sampling, so it is likely that these small individuals were simply unable to compete for resources in this light-starved environment. One final plot exhibiting high mortality was Spruce Run plot A, but in this case the high rate of mortality is more likely an artifact of the low initial density of trees. Since Spruce Run plot A only included 18 individuals to begin with, the loss of a relatively small number of trees represents mortality of a comparatively large portion of the trees in the plot.

Much more severe in some cases was mortality among hemlock saplings. The initial number of saplings in the plots ranged from zero to over 100, so once again a high mortality rate does not always translate to a large number of dead trees. High mortality rates in plots with comparatively few saplings may be a result of random events or chance, as a similar number of plots (seven total) experienced no mortality of hemlock saplings. However, the plots with the highest number of saplings (>50) ca 2010 all experienced high mortality, losing anywhere from 35% to 71% of their saplings by 2020. Ash Cave plot A, Crane Hollow plot A, Long Hollow plots B and C, Rocky Branch plot C, and Sheick Hollow plot B all displayed this pattern. Therefore, this seems likely to be another case of competitive thinning among the smallest individuals in the plots where initial numbers are dense. An unusual possible exception to this rule was found at Hamilton-Red Rock. Both plots at this location experienced a small increase in saplings despite already dense growth of adult trees. Given the aforementioned mortality of adult hemlocks in the smallest size class, this at first seems unusual. However, this increase in saplings could perhaps be explained as a recent response to adult mortality. Whether or not that is the case, Hamilton-Red Rock plots B and C were among only four plots in which the number of saplings increased, and only two saplings in all thirty plots grew into the adult size class. Though competitive thinning appears to be an easily identifiable cause in several cases, it is clear that mortality rather than growth of hemlock saplings is much more common in these plots. Whether or not this trend is similar to that seen elsewhere in the range of eastern hemlock appears impossible to say, as little published research is available documenting hemlock mortality or growth rates outside of an HWA infestation context.

4.4: Composition of Transects and Comparisons to Plots

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. These conditions favor hemlock due to their shade tolerance and the need for moist soil for their seedlings to establish. For those same reasons, the hemlock population tends to diminish as one moves upslope toward the drier and more exposed upper slopes and ridge tops. This was certainly the case in this study's sites, as moving upslope (where the transects were established) always resulted in a reduction in hemlock and a corresponding increase in the density of non-hemlock species (Fig. 4.4). 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.

Figure 4.4: Winter in the Hocking Hills, clearly demonstrating the affinity of the evergreen eastern hemlock for ravine and slope environments, with deciduous species dominating the surrounding hilltops. (Image created by Nicole Stump).

Sugar maple, sweet birch, and tulip poplar all grew in significantly fewer numbers in the transects compared to the plots. Beech was also less important, but this was largely a result of reduced basal area, as there was not a major decrease in the number of individuals, but those individuals tended to be much smaller. Sugar maple, sweet birch, and tulip poplar changed very little in terms of size class distribution as one moved upslope, but experienced dramatic reductions in number. Such shifts should be expected, though, as all of these species tend to occur in the same moist conditions preferred by hemlock (Nowacki & Abrams 2008). As such, these mesophytic deciduous species are likely to maintain their positions in the sheltered lower valleys and could perhaps expand in number due to reduction in competition from hemlock mortality. Furthermore, although the numbers of these mesophytic species on the upper slopes and ridge tops are low, these trees could certainly seed in to the prime habitat below.

In contrast to sugar maple, the number of red maples more than doubled in the transects compared to the plots. Most of these trees are in the smaller size classes, indicating that the majority of red maples in the transects were recently recruited, similar to the plots below. Oaks were also well-represented in the transects, with white oak, chestnut oak, and red oak all growing in significantly higher number. All of these species are associated with more xeric upper slope or ridge positions in southeastern Ohio (Dyer & Hutchinson 2019), so the shift from hemlock-mixed hardwood to oak-maple stands moving upslope is easily explained by established topographic associations. For that reason, the transition toward oak domination on upper slopes and ridge tops is comparable to that seen elsewhere in hemlock's range. This trend has been observed from as nearby as other Unglaciated Allegheny Plateau sites (Martin & Goebel 2013) to as far as Connecticut (Small et al. 2005), though the black oak and scarlet oak seen in the latter are largely absent from this study's transects. Regardless of the exact species composition, though, previous studies have documented the potential for oak species in general to grow rapidly in response to hemlock mortality (Orwig & Foster 1998, Small et al. 2005). Due to their abundance in both the plots and the transects above, this growth response indicates that oak could relatively quickly become dominant components of the post-HWA canopy regardless of slope position.

However, studies which predict post-HWA forest composition based on the trees which currently occur alongside hemlock do not take into account that current forests themselves are in a state of transition. Mesophication refers to the transition of forests in eastern North America formerly adapted to dry, fire-prone conditions toward a cooler, wetter state dominated by shade-tolerant, mesophytic species (Nowacki & Abrams 2008). Initially attributed primarily to fire suppression, mesophication may in fact be a multifaceted process resulting from a combination of the lack of fire, wetter and cooler climatic conditions, changes in land use, and increases in populations of herbivores like white-tailed deer (*Odocoileus virginianus*), among other factors (McEwan et al. 2011). This has already lead to a marked decrease in the recruitment of some oak species and a corresponding increase in mesophytic species like sugar maple and red maple. Therefore, mesophication is a likely driver behind the large number of young red maples seen in the transects. This increased competitiveness of red maple makes them especially capable of expanding their populations in hemlock's future absence, just as they did in HWA-impacted Connecticut forests (Orwig & Foster 1998). At the same time, in Ohio and elsewhere across eastern forests, mesophication has led to a decrease in white oak, formerly a dominant species (Dyer 2001). White oak is still a dominant species in the transects (attaining the second highest importance value overall by virtue of its large size on average). However, a decrease in the number of white oak trees in the plots, the near-complete lack of individuals in the smallest size class in both plots and transects, and the absence of white oak saplings all point to a similar pattern of white oak decline in these hemlock stands.

Although red maple is likely to continue to become more important in the future, and white oak less so, the current abundance of chestnut oak and red oak may be a good reflection of future forest composition. Populations of red oak and chestnut oak have been observed to expand in the eastern U.S. even as white oak declines. Abrams (2003) attributes this change to the rapid growth of red and chestnut oaks compared to white oak, allowing them to more easily colonize new sites following disturbances even in mesic conditions. This was reflected in both the plot and transect surveys. 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, dominance (basal area), and frequency of occurrence. Red oak, while not as numerous, is also found in greater numbers in the transects away from competition with hemlock.

Although the 20th century has been wet, and modern forest dynamics have thus dominated by growth of mesophytic species (Pederson et al. 2015), climate change projections indicate warmer and drier conditions in the future. The process of mesophication which has resulted in white oak decline could potentially be reversed, creating conditions favorable for oak once more (Vose & Elliott 2016). Still, the potential for extreme drought in some regions make such long-term predictions difficult (Dey 2014). At the very least, although conditions may not be ideal for white oak and other xerophytic species under current conditions, the possibility exists that these species could dominate the canopy once more under climate change conditions.

In the short term, it appears that chestnut oak and red oak are in an especially good position to disperse into the large gaps left below following future HWA-induced mortality, as is the aggressively expanding red maple. White oak, also a dominant non-hemlock species in the area, could certainly seed in below as well. However, its slow growth and declining recruitment ability due to mesophication mean that it is likely to be initially outcompeted by faster-growing species which can better cope with cool, wet environments, such as red maple, red oak, and chestnut oak.

4.5: Invasive Species

The association between disturbance and subsequent invasion of exotic plants is well-documented. Opportunistic invasive species exploit increased resource accessibility due to native plant mortality to establish themselves or expand their range in areas affected by disturbance. A literature review by Lozon and MacIsaac (1997) found that 68% of documented cases of invasive plant establishment were preceded by some form of disturbance. The opening of the canopy due to hemlock woolly adelgid would be one such example of disturbance, and a large-scale one at that. Multiple studies of New England hemlock forests affected by HWA have shown a resulting increase in invasive shrubs and vines (Orwig & 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). A similar increase in invasive plants will likely be observed in Ohio.

Worryingly, invasive herbaceous plants and shrubs were already observed in or near several of this study's sites, including garlic mustard, Japanese barberry, multiflora rose, and autumn olive. Although all of these plants are currently represented by only a few scattered individuals, HWA-induced mortality could afford these species the opportunity to expand their populations in the Hocking Hills, potentially supplanting native species. Much more common and numerous across the study sites was Japanese stiltgrass, which was most often found growing thickly alongside trails and roads. Currently existing primarily in edge habitat, HWA-induced mortality could give stiltgrass the perfect opportunity to penetrate into the forest. Stiltgrass is also capable of aggressive growth even in the shade (Leicht et al. 2005), so once colonization of the post-HWA forest occurs, these populations will likely persist. Furthermore, the existing edge populations form narrow but dense monocultures in which few other herbaceous species grow, so it already displays a propensity for outcompeting native plants.

Given this density, shade tolerance, and frequency of occurrence, stiltgrass currently appears to be the greatest invasive plant threat in the study area, at least in the vicinity of sampled sites.

5. Conclusion

As a foundation species, eastern hemlock acts as the pillar of a unique ecosystem, supporting a wide variety of organisms including fish, aquatic invertebrates, amphibians, birds, and fungi that all depend upon it for survival (Snyder et al. 2002, Ross et al. 2003, Ellison et al. 2005, Fassler et al. 2019). For the sake of all of these organisms and the hemlock itself, not to mention the tourism-dependent economy of the Hocking Hills region (Tourism Economics 2016), protecting as much hemlock forest as possible from hemlock woolly adelgid is the best course of action. This can be accomplished through an integrated pest management strategy of pesticide application and establishment of biocontrol species (ODNR 2017). However, because neither the budget nor the time and labor exist to treat every hemlock tree, HWA will in all likelihood eventually lead to the loss of hemlock where protection strategies are not implemented. Therefore, understanding the transition from hemlock forest to deciduous forest that will follow that mortality in southeast Ohio is important from both ecological and economic perspectives, potentially guiding conservation and land management efforts.

Unfortunately, predicting the composition of post-HWA forests in Ohio is not a simple matter. Forests in the eastern United States are already in a state of transition due to a host of factors including ongoing processes of mesophication and climate change, the invasion of exotic pests and diseases, increases in herbivore populations, human land use, and more. In such an ever-changing environment, predicting the composition and structure of future forests involves some speculation. Furthermore, the infestation of Ohio's hemlock forests by HWA is only just beginning, not yet resulting in widespread mortality. Still, there are limitations that can be overcome and further research that can be undertaken to enhance our ability to predict and understand the composition of these future post-HWA forests. For example, models are sometimes used to project future forest conditions, but past applications of widely used models like the US Forest Service's Forest Vegetation Simulator and its HWA Event Monitor only predicted mortality. They do not account for recruitment, nor do some variants include shrubs, vines, and herbaceous plants (invasive or otherwise) that can complicate predictions (Spaulding & Rieske 2010). The development of more inclusive models could therefore be a useful addition to observational studies that could lead to more accurate predictions of future forest composition. Despite these limitations and complications, we can make predictions of future forest composition based on what we can currently observe growing alongside hemlock in the field and how those species are likely to respond to ongoing challenges and predicted future conditions.

Using this approach, there is much that can be said about the ways in which the hemlock stands of the Hocking Hills have changed in the past decade as well as the non-hemlock species currently growing alongside them. Little mortality attributable to HWA has yet occurred in this study's plots, with most mortality of both hemlock and deciduous species occurring as a result of storm damage and competitive thinning. Although growth rates of adult hemlock is comparable to other species in the plots and hemlock is still the most numerous species in the sapling class, mortality of hemlock saplings is widespread and recruitment of new adults rare. Most growth or recruitment in the sapling size class was instead observed among deciduous species, and it is these saplings (especially beech) which will likely benefit from future hemlock mortality.

A mixture of deciduous trees are also already growing alongside hemlock in the canopy. The most common of these include tulip poplar, chestnut oak, white oak, sweet birch, and red maple. These species are quite literally in the best position to dominate in the plots after hemlock mortality, as they are likely to experience an immediate growth response to the increased resource availability left behind by so many dead hemlocks. Furthermore, mesophytic pioneer species like tulip poplar and sweet birch are well suited to quickly expand in number in the moist valleys and slopes of the Hocking Hills, particularly as the process of mesophication makes certain oak species less competitive. Chestnut oak and red oak, however, have also been proven to tolerate these moist conditions well (Abrams 2003), and the former is an especially common non-hemlock species in this study's plots. Additionally, along the ridges and upper slopes above these plots, chestnut oak, white oak, red oak, and red maple are all common. Given the abundance, fast growth, and tolerance of mesic conditions seen in red and chestnut oaks, as well as the expanding number of red maples in eastern forests (Abrams 1992), these species appear especially likely to successfully seed in to the empty spaces in the valleys below following hemlock mortality. As such, stands currently dominated by hemlock might be expected to become dominated by mesophytic hardwoods such as tulip poplar and sweet birch as well as red maples, red oaks, and chestnut oaks which appear poised to expand in number and disperse from above. However, since climate change is likely to produce warmer, drier conditions in the future, xerophytic species like white oak should not be counted out, especially considering the longevity of the species. No matter the species present in the canopy, though, a number of invasive plants, chief among them Japanese stiltgrass, are also present and capable of expanding in number and potentially outcompeting native species given the right disturbance. Widespread hemlock mortality could certainly provide such a disturbance, so removal or control of exotic species should be a management priority whatever the future canopy composition may be.

In short, this study has recorded growth and mortality rates over time for eastern hemlock dominated stands, which is largely absent from the literature in forests not yet affected by hemlock woolly adelgid. Furthermore, this study has provided a snapshot of hemlock forests in southeast Ohio's Hocking Hills region just prior to infestation by HWA, as well as the deciduous trees growing among and adjacent to these hemlock stands. This information represents a new contribution for the isolated hemlock stands of Ohio which could be valuable for management and conservation efforts in this unique environment on the edge of hemlock's range.

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7. Appendix

7.1: Plot & Transect Coordinates

Site	Plot	Lat_plot	Lon_plot	Lat_trans	Lon_trans
Ash Cave	A	39.397409	-82.544496	39.39744	-82.54409
Ash Cave	B	39.399612	-82.545697	39.39991	-82.54570
Ash Cave	C	39.395522	-82.537627	39.39428	-82.54021
Cantwell Cliffs	A	39.555327	-82.586316	39.55453	-82.58695
Cantwell Cliffs	B	39.551880	-82.589180	39.55147	-82.58903
Cantwell Cliffs	C	39.547398	-82.579761	39.54753	-82.57934
Clear Creek	A	39.595120	-82.550480	39.59558	-82.55003
Clear Creek	B	39.591030	-82.563597	39.58992	-82.56386
Clear Creek	C	39.595650	-82.590900	39.59549	-82.58989
Crane Hollow	A	39.464215	-82.567437	39.46494	-82.56763
Crane Hollow	B	39.465103	-82.570501	39.46530	-82.57143
Crane Hollow	C	39.462945	-82.570884	39.46370	-82.57203
Hamilton-Red Rock	B	39.431799	-82.569862	39.43105	-82.56992
Hamilton-Red Rock	C	39.428202	-82.565463	39.42838	-82.56579
Lake Katharine	A	39.090560	-82.686740	39.09054	-82.68703
Lake Katharine	B	39.091855	-82.685090	39.09167	-82.68478
Lake Katharine	C	39.092282	-82.684499	39.09204	-82.68382
Long Hollow	A	39.467401	-82.556708	39.46740	-82.55688
Long Hollow	B	39.466644	-82.558995	39.46660	-82.55856
Long Hollow	C	39.464513	-82.559347	39.46514	-82.55814
Old Man's Cave	A	39.428165	-82.543748	39.42809	-82.54356
Old Man's Cave	B	39.425955	-82.543588	39.42616	-82.54330
Old Man's Cave	C	39.423120	-82.540250	39.42360	-82.53979
Rocky Branch	B	39.491457	-82.531606	39.49144	-82.53117
Rocky Branch	C	39.492894	-82.532355	39.49333	-82.53194
Sheick	A	39.473795	-82.550153	39.47391	-82.54984
Sheick	B	39.471875	-82.548730	39.47204	-82.54832
Sheick	C	39.470387	-82.545367	39.46985	-82.54478
Spruce Run	A	39.451710	-82.603116	39.45143	-82.60313
Spruce Run	B	39.453004	-82.603498	39.45310	-82.60348

Note: Transect coordinates were taken with smart phone and are less accurate than plots.

7.2: Plot Characteristics: Plot slope, aspect, and soil data collected in initial sampling period. All soil measurements based on samples from 2009 with the exception of Old Man's Cave Plot C (2011).

Plot	Slope	Aspect	pH	C	N	C:N
Ash Cave A	24	284	4.2	3.25	0.12	27.08
Ash Cave B	13	142	4.8	2.04	0.12	17.00
Ash Cave C	24	304	4.2	2.57	0.10	25.70
Cantwell Cliffs A	26	342	4.3	2.02	0.12	16.83
Cantwell Cliffs B	26	19	5.3	2.58	0.25	10.32
Cantwell Cliffs C	16	320	4.5	2.98	0.21	14.19
Clear Creek A	26	340	4.7	1.92	0.16	12.00
Clear Creek B	12	340	4.5	1.46	0.14	10.43
Clear Creek C	26	268	4.1	1.59	0.07	22.71
Crane Hollow A	21	313	4.5	1.69	0.10	16.90
Crane Hollow B	17	76	4.7	2.42	0.18	13.44
Crane Hollow C	9	139	4.5	1.89	0.12	15.75
Hamilton-Red Rock B	26	160	4.0	1.73	0.06	28.83
Hamilton-Red Rock C	21	278	4.2	3.36	0.14	24.00
Lake Katharine A	19	20	5.0	2.14	0.15	14.27
Lake Katharine B	23	325	4.5	1.65	0.08	20.63
Lake Katharine C	26	29	4.4	0.73	0.01	
Long Hollow A	17	332	4.7	4.07	0.26	15.65
Long Hollow B	17	245	4.1	2.26	0.09	25.11
Long Hollow C	18	304	4.0	4.00	0.13	30.77
Old Man's Cave A	12	260	5.1	3.36	0.19	17.68
Old Man's Cave B	7	290	5.6	2.93	0.12	24.42
Old Man's Cave C	20	235	5.0	1.84	0.12	15.33
Rocky Branch B	30	251	4.2	2.36	0.10	23.60
Rocky Branch C	16	280	4.6	2.92	0.13	22.46
Sheick Hollow A	28	229	4.5	1.39	0.08	17.38
Sheick Hollow B	22	215	4.4	2.47	0.14	17.64
Sheick Hollow C	19	300	4.1	1.76	0.09	19.56
Spruce Run A	31	30	4.8	2.95	0.23	12.83
Spruce Run B	20	183	4.5	2.36	0.13	18.15

7.3: Plot Age: Inferred age of plot establishment assigned by the minimum year of establishment of the oldest tree in each plot as identified by core samples. Ten trees per plot were randomly selected for coring.

Site	Plot	Min Establishment Year
Ash Cave	A	1769
Ash Cave	B	1845
Ash Cave	C	1872
Cantwell Cliffs	A	1894
Cantwell Cliffs	B	1890
Cantwell Cliffs	C	1880
Clear Creek	A	1878
Clear Creek	B	1886
Clear Creek	C	1894
Crane Hollow	A	1857
Crane Hollow	B	1895
Crane Hollow	C	1914
Hamilton-Red Rock	B	1900
Hamilton-Red Rock	C	1870
Lake Katharine	A	1883
Lake Katharine	B	1899
Lake Katharine	C	1879
Long Hollow	A	1907
Long Hollow	B	NA
Long Hollow	C	1864
Old Man's Cave	A	1867
Old Man's Cave	B	1814
Old Man's Cave	C	1867
Rocky Branch	B	1874
Rocky Branch	C	1841
Sheick	A	1900
Sheick	B	1894
Sheick	C	1923
Spruce Run	A	1863
Spruce Run	B	1888

7.4: Descriptive Calculations & Data Analysis

Density: An expression of the number of trees growing within a defined area.

a. Stand Density (density of trees of all species across the entire stand, plot or transect, expressed in trees/hectare):

$$D = \frac{\#of\ trees}{Area\ sampled}$$

b. Relative Density (of an individual species, expressed as percentage):

$$D = \frac{\#\ of\ trees\ of\ species\ A}{Total\ \#\ of\ trees\ sampled}$$

c. Absolute Density (of an individual species, again expressed in trees per hectare):

$$D = \frac{\#\ of\ trees\ of\ species\ A}{Area\ sampled}$$

Dominance: An expression of tree size in terms of area. To perform dominance calculations, it is necessary first to calculate basal area (BA) from the diameter measurements taken in the field. This was accomplished with the equation Area = πr^2, adjusted to account for the transition from centimeters to meters, resulting in a final equation of $BA = \pi \left(\frac{DBH}{200}\right)^2$. With basal area calculated for each individual tree, it then became possible to perform the following dominance calculations:

a. Stand Basal Area: A measure of the basal area of all trees, expressed in m^2/ha

$$Stand\ BA = \frac{Total\ BA\ for\ all\ trees\ sampled}{Area\ sampled}$$

b. Relative Dominance (of an individual species, expressed as a percentage):

$$Relative\ Dom = \frac{Total\ BA\ of\ species\ A}{Total\ BA\ of\ all\ trees}$$

c. Absolute Basal Area (of an individual species, expressed as m^2/ha):

$$Absolute\ BA = \frac{Total\ BA\ of\ species\ A}{Area\ sampled}$$

Frequency of Occurrence: An expression of how frequently a given species is encountered.

a. Percent Frequency:

$$PF = \frac{\#\ of\ plots\ containing\ species\ A}{Total\ \#\ of\ plots}$$

b. Relative Frequency (%):

$$RF = \frac{PF\ of\ species\ A}{Total\ PF\ of\ all\ species}$$

Importance Value: A single value taking the previous three metrics into account. There are two ways of calculating importance values, both of which were used in this study under different circumstances.

a. $IV = \frac{Relative\ Density + Relative\ Dominance}{2}$

(This IV formula was used for individual plot or transect level calculations. Due to the fact that frequency of occurrence takes the entire study area into account, it cannot be calculated for individual plots and thus must be omitted from the importance values at this level).

b. $IV = \frac{Relative\ Density + Relative\ Dominance + Relative\ Fequency}{3}$

(This IV formula includes frequency of occurrence metrics and thus was used for individual species calculations across the entire study area).

Growth and Mortality Rates:

a. Growth Rate (%):

$$Growth\ Rate = \frac{Final\ BA - Initial\ BA}{Initial\ BA} * 100$$

$$Annual\ Growth\ Rate = \frac{Growth\ Rate}{\#\ of\ years\ since\ initial\ sampling}$$

b. Mortality Rate (%):

$$\frac{Initial\ Count - Final\ Count}{Initial\ Count} * 100$$

Size Class Analysis Methodology: Individual species were broken down into DBH classes of 16 cm for size class analysis. Living trees within each size class were counted and these counts were then divided by the total area in hectares to arrive at absolute density of trees within each size class. Size class histograms were then created from these data for major species (here defined as species with more than ten representatives). Species under this threshold and were thus lumped together into an “other” category. Histograms showing the combined size distributions of mesophytic species (those which thrive in wet environments) versus xerophytic species (those which thrive in drier environments) were also created.