

PREPARING FOR HEMLOCK WOOLLY ADELGID IN OHIO: COMMUNITIES ASSOCIATED WITH HEMLOCK-DOMINATED RAVINES OF OHIO'S UNGLACIATED ALLEGHENY PLATEAU

Katherine L. Martin and P. Charles Goebel¹

Abstract.—Hemlock woolly adelgid (HWA) is an invasive insect causing widespread mortality in eastern hemlock (*Tsuga canadensis* [L.] Carr; hereafter “hemlock”) throughout eastern forests. Hemlock is a foundation species, regulating ecosystem structure and function (e.g., microclimate, nutrient cycling). Across the central and southern Appalachians, hemlock tends to dominate ravine and riparian forests; thus its loss will have dramatic effects across ecosystem boundaries. Prior to invasion by HWA, we are collecting data on hemlock in southeastern Ohio. We found hemlock associated with short, steep slopes regardless of aspect. Hemlock is dominant at lower slope positions adjacent to streams, where few other woody species are found in either the overstory or sapling layers. At upper slope positions, increases in diversity indices are small. Nonmetric multi-dimensional scaling analyses indicate additional species (deciduous hardwoods) form predictable associations along environmental gradients within ravines. Thus, at upper slope positions, communities of oaks and other deciduous hardwoods similar to other ecosystems of the region may develop should widespread hemlock mortality occur. At the same time, riparian forests will experience nearly complete shifts in species composition and, thus, function. Hemlock mortality remains a serious challenge for the Central Hardwoods region, where hemlock-dominated ravine systems are important recreation and tourism sites.

INTRODUCTION

Over the past two centuries, the forests of eastern North America have changed dramatically as introduced pests and pathogens have reshaped forest ecosystem structure and function (Lovett and others 2006). Some of the species lost were considered foundation species (Ellison and others 2005), as they were the dominant species in an ecosystem in terms of both abundance and influence. The loss of such species has likely had significant ramifications for the stability of ecosystem processes. In particular, foundation species are thought to structure exchanges of energy through a limited number of strong interactions (Ellison and others 2005). American chestnut (*Castanea dentata* [Marsh. Borkh.]) once filled such a foundational role across more than a million square hectares of eastern forests, but was eliminated by chestnut blight (*Cryphonectria parasitica* [Murr.] Barr) in the early 20th century (Anagnostakis 1987). As chestnut declined, eastern hemlock (*Tsuga canadensis* [L.] Carr; hereafter “hemlock”) replaced it as the foundation species in many of these forest ecosystems, particularly in riparian communities of the central and southern Appalachians (Elliott and Swank 2008). Yet hemlock may soon also be eliminated as another introduced pest, the hemlock woolly adelgid (*Adelges tsugae*; HWA), is causing widespread hemlock mortality throughout an expanding portion of its range.

¹Ph.D. candidate (KLM), Associate Professor (PCG), School of Environment and Natural Resources, 127A Williams Hall, 1680 Madison Avenue, The Ohio State University, Wooster, OH 44691. KLM is corresponding author: to contact, call (330) 202-3549 or email at martin.1678@osu.edu.

The full impact of hemlock mortality is not completely understood, but initial studies indicate forest dynamics including species composition, diversity, and nutrient and energy exchanges will be affected. Hemlock stands support a unique suite of species, and therefore contribute to landscape or beta and gamma diversity (Snyder and others 2002, Tingley and others 2002, Ross and others 2003). Changes following hemlock mortality will likely be dependent on the post-hemlock community dynamics and therefore may be region-specific (Orwig and Foster 1998, Jenkins and others 1999, Kizlinski and others 2002, Eschtruth and others 2006, Stadler and others 2006, Ford and Vose 2007, Nuckolls and others 2008, Orwig and others 2008). Whereas most efforts are currently focused on finding biological controls for the current and future spread of HWA along the invasion front (Onken and Reardon 2008), data are needed to initiate restoration and management planning strategies for forests impacted by HWA. To inform these plans, we are collecting baseline data on these hemlock forest ecosystems in southeastern Ohio prior to HWA invasion.

The objective of this investigation was to document the current community composition in southeastern Ohio hemlock ravine forest ecosystems. These data would allow us to test the following hypotheses:

1. Hemlock is particularly dominant immediately adjacent to small streams, which indicates hemlock mortality will have a direct impact across forest and stream ecosystems.
2. Species that co-occur with hemlock are structured along physiographic gradients; thus post-hemlock forest dynamics will differ across these gradients.

STUDY AREAS

Study areas are located within the unglaciated Allegheny Plateau physiographic province of southeastern Ohio (Brockman 1998) and characterized by sandstone bedrock that forms deep valleys and cliffs. This region supports the majority of the hemlock stands within Ohio (Black and Mack 1976, Prasad and others 2007). Our study areas are part of the Ironton and Shawnee-Mississippian Plateau physiographic subsections (Brockman 1998). We sampled three sites within Lake Katharine State Nature Preserve in Jackson County, a 817-ha preserve with limited areas of hiking trails. In Hocking County, five sample sites were located within Sheick Hollow State Nature Preserve and the Hocking State Forest. Sheick Hollow is a 61-ha preserve adjacent to the state forest and accessible by permit only, while Hocking State Forest contains 3,924 ha managed for multiple uses, although hemlock timber is not extracted. Hocking and Jackson Counties have continental climates with cold, snowy winters (0 °C average) and warm, humid summers (21.6 °C average) (Kerr 1983, Lemaster and Gilmore 1989). Across both counties, an average rainfall of approximately 102 cm is distributed evenly throughout the year. Hocking County is characterized by sedimentary bedrock of the Mississippian and Pennsylvanian Systems. In the Mississippian system, the Logan formation of sandstone, shale, and conglomerate overlays the Cuyahoga formation of Cuyahoga Shale and Blackhand Sandstone (Lemaster and Gilmore 1989). The bedrock of Jackson County is similarly porous, formed by Sharon conglomerate and Pottsville sandstone (Beatley 1959, Runkle and Whitney 1987). Soils in the upland and slope portions of Lake Katharine are well drained hapludults, mainly the Clymer silt loam formed from sandstone residuum and Rigley sandy loam formed by colluvium at the base of slopes. Orville fluvaquents occur in the floodplains of some small coves (Kerr 1983, Runkle and Whitney 1987). In Hocking County, Lemaster and Gilmore (1989) describe the predominant soils of Hocking State Forest as part of the Cedar Falls-rock outcrop complex with 40- to 70-percent slopes. Cedar Falls is the predominant soil series, a steep and well drained soil. All sites were selected in valley/ravine riparian areas within second-growth forests with little evidence of recent human disturbance and a dominance of hemlock (approximately 50 percent or greater of the total overstory basal area).

METHODS

FIELD METHODS

At each of the eight study sites, we established three transects parallel to the stream at 10, 30, and 50 m from the stream bank. The side of the ravine chosen for sampling was determined haphazardly, in some cases based on logistical considerations due to the location of cliffs. In each transect, we used a series of five 100-m² circular plots (5.62-m radius) for a total of 15 plots per study site. Within each circular plot, we recorded basic physiographical data, slope percent (using a clinometer), slope shape, slope position, and aspect. All species and diameter at breast height (d.b.h) of the woody vegetation (all stems >2.5 cm d.b.h.) were recorded. Stems between 2.5 cm and 10 cm d.b.h. were classified as saplings, while those >10.0 cm were classified as overstory. The five subplots along each transect were combined for data analyses.

STATISTICAL ANALYSES

All statistical analyses were performed using R version 2.10.0 (online documentation available at <http://www.r-project.org/>). For the overstory layer (>10 cm d.b.h.), analyses are based on relative basal area; for the sapling (2.5-10 cm d.b.h.) layer, stem counts are used. We calculated metrics of heat load and direct incident radiation for each plots using latitude, slope percent, and aspect in Eqn. 1 from McCune and Keon (2002).

To understand the change in community characteristics across our transects going upslope from the stream, we compared measures of species richness (S), Shannon's diversity (H'), and Pielou's evenness (J') using an analysis of variance. Prior to analyses, we ensured that each metric (S, H', and J') fit the model assumptions, using a Shapiro-Wilk test for normality and Levene's test for homogeneity of variance. Skewness and kurtosis were examined with the D'Agostino and Bonett-Seier tests, respectively. Analyses of variance were then used for all three metrics (S, H', J') and significant results were examined in detail with Tukey's honestly significant difference. These metrics were calculated once for the overstory and once for the sapling layers.

To examine the environmental gradients structuring hemlock ravine communities in Ohio, we used multivariate techniques. To extract measures of community composition, we subjected the overstory and sapling layers to nonmetric multidimensional scaling analysis (NMDS). For the purposes of analysis, species appearing on fewer than 5 percent of subplots were excluded (six subplots out of a total of 120). NMDS is an unconstrained ordination method regarded as highly robust for community data (Minchin 1987). We used the metaMDS procedure with a Bray-Curtis distance matrix using the vegan package for community ecology (Dixon and Palmer 2003, <http://finzi.psych.upenn.edu/R/library/vegan/html/metaMDS.html>). The metaMDS procedure automatically transforms data with large ranges using square root and Wisconsin double standardization. The metaMDS procedure uses an iterative approach with random starts to insure against entrapment by local minima while converging on a solution that minimizes stress. The procedure also rotates the final solution so that the first axis explains the most variance. To examine associations with specific factors, environmental vectors determined by principal components analysis (PCA) were overlaid on the community NMDS diagram using the envfit procedure, also part of vegan (Dixon and Palmer 2003, <http://finzi.psych.upenn.edu/R/library/vegan/html/envfit.html>). We allowed NMDS iterations to continue until the convergence on a global solution. Categorical variables including slope shape and slope position were coded as dummy variables.

To examine community structure along physiographic gradients without the dominant influence of hemlock, we constructed an additional NMDS. Relative basal area was re-calculated without hemlock; then an NMDS solution was calculated with an overlay of environmental PCA axes as above. This analysis is intended only to examine gradients that may have been obscured by the presence of hemlock. It is not intended as a simulation of hemlock mortality, as modeling this complex disturbance is beyond the scope of this investigation.

RESULTS

Comparisons of species richness and diversity indicated that hemlock is dominant throughout our study ravine and riparian areas (Fig. 1). In the overstory, species richness measures indicate that hemlock is particularly dominant at lower slope positions, where few other species are found. However, hemlock seems to exert a greater influence than we expected at upslope positions. Although additional species occur, evenness remains low and exhibits a slightly decreasing trend upslope as additional infrequent species occur. Thus, upslope gains in Shannon's diversity are minimal.

In the overstory, NMDS axis one was associated with slope shape, slope position, heat load, and the middle (30-m) transect (Fig. 2). Axis two was more strongly associated with the lower (10-m) and upper (50-m) transects, slope percent, and incident radiation. The ordination diagram places hemlock near the origin of the environmental gradients, suggesting a ubiquitous distribution of this foundation species in steep ravines. Lower slope positions are characterized by species such as sweet birch (*Betula lenta* L.), American beech (*Fagus grandifolia* Ehrh.), and yellow-poplar (*Liriodendron tulipifera* L.). Moving up the slope, species including sugar

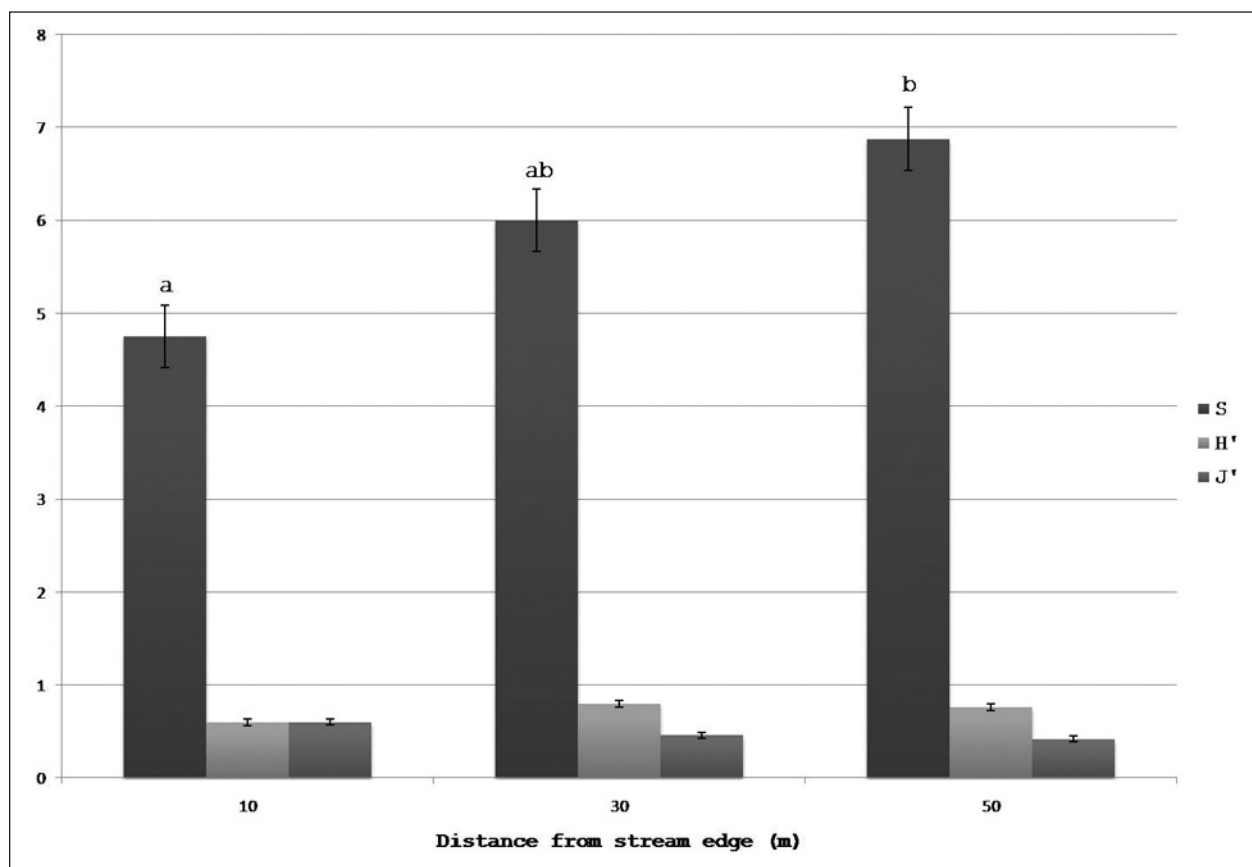


Figure 1.—Mean (± 1 SE) overstory species diversity. S refers to species richness, H' to Shannon diversity, J' to Pielou's evenness. Only species richness was determined to be different at $\alpha = 0.05$. Letters represent Tukey's HSD separation of the means.

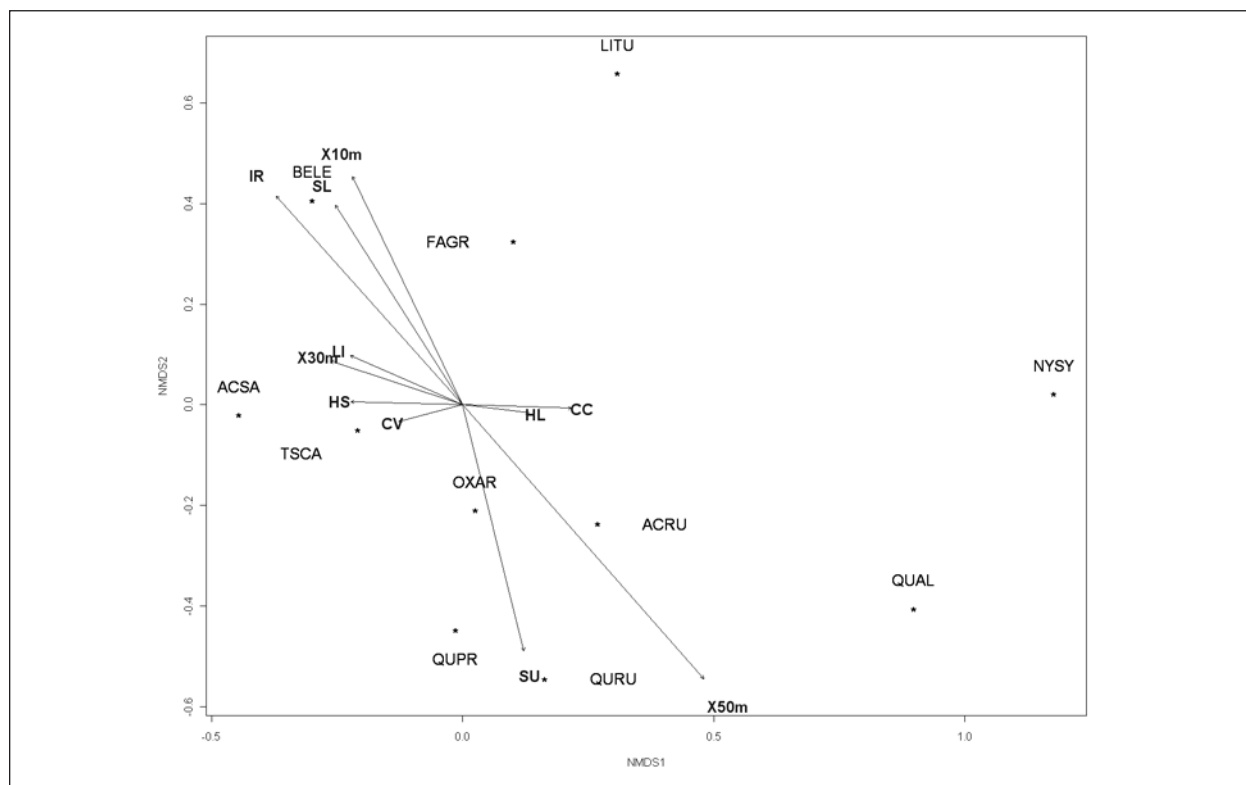


Figure 2.—Nonmetric multidimensional scaling (NMDS) ordination for overstory species with environmental principal components axes. The distance matrix for the NMDS is Bray-Curtis, based on relative basal area. Species are coded as follows: ACRU – red maple, ACSA – sugar maple, BELE – sweet birch, FAGR – American beech, LITU – yellow-poplar, NYSY – blackgum, OXAR – sourwood, QUAL – white oak, QUPR – chestnut oak, QURU – red oak, TSCA – hemlock.

maple (*Acer saccharum* Marsh.), red maple (*A. rubrum* L.), and white oak (*Quercus alba* L.) become more abundant, with red oak (*Q. rubra* L.) and chestnut oak (*Q. prinus* L.) on summits.

When the overstory was reanalyzed without the dominant influence of hemlock, environmental gradients exerted a stronger influence on community composition (Fig. 3). In this case, NMDS axis one was driven by the upper and lower transects and incident radiation. Heat loading and the 30-m distance had a greater influence on the second axis. As in the previous ordination, sweet birch and yellow-poplar were associated with lower and steeper slopes, while white and red oaks and blackgum (*Nyssa sylvatica* Marsh.) were found at upper slope positions. In this analysis, American beech and chestnut oak were separated from other species, but were not strongly associated with the environmental vectors. These two species may be influenced by metrics not included, such as soil chemistry or moisture, which are known to be influential in the region (Runkle and Whitney 1987, Hutchinson and others 1999, Small and McCarthy 2005).

The sapling layer was species-poor, and some sample transects did not have any non-hemlock saplings. As species occurred infrequently in the sapling layer, we completed an NMDS with all species to examine possible environmental gradients (Fig. 4). Species including sourwood (*Oxydendrum arboreum* [L.] DC.), umbrella magnolia (*Magnolia tripetala* L.), blackgum, red maple, and black walnut (*Juglans nigra* L.) grouped on convex slopes, associated with axis one. As in the overstory layer, hemlock's ubiquity was apparent from its position near the origin. Slippery elm (*Ulmus rubra* Muh.), hornbeam (*Carpinus caroliniana* Walter), and sugar maple grouped together on summits and convex slopes. The short environmental vectors indicate sapling distribution may be driven by a factor not included in the analysis, or there were too few saplings to indicate a clear pattern.

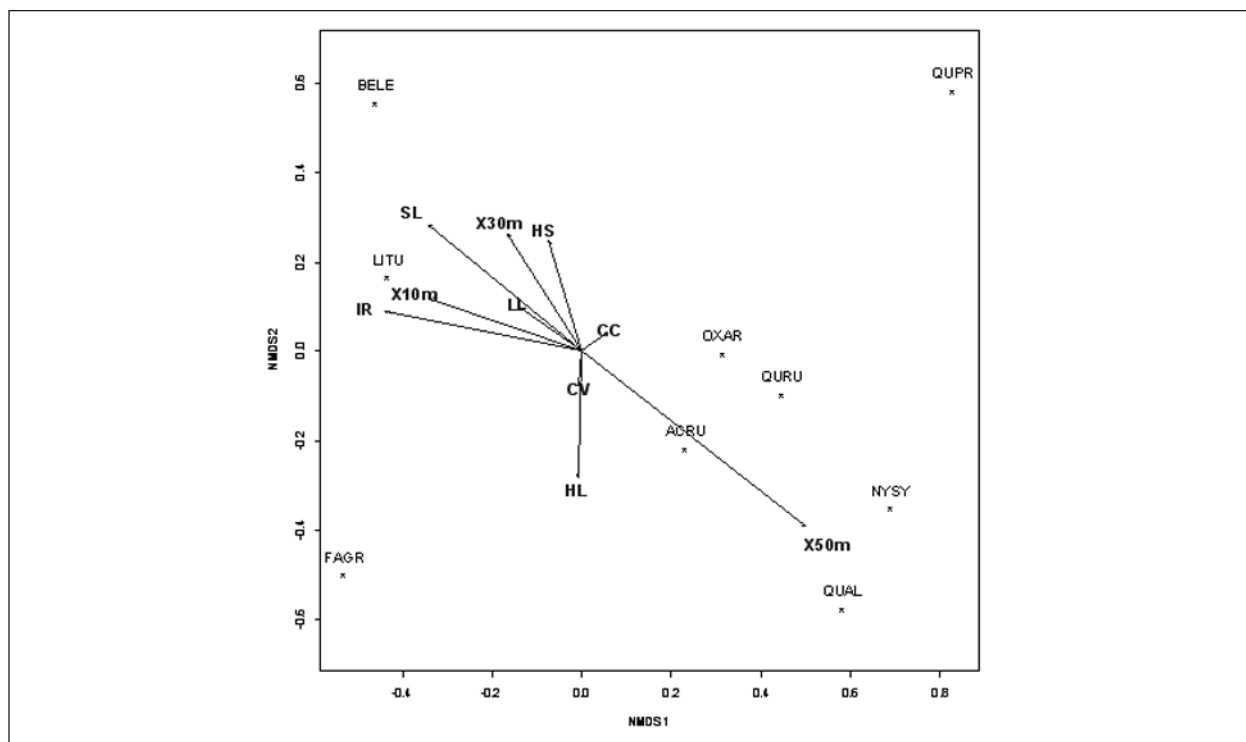


Figure 3.—Nonmetric multidimensional scaling (NMDS) ordination for overstory species with hemlock removed. Environmental vectors are principal components axes. The distance matrix for the NMDS is Bray-Curtis, based on relative basal area. Species are coded as follows: ACRU – red maple, ACSA – sugar maple, BELE – sweet birch, FAGR – American beech, LITU – yellow-poplar, NYSY – blackgum, OXAR – sourwood, QUAL – white oak, QUPR – chestnut oak, QURU – red oak.

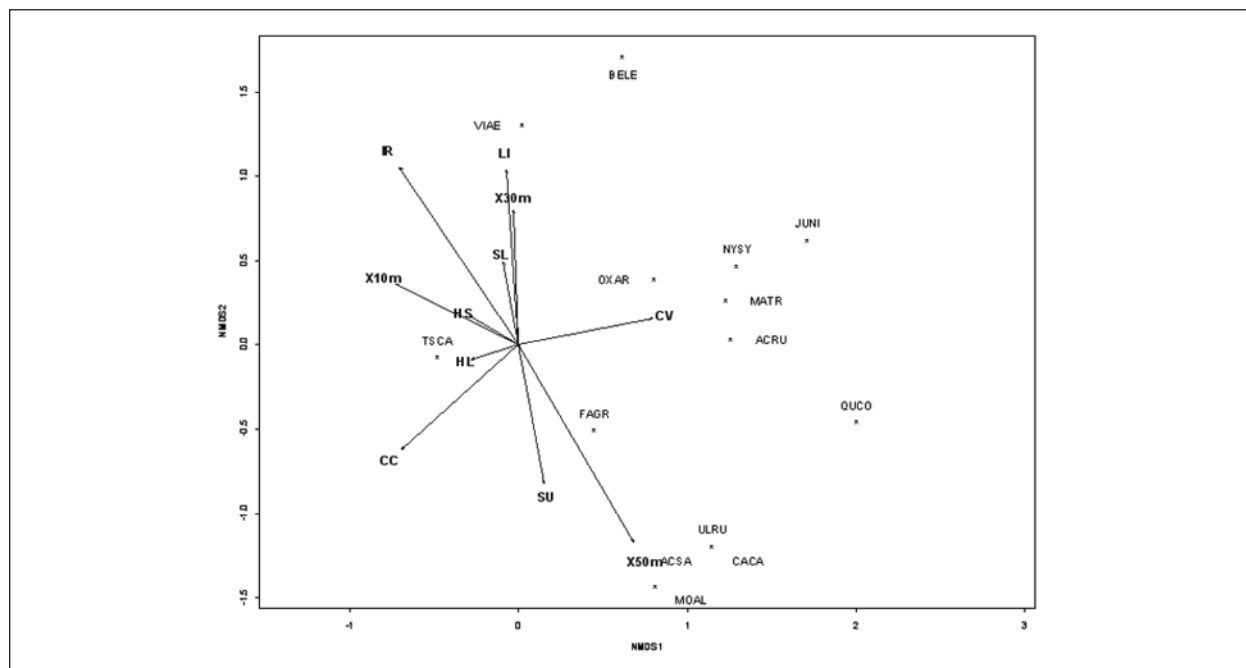


Figure 4.—Nonmetric multidimensional scaling (NMDS) ordination for sapling species with environmental principal components axes. The distance matrix for the NMDS is Bray-Curtis, based on stem counts. Species are coded as follows: ACRU – red maple, ACSA – sugar maple, BELE – sweet birch, CACA – hornbeam, FAGR – American beech, JUNI – black walnut, MATR – umbrella magnolia, MOAL – mulberry (*Morus alba* L.)*, NYSY – blackgum, OXAR – sourwood, QUCO – scarlet oak (*Quercus coccinea* Munchh.), TSCA – hemlock, ULRU – slippery elm, VIAE – wild grape (*Vitis aestivalis* Michx.).

*invasive

DISCUSSION

Throughout Ohio, hemlock is not broadly distributed; in the specialized habitats where it does occur, however, it dominates both the overstory and sapling layers, regardless of aspect. As few other species occur in either the overstory or sapling layers of these steep riparian ravines, the arrival of HWA would be a major disturbance in key headwater areas of the Ohio River watershed. Successional patterns that result following hemlock mortality will differ moving upslope away from first- and second-order streams as environmental gradients drive the re-initiation of deciduous hardwood communities.

The successional patterns we can expect for Ohio and central hardwood forest ecosystems where hemlock is a dominant overstory species will be unique and illustrative of the variance of the impact of HWA. Pollen records indicate that historic hemlock declines resulted in a transition to birch, followed by maple and oaks in the southern Appalachians (Allison and others 1986). These large-scale patterns from pollen records provide a general model that can be refined on regional and local scales for management purposes. For example, following the historic pattern, studies indicate that hemlock will likely be replaced by sweet birch in the Northeast, where hemlock occurs across the landscape (Orwig and Foster 1998, Kizlinski and others 2002). In the Connecticut Arboretum, Small and others (2005) found that hemlock ravines shifted toward a mixed hardwood overstory with a more developed understory.

The future composition and structure of ravine and riparian forests is not as clear for the central and southern portions of the hemlock's range (Ellison and others 2005). We found sweet birch sporadically, generally at lower slope positions. Birch was rarely found in the current understory. However, our study may underestimate the role of birch, as all birch at Lake Katharine were identified as yellow birch, in agreement with Runkle and Whitney (1987). For analysis purposes, the species were treated separately and yellow birch was later removed from analyses as very infrequent (present on less than 5 percent of all plots). Thus, the future influence of sweet birch and/or ecologically similar yellow birch will depend on its ability to disperse and germinate more widely throughout the forest. Birch is known as an opportunistic species well adapted to disturbances from canopy gaps created by hemlock mortality (Orwig and Foster 1998, Catovsky and Bazzaz 2000). At the same time, birch is a shade-intolerant, short-lived species that would not be expected to remain dominant after one generation (Ford and Vose 2007). Shade-tolerant, later successional mesophytic species well suited to the cooler microclimate of ravines, including sugar maple and basswood (*Tilia americana* L.), were infrequent and absent (respectively) from our plots. Runkle and Whitney (1987) suggest the low pH and poor soil quality may exclude these species. In addition to birch, yellow-poplar may also expand (Ford and Vose 2007), particularly as it is already more abundant at lower slope positions.

Additional data such as soil properties may be particularly illustrative to refine future successional trajectories (e.g., Boerner 2006). The influence of basic physiographic variables was particularly evident when the dominant influence of hemlock was removed from the overstory ordination. These gradients could be compared to known gradients within southern Ohio (e.g., Goebel and Hix 1997, Hix and Percy 1997, Hutchinson and others 1999, Small and McCarthy 2005), particularly with additional environmental data. Several studies indicate that nitrogen and soil moisture may be particularly influential in the region (Runkle and Whitney 1987, Hutchinson and others 1999, Small and McCarthy 2005). While such studies provide a solid foundation for the environment-vegetation relationships in the unglaciated Allegheny Plateau, hemlock-dominated ravines are not represented, and thus, the interaction of the unique physiographic setting and soil properties on the occurrence of species besides hemlock merits additional inquiry. The environmental

gradients measured as part of this study provide valuable insight, and we plan to build on this foundation with further analyses. In particular, future analyses of soil properties within the ravines will allow exploration of how varied soil properties are within 50 m of these streams and among ravines of the unglaciated Allegheny Plateau. It is reasonable to expect we will identify decreasing soil moisture moving upslope as an additional factor driving the transition from mesic species such as sugar maple and beech to increasingly dry-mesic and xeric oaks (Fig. 2).

The role of hemlock as a foundation species may be particularly important in the central and southern Appalachians, including the Central Hardwoods region. Hemlock dominates headwater riparian areas from ravine bottoms upslope, in many cases to the summit of short hills. Hemlock ravines contribute a unique community to landscape diversity. In riparian areas, hemlock is more likely to be replaced by species such as birch and yellow-poplar. These fast-growing, deciduous species that produce higher quality, faster-decaying leaf litter than hemlock will likely alter the cycling of nutrients and energy across riparian and headwater streams (Kominoski and others 2007, Ball and others 2008). At upper slope positions, if oak and hickory species are able to expand, species composition and function may not shift quite as far. This outcome may indicate more resilience to the loss of hemlock. Yet the future overstory will depend in part on the response of the seedling and sapling layer (Collins and Carson 2004), which is currently sparse. In a region with significant recreation and tourism centered in hemlock-dominated ravines, work to further understand hemlock ecosystem ecology and continue refining successional predictions is critical before the arrival of HWA.

ACKNOWLEDGMENTS

Salaries and funding for this study were provided in part by the state of Ohio through funds to the Ohio Agricultural Research and Development Center (OARDC). Additional funding was provided to the lead author via an OARDC SEEDS grant. We are grateful for access to research sites, granted by the Ohio Division of Natural Areas and Preserves and the Ohio Division of Forestry, and for logistical advice provided by Randy Beinlich at Lake Katharine and David Glass at Hocking State Forest. Stephen Rist, Cody Clifton, Keely Davidson-Bennett, and Jack Martin provided valuable field assistance. Finally, we thank two anonymous reviewers for their comments on an earlier version of the manuscript.

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