

Spatial Patterns of Spread
of the Invasive Forest Pest, Hemlock Woolly Adelgid,
in the Finger Lakes Region of NYS

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INTRODUCTION

Geographic Context: Invasive Species

When a species is introduced from its native range into a new environment, it typically does not survive without the intervention of humans. This is because the organism, plant or animal, has evolved in a separate habitat with unique environmental and climactic variables. When it is introduced into a new habitat, it finds itself unsuited to the physical conditions of the area or to the competition of native organisms. Nonetheless, in rare circumstances, the introduced organism may find itself *too* well suited for the environment. This is when invasive species arise.

An invasive species is an organism which is both non-native to the area and deleterious to the native flora and fauna of the area. Invasive species are typically generalists in their native ranges, meaning they are very adaptable to different physical environments and are good competitors. When invasive species are introduced into an area similar enough to their native habitat, they often find themselves without natural predators or competitors, and their populations increase rapidly. In their native ranges, this does not happen because their numbers are kept in check by predators and competitors which have co-evolved over centuries to keep the ecosystem in balance. Without this balance, invasive species outcompete native species—not only harming these native species directly, but also affecting all the organisms that rely on the native species for survival.

It is imperative to study invasive species for a number of different reasons: the biology of the organism must be understood to realize how they breed and reproduce, the ecology of the organism must be understood to comprehend how it interacts with other organisms in the ecosystem, and the geography of the organism must be understood to be able to predict where it

will be found and where it may travel. By understanding how invasive species spread and what environments they thrive in, researchers can conserve native organisms threatened by specific nonnative pests. Knowing where the invasive may be found can help identify new areas of infestation, and early intervention is often the only way to eradicate an invasive species. Understanding how invasive species spread and what habitats are threatened can help focus conservation efforts to the most critical areas.

Invasive species research falls into the realm of four of the five main geographic themes: the natural environment, human-environmental interactions, movement, and spatial themes. The natural environment theme encompasses patterns and processes provided by natural earth systems. The biology of invasive species falls into this theme because in their natural habitats, these species play a role in the ecosystem processes of the area. Even though the species has been transported somewhere new, it still plays a part in the natural pattern of the world. This transitions into the second theme, human-environmental interactions. Without human interference, there would be few invasive species. This is because humans have played a role in the transportation, either deliberately or accidentally, of invasive species for hundreds of years. This leads directly into the third theme, movement which refers to motion or flows of energy around the world. These movements have a structure and impacts which can be measured. When invasive species are moved into an area, they increase in population and spread from the origin of introduction. How they spread leads into the fourth and final theme, spatial. The spatial theme refers to differentiating geographic space based on distinctive features that allow them to be separated from other geographic areas. In terms of invasive species, this signifies the environmental variables which makes a habitat suitable or unsuitable and explains the spatial patterns of spread.

General Information: Hemlock Woolly Adelgid

The hemlock woolly adelgid (*Adelges tsugae* or HWA) is an insect within the family Adelgidae, or conifer woolly adelgids. Adelgids are closely related to aphids, but consist of a relatively small family, made up of only about named 70 species (Footitt et al., 2009). Adelgids feed on the sap of coniferous host trees, typically a primary host from the genus *Picea* (spruce) and a secondary host from either *Abies*, *Larix*, *Pinus*, *Pseudotsuga*, or *Tsuga* (Havill et al., 2006). HWA received its name because its secondary host is hemlock, or *Tsuga*. HWA is native to Japan and China, but non-native populations can be found in western North America and the eastern United States. In its introduced range in North America, there are no suitable spruce species, so the insect remains on hemlock for its entire lifecycle. In the western North America, HWA feeds on the native hemlock species *T. heterophylla* and *T. mertensiana*, but the insect does not cause mortality, probably due to a native predator or host resistance. In the eastern United States, though, it is a different matter.

HWA was first recorded in the eastern United States in Virginia in the 1980's. It was found on both species of hemlock naturally occurring in the area, *T. canadensis* and *T. caroliniana*. Trees infected with the insect first lost their needles, then limbs, and eventually died, sometimes in as little as four years (McClure, 1991). Since its introduction, HWA has spread to 19 states from Georgia to Maine. It encompasses the entire native range of the Carolina Hemlock (*T. caroliniana*) and most of the southern and eastern range of the Eastern Hemlock (*T. canadensis*) (Figure 1). It has reached its southern and eastern limit in terms of host trees, but it continues to spread north and west at a rate of about 18 miles a year (McClure, 1991).

There are chemical and biological controls which can be used in defense of the insect, but they are both costly and time intensive. Chemical controls must be applied to the trunks of

individual trees—this may be effective in urban settings or for a small, ecologically important stands, but chemical treatment is not effective on a regional scale. Biological controls are more effective for regional conservation, but it takes a great deal of time and research to get the approvals to release a biological control, and then it takes more time for the populations of the control to reach a level which would impact the invasive species.

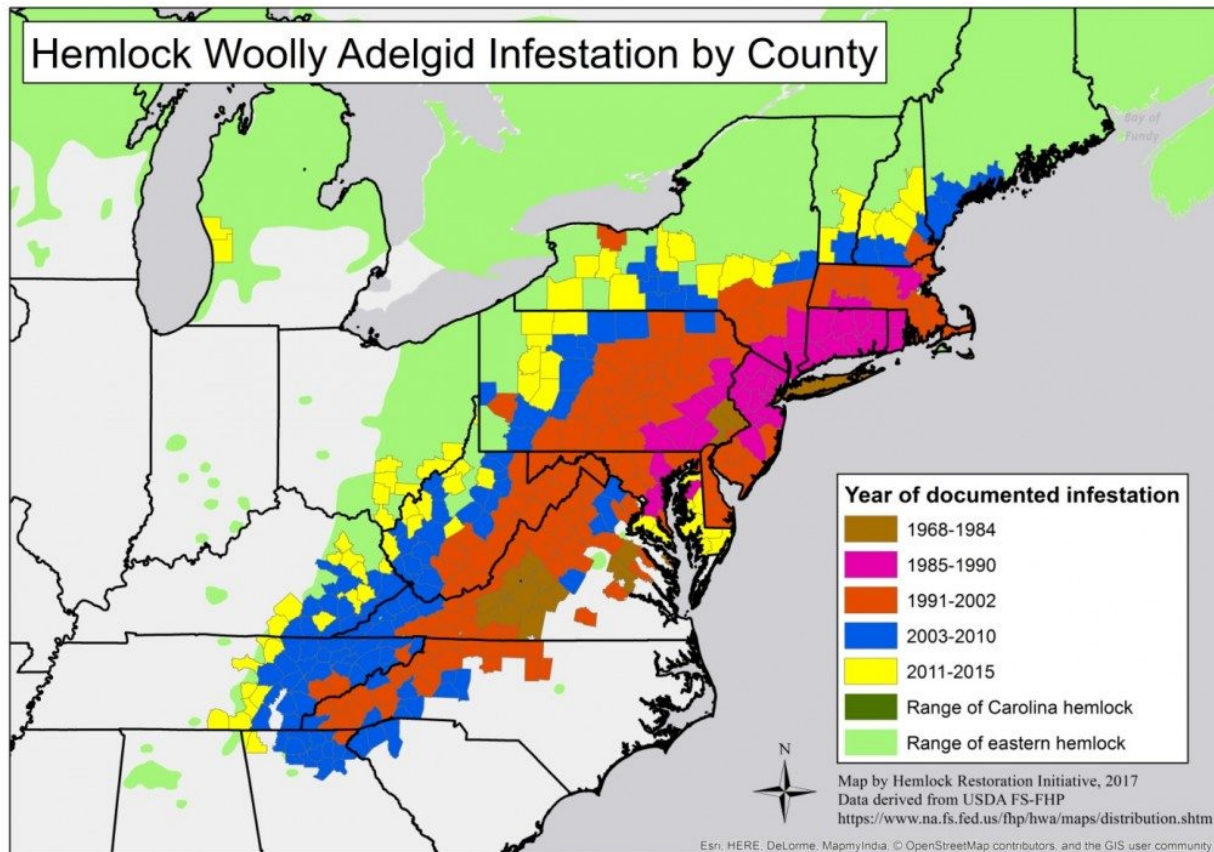


Figure 1: Map by USDA (2017) showing the spread of HWA throughout the Northeast from 1968-2015

Overall Theme & Research Questions

Understanding how invasive species spread helps conservationists slow and possibly stop the movement of invasive species. If we can understand how HWA spreads, we may be able to slow the spread enough to allow a biological control to establish, and in turn, we may be able to protect hemlocks and the organisms they support. With that in mind there are two specific research questions I plan to investigate in this study: 1) What are the small-scale spatial patterns

of HWA spread? and 2) What are the environmental variables that make particular hemlock stands more vulnerable to an initial HWA infestation? Most studies looking into the spread of HWA have been conducted on a county or township level. I want to look at a finer-scale to search for patterns of spread on a landscape level, and I want to know what environmental variables may prove to make a particular stand more at-risk.

LITERATURE REVIEW

To learn how to study and answer these research questions, a review of the literature was completed to understand major concepts and the framework of the problem. Different disciplines were considered at to understand the over-all geographic context.

Ecology: Hemlocks as a Foundational Species

To understand the importance of this work, one must first understand why hemlocks are worth saving. Numerous studies have been implemented studying both the significance of hemlocks as a foundational species, and the effects on the ecosystem caused by the loss of hemlocks after an HWA infestation. Eastern hemlocks, in particular, are one of the most long-lived, shade-tolerant trees in North America. They grow on steep ravines where other species struggle to survive and keep eroding banks at bay. They grow in thick stands which keep the understory cool and dark. Many organisms depend on the habitat hemlocks provide.

In 1994, a study was started in the Delaware Water Gap National Recreation Area in Pennsylvania. This study took place from 1994 to 2003 and was the first to look at an area before, during, and after HWA infestation. Permanent plots were established in hemlock groves to monitor tree and vegetation health before HWA, with the expectation that it would arrive shortly. Before infestation, hemlock plots were healthy. The understory had low light levels and contained 316 different understory plant species. By 2003, after HWA had reached the area, 19%

of hemlock trees showed a decline in vigor from healthy to “severe decline” and 13% of the trees had gone from healthy to dead. Change in light levels increased by 7.8% and both species richness and understory plant-cover increased (Eschtruth et al., 2006). An increase in species richness may seem like a good thing, but as another study performed in 2013 shows, hemlocks may lower diversity, but in turn, they increase local stability.

Hemlocks are considered a foundation species because they alter the microclimate of the area (Ford et al., 2005). The deep shade and acidic soils from the needles results in cool, damp environments with nutrient-poor soils and slow nitrogen cycling. The 2013 study looked at the biotic influence hemlocks played on their environments. Transects were set up running from streams, uphill into hemlock dominated stands. They found that the biotic effect of hemlocks is more influential on species richness and ecosystem processes than the abiotic factors of soil and physiography (Martin and Goebel, 2013). In most cases, as you move from a stream upland, soil quality and moisture content change: these are the abiotic factors. In hemlock stands, the soil quality and moisture remained the same. This is important because when hemlocks die and are replaced with other overstory species, this stable microclimate will change, displacing the organisms that rely on it.

Biology: HWA Lifecycle

The lifecycle of the HWA is important for studying dispersal because there are only a few times during the year when the insect is mobile. HWA has an extremely complex lifecycle with up to five different morphological forms, including crawlers (newly hatched adelgids), numerous nymph instars, and winged and nonwinged adults. Within their lifecycles, HWA can utilize alternating coniferous hosts and can be either holocyclic, meaning they undergo a sexual generation in their lifecycle, or anholocyclic, meaning they are parthenogenic or asexual (Havill

et al., 2007). Holocyclic generations always take place on the primary host, a spruce species. Since there are no suitable spruce species in North America for the adelgids to undergo their sexual generations, it is completely parthenogenetic here. Because of this, it only takes one insect to start a new population (Tobin et al., 2013). HWA goes through two generations each year. The overwintering generation lays eggs in woolly-ovisacs which each contain about 50 eggs (McClure, 1987). During the spring, eggs hatch into larva, called crawlers. This is the only stage of the insect that can move, the other life stages are sessile, as they attach themselves to the base of a needle. Crawlers transition through a number of nymph stages before becoming the second generation of adults during the summer. These second-generation adults lay eggs, and these insects then over winter to reproduce the following spring.

Eco-Geography: HWA Dispersal

Because of the sessile nature of the nymphs and adults, spread only occurs when the crawlers are active and when ovisacs are manually dispersed. Wind, birds, and mammals have all been found to be vectors of dispersal for both crawlers and eggs (McClure, 1990). The woolly egg cases get picked up by the wind and have been transported many miles. Egg sacks and crawlers also are inadvertently picked up by birds and mammals and are moved with the animals from one tree or stand to another. Mist net studies on birds have found both eggs and crawlers stuck on feathers and legs, and a study on hemlock saplings found higher adelgid occurrence on deer-browsed saplings than on untouched saplings (McClure, 1990).

Geography: Spatial Patterns of Infestation

Most studies done on HWA spread have been at a county level, and a steady pattern of dispersal outwards from the source point has been noted. Only a few studies have looked at spread at a landscape level. One such study conducted in Connecticut in 2002 looked at the

spatial patterns of HWA damage, and examined the environmental factors associated with hemlock health and mortality. They found a strong spatial correlation between HWA infestation and latitude and weak correlations to slope, aspect and location. Mortality was significantly higher on W and SW aspects and significantly correlated with stand size (Orwig et al., 2002). A second study done on hemlocks in Shenandoah National Park, Virginia also looked at landscape-level impacts of HWA. They used elevation, slope, slope direction (e.g., aspect), slope shape, moisture index, and distance to streams and roads as dependent variables and regression tree statistical modeling techniques (CART) to estimate areas at risk of infestation. They found elevation, followed by distance to streams, to be the most important variables when predicting where HWA might be found (Young and Morton, 2002).

Summary: Improving Current Research

Previous studies done on the spatial patterns of HWA spread have been done in areas that have been exposed to HWA for more than a decade. Because an HWA infestation can start with only one individual, and populations can increase rapidly with multiple, asexual generations each year, the insect spreads quickly once introduced to an area. Information on what variables may have made hemlock stands vulnerable to HWA infestation in the first place is quickly lost with time as hemlock decline reaches a uniform level across the area (Young and Morton, 2002). To define the small-scale spatial patterns of HWA spread and the environmental variables that make particular stands more vulnerable, I want to specifically look at newly infested areas.

CONCEPTUALIZATION

Interactions Between Concepts and Variables

There are different variables which can lead to one hemlock stand being more vulnerable to HWA infestation than another. By looking at newly infested areas, I believe we can pinpoint

what these variables are. From a review of the literature, it has been shown that adelgids can be transported during the spring and summer months while the crawlers are active and eggs are being laid. It has also been shown that spread is can be stimulated by wind, birds, and mammals. From previous studies done on spatial patterns of spread, we know that there are certain environmental variables that show at least weak correlations with HWA infestation. Based on these concepts, I propose the following model to explain the relationship between the dependent variable, where HWA can be found, and the environmental factors which make up the dependent variables (Figure 2).

Conceptual Diagram

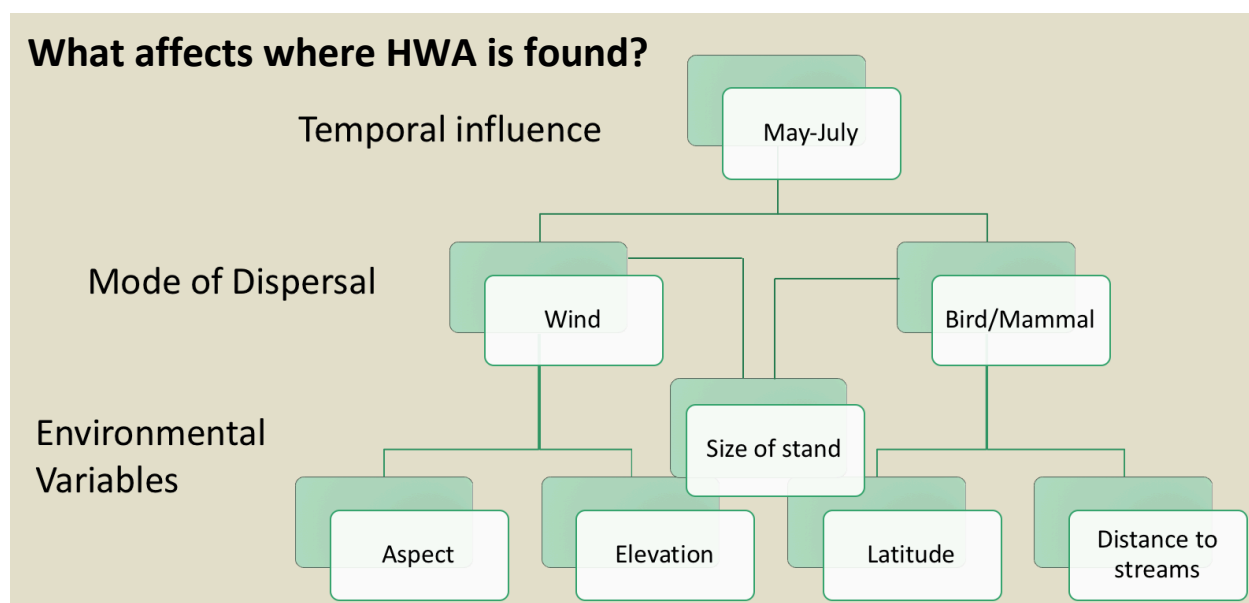


Figure 2: Conceptual diagram linking the dependent variable to the independent variables

To begin looking at where HWA is more likely to occur, you must first look at what influences its spread. The timing, modes of dispersal, and environmental variables all play a part in where HWA will initially be deposited and where infestations will start. HWA can only be spread during the months of May through July. During this time, birds are in the process of migrating and breeding, and deer are actively looking for food. Prevailing winds in the eastern

United States at this time come from the southwest and blow northeast. Both of these modes of dispersal play a role in what size hemlock stands are most at risk for initial infestation. Wind specifically plays a role in the elevation at which initial stands are infected and the aspect of which stands are facing. Bird and mammal modes of dispersal affect which latitudes are infected first and how far away from streams initially infected stands are.

Hypotheses

Based on the diagram above and information gleaned from the literature review, I propose a null hypothesis (H_0) which states:

HWA spread is not associated with landscape patterns such as elevation, aspect, latitude, and distance to streams, and that initial spread is random.

I hope to reject this hypothesis and support my alternate hypothesis (H_a):

HWA spread is associated with landscape patterns such as elevation, aspect, latitude, and distance to streams during the initial stages of infestation.

Specifically, I hypothesize that there will be a higher probability of initial HWA infestations 1) in low elevations, 2) on SW aspects, 3) in larger stands, 4) closer to streams, and 5) along lower latitudes.

I hypothesize that lower elevations are more prone to initial infestation than high elevations because wind and gravity will work together to blow egg sacks and crawlers down slopes and ravines. They will be more likely to settle in lower elevations than high elevations. Because prevailing winds come from the SW and blow NE, I believe that stands on SW aspects will be more likely to be infected than other aspects. Larger stands are more susceptible to initial infestation because the probability of an egg sack or crawler being blown in or carried in on an animal increases with size of stand. Hemlock stands closer to streams will be more at risk to initial infestation than stands farther from streams because there is more animal activity near

streams and water bodies. Animals carrying adelgids, both birds and mammals, will be more prevalent near these bodies of water. Finally, since current HWA infestations are in lower latitudes, I believe because of proximity, animals will transport adelgids to stands in lower latitudes before higher latitudes. These are the five variables I believe I will find positive correlations with HWA presence, but I will include others from previous research to see if there are further factors I am missing.

STUDY AREA

Importance of New York State

New York State is one of the most heavily infested states in terms of invasive species. A study done on the geographical distribution of invasive forest pests shows a distinct

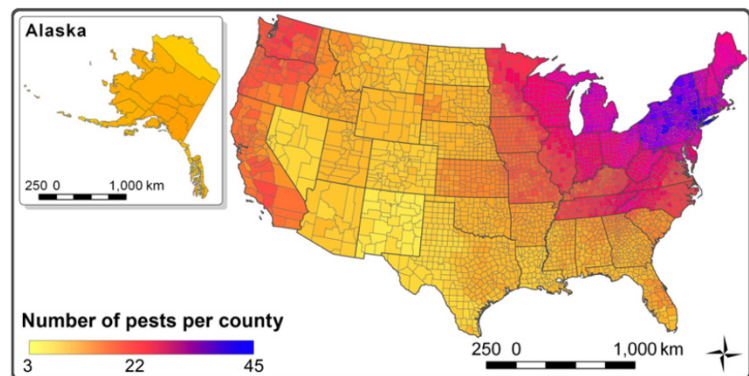


Figure 3: Map by Liebhold et al. (2013) showing distribution of invasive forest pests in the US

pattern of increasing pests in the north-eastern region (Figure 3). At least 40 invasive forest pest

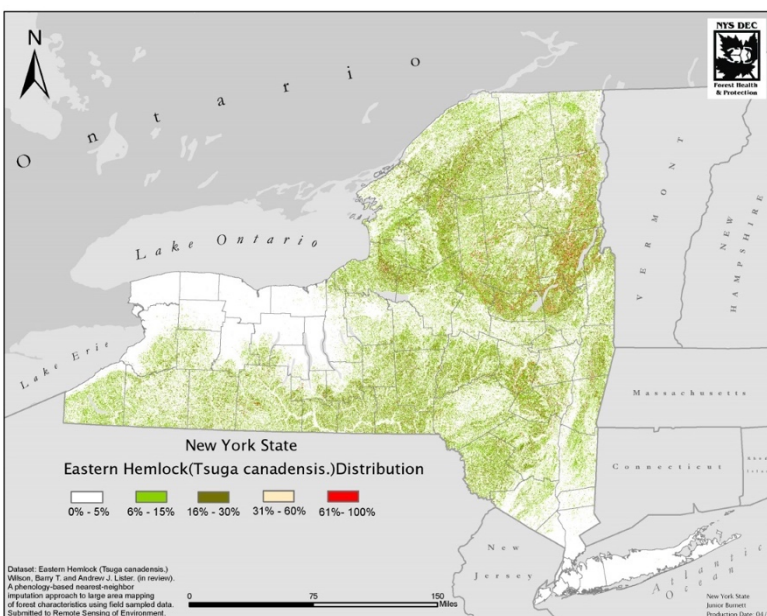


Figure 4: Map from the NY DEC showing Eastern Hemlock distribution in NYS

species are present in NY (Liebhold et al., 2013). This is alarming because NY is also home to the largest forest preserve in the continuous United States, the Adirondack State park. As seen in Figure 4, NY forests are comprised of a large proportion of hemlock trees, but

this is especially so in northern NY, where the Adirondack park is. The outline of the park can be seen in darker green and brown shades in this map. These darker shades represent higher densities of Eastern Hemlock trees. It is vital that HWA is kept from this area. If hemlocks were to become infected within the park, the ecosystem functions of the whole area could change. Unfortunately, HWA is moving closer to the park (Figure 5). In 2017, HWA was found on a few isolated trees in the south of the park. These trees were chemically treated, as were all the trees in the area. It is believed that because so few trees were infected when the infestation was found, eradication efforts were successful.

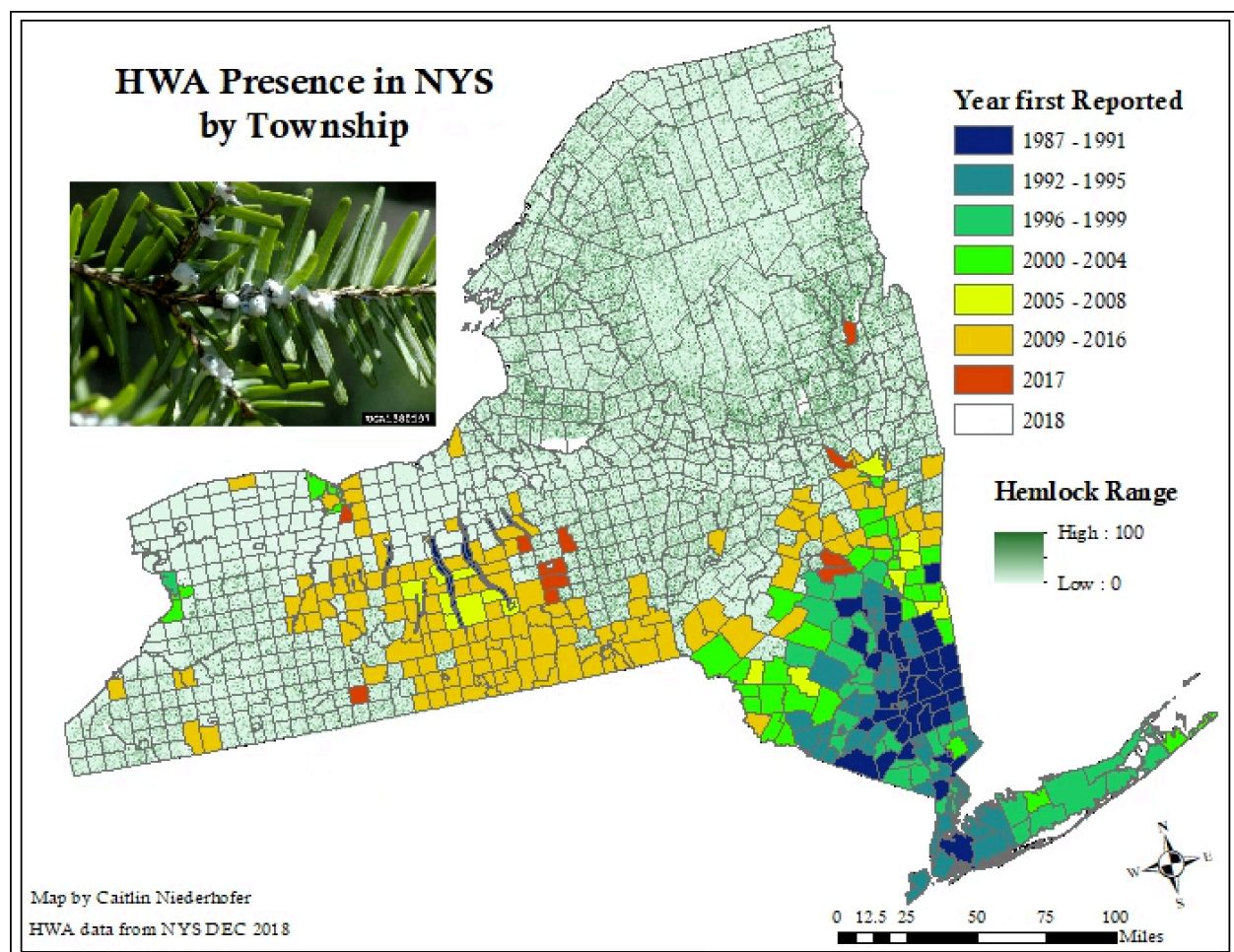


Figure 5: Map by Caitlin Niederhofer showing HWA spread through NYS by township and hemlock densities

Specific Study Area

For my specific study area, I chose to look at the counties of Schuyler, Chemung, Tioga, Tompkins, Cortland, and Broome (Figure 6). I chose these counties for three reasons, first of all, from Figure 4, it can be seen that there is a high density of hemlock trees in the area south and

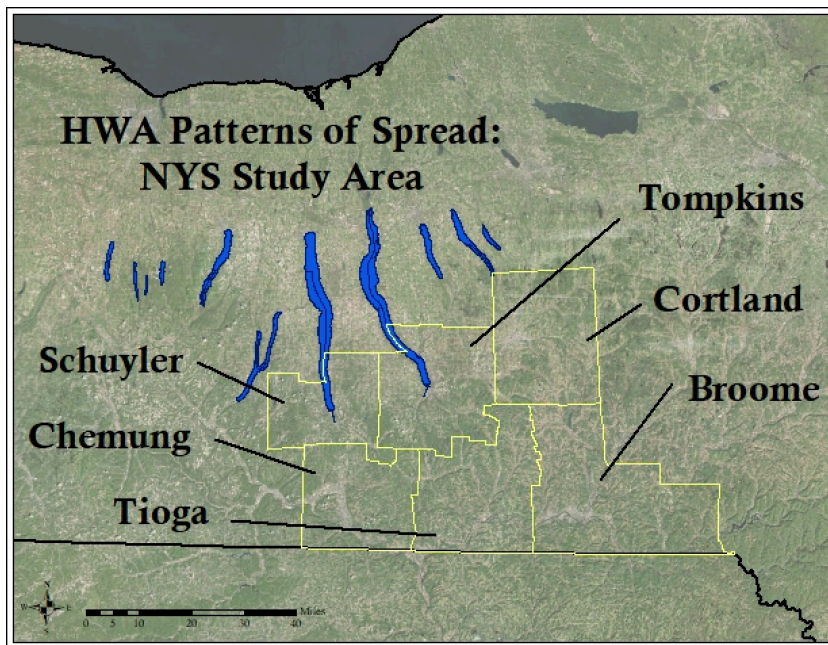


Figure 6: Map by Caitlin Niederhofer showing study area for HWA research

east of the Finger Lakes. This is also a region full of valleys and steep ridges where hemlocks prefer to grow. Secondly, HWA is relatively new to these counties. There are areas along the Finger Lakes in Schuyler and Tompkins counties which have had HWA since 2008,

but Tioga, Chemung and Broome counties have only had HWA for less than five years.

Evidence of HWA in Cortland county has only been seen in the last year. Although HWA has been found in most of the townships in these counties, there are still hemlock stands which are presumably HWA free.

The third reason I chose these counties is for ease of data collection. I will be conducting field test myself and need to feasibly reach all study plots. Since I live in Cortland county, go to school in Broome, and have worked in Tompkins, I am familiar with the area. Schuyler, Chemung, and Tioga are close enough to make travel during the summer field season possible.

METHODOLOGY

Data Acquisition: Sources and Structure

From a contact in the DEC and the department of Forest Health, I will obtain hemlock range maps and HWA occurrence data. The Forest Health department does yearly flyovers of NYS to visually assess the health of trees in the area. Photos are taken of forested areas that show signs of defoliation or reduced health. Field surveys are then organized throughout the year to assess what is causing the damage. DEC collects data on many forest pests, including HWA. The data I obtain from the department of Forest Health will be GIS polygon and point data. From this data, I hope to be able to come up with a list of all hemlock stands within the study area, complete with information whether HWA has been surveyed, if HWA is present, and if so when it was first detected in the stand.

Data on environmental variables such as those listed in the hypothesis will come from the USGS. I will use digital elevation models (raster datasets) and GIS overlays to collect information on slope, aspect, latitude, and elevation. Distance from streams will come from a hydrology shapefile of NYS from GIS open data.

Finally, data on the most recent HWA infestation sites will be primary data that I collect via ground work and field testing. From the data from DEC, I will generate a random sample of hemlock stands that either are not known to contain HWA or have HWA which has been found within only the past two years. This two-year time frame should ensure that variables which caused the stand to be vulnerable to HWA are still measurable. I will survey trees in each stand looking for the presence or absence of HWA. Since I am only looking at what causes a stand to be vulnerable to initial infestations, and not how bad the infestations are, I only need binary data, or “yes, no”. If I find evidence of any HWA in the stand, it will be marked as present, if I find no

evidence, it will be marked as absence. I will try and survey 100 random plots. I am including plots where HWA has not been detected yet, because it is important to include these in the analysis, but also because I assume I will find new infestations.

Data Portrayal

DEC data will be brought into ArcGIS and maps of current HWA infestations will be made, as well as maps of hemlock stands. Variation in environmental variables from the 100 random test plots will be summarized in tables showing mean, median, and mode values. Presence and absence data from the test plots will be color-coded and mapped in ArcGIS. Environmental variables from “presence” plots will be averaged by variable and displayed in contrast to the averages from the “absence plots”.

Prior to analysis, aspect values (one of the environmental variables) will need to be changed from a cardinal direction to a numerical value that can be used in the regression. A cosine transform will be applied to change the circular direction variable (azimuth degrees) to a value from -1 (South) to 1 (North).

Data Analysis

I will use Mantle regression tests to study the relationships between HWA presence in hemlock areas and environmental variables. Mantel tests include the geographical location as a variable in the analysis and have been used in similar studies looking at the relationship between environmental variables and species ranges. Mantel tests performs a linear regression on distance matrices generated from independent and dependent variables. This is important because HWA infestation rates are spatially autocorrelated with one another. These mantel regression results will show me what environmental variables correlate with initial HWA infestations and whether

or not they are statistically significant. I can then map areas in high risk of HWA spread based on these significant independent variables.

Methodology Table

The information previously stated in this methodology section is visually summarized in the following table (Table 1). The hypothesis is stated in the top left followed by each environmental variable separately.

Table 1: Visual summary of methodology

Hypothesis:	Data Acquisition & Preparation			Data portrayal & Analysis	
	Source	Structure	Manipulation	Method Portrayal	Method of analysis
There is a relationship between HWA infestation and landscape characteristics:	DEC hemlock range maps	Polygon	Original data	Maps	Descriptive analysis
	DEC HWA occurrence data	Point and polygon	Show temporal change	Maps	Descriptive analysis
	Field collection of new infestation	Binary data	Original data	Maps	Descriptive analysis
S and SW facing slopes	USGS: DEM	Nominal	Cosine transform	Table	Mantel regression
Low Elevation	USGS: DEM	Continuous	Original data	Table	Mantel regression
Large Stand Size	DEC range maps	Polygon	Generate area	Table	Mantel regression
Latitude	USGS: DEM	Continuous	Original data	Table	Mantel regression
Distance to streams	GIS Open data NYS hydrology	Continuous	Distance calculation (GIS)	Table	Mantel regression

UTILITY AND RELEVANCE

Expected findings

This study aims to look at the relationship between environmental variables and initial HWA infestation. If HWA dispersal can be predicted, the spread of HWA may be slowed, or even stopped. If this study can identify variables which place hemlock stands at risk of initial infestation, those areas can be monitored closely. When HWA is found in the initial stages of infestation, chemical means of eradication are an option. Biological controls could also be released in “at risk areas” preemptively, giving the predatory control insects time to build their populations before HWA infestations reach levels which cause mortality in hemlocks. By slowing the spread of HWA, both hemlocks and the organisms they support can be saved in NY and the Northeast. This will intern preserve biodiversity and important ecosystem functions across the Northeast.

Limitations

There are a number of limitations that present themselves in this study. The first is the availability of data. I have been in contact with the DEC, but I am still not sure at what scale the data on hemlock stands and HWA presence will be. Preferably, I will receive detailed GPS coordinates of HWA presence and accurate polygons of hemlock stands, but this may not be the case. If I cannot obtain this data from the DEC, I will have to create my own hemlock stand polygons. This may be possible through remote sensing and high-resolution satellite data. Another limitation is time. I will not be able to search each tree in a stand for the presence of HWA, so transects will be utilized. If no HWA is found in the transect, the stand will be considered free of HWA. I also do not own scaling equipment, so HWA surveys will be taken from the ground.

LITERATURE CITED:

- Eschtruth, A. K., N. L. Cleavitt, J. J. Battles, R. A. Evans, and T. J. Fahey. 2006. Vegetation dynamics in declining eastern hemlock stands: 9 years of forest response to hemlock woolly adelgid infestation. *Canadian Journal of Forest Research* 36 (6):1435–1450.
- Footitt, R. G., H. E. L. Maw, N. P. Havill, R. G. Ahern, and M. E. Montgomery. 2009. DNA barcodes to identify species and explore diversity in the Adelgidae (Insecta: Hemiptera: Aphidoidea). *Molecular Ecology Resources* 9 (SUPPL. 1):188–195.
- Ford, C. R., D. R. Foster, B. D. Kloeppel, J. D. Knoepp, and M. Gary. 2005. Loss of foundation species : consequences for the structure and dynamics of forested ecosystems. *Frontiers Ecology Environment*; 3(9): 479–486:1–29.
- Havill, N., M. Montgomery, and M. Keena. 2006. Chapter 1 : Hemlock Woolly Adelgid and Its Hemlock Hosts : a Global Perspective. 3–14.
- Havill, N. P., R. G. Footitt, and C. D. von Dohlen. 2007. Evolution of host specialization in the Adelgidae (Insecta: Hemiptera) inferred from molecular phylogenetics. *Molecular Phylogenetics and Evolution* 44 (1):357–370.
- Liebholt, A. M., D. G. Mccullough, L. M. Blackburn, S. J. Frankel, B. Von Holle, and J. E. Aukema. 2013. A highly aggregated geographical distribution of forest pest invasions in the USA. *Diversity and Distributions* 19 (9):1208–1216.
- Martin, K. L., and P. C. Goebel. 2013. The foundation species influence of eastern hemlock (*Tsuga canadensis*) on biodiversity and ecosystem function on the Unglaciated Allegheny Plateau. *Forest Ecology and Management* 289:143–152. <http://dx.doi.org/10.1016/j.foreco.2012.10.040>.
- McClure, M. S. 1987. Biology and Control of Hemlock Woolly Adelgid. The Connecticut Agricultural Experiment Station Bulletin 8:3–9.
- McClure, M. S. 1990. Role of Wind, Birds, Deer, and Humans in the Dispersal of Hemlock Woolly Adelgid (Homoptera: Adelgidae). *Environmental Entomology* 19 (1):36–43. <http://ee.oxfordjournals.org/cgi/doi/10.1093/ee/19.1.36>.
- McClure, MS. 1991. Density-dependent feedback and population cycles in *Adelges tsugae* (Homoptera: Adelgidae) on *Tsuga canadensis*. *Environmental Entomology* 20: 258–264
- Orwig, D. A., D. R. Foster, and D. L. Mause. 2002. Landscape patterns of hemlock decline in New England due to the introduced hemlock woolly adelgid. (Insights from Historical Geography to Ecology and Conservation: Lessons from the New England Landscape.). *Journal of Biogeography* 29 (10):1475–1487.
- Tobin, P. C., R. M. Turcotte, and D. A. Snider. 2013. When one is not necessarily a lonely number: Initial colonization dynamics of *Adelges tsugae* on eastern hemlock, *Tsuga canadensis*. *Biological Invasions* 15 (9):1925–1932.
- Young, J. A., and D. D. Morton. 2002. Modeling landscape-level impacts of HWA in Shenandoah National Park. *Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium. Agricultural Experiment Station, Rutgers University. New Brunswick, USA* (Teeter 1988):73–85. http://www.lsc.usgs.gov/aeb/2055/young_morton_hwa_modeling.pdf