Potential Effects of Climate Change on Mortality of the Invasive Species Hemlock Woolly Adelgid (*Adelges tsugae*) in Nova Scotia, Canada

by

Anna K. J. Irwin-Borg

Submitted in partial fulfillment of the requirements for the degree of Bachelor of Science

at

Dalhousie University

Halifax, Nova Scotia

April 2019

DALHOUSIE UNIVERSITY

DATE: April 15th, 2019

AUTHOR: Anna Irwin-Borg

TITLE: Potential Effects of Climate Change on Mortality of the Invasive Species Hemlock Woolly Adelgid (*Adelges tsugae*) in Nova Scotia, Canada

DEPARTMENT OR SCHOOL: College of Sustainability

DEGREE: Bachelor of Science Environment, Sustainability and Society, and Environmental Science

Convocation: May 2019

Signature of Author

Table of Contents

List of Figures

Abstract

Hemlock woolly adelgid (HWA) kills hemlock trees by injecting poison into their stems as the feed on sap, defoliating the trees. This insect has caused widespread eastern hemlock death across the northeastern United States (US) and its presence was confirmed in Nova Scotia in 2017. Eastern hemlock trees are foundation species, creating unique ecosystem dynamics in their habitats, and they are also a defining species of tolerant coniferous old-growth Acadian forests, which are valuable biodiversity hubs in Nova Scotia. HWA mortality after exposure to extreme low winter temperatures has been well studied, and 91% mortality has been found to keep HWA populations under control. This study used an equation developed for northeast US forests to determine theoretical HWA mortality using mean winter temperatures for a past (1981-2010) scenario and representative concertation pathway (RCP) 2.6, 4.5, and 8.5 scenarios for the near future (2041-2070) and distant future (2071-2100). Stands containing hemlock are also shown in the maps to depict areas of concern. It was found that some high-elevation, northern regions of Nova Scotia would have kept HWA populations under control, causing >90% HWA mortality, but stands containing hemlock are generally not present in these areas. Areas with >90% mortality were not found in any of the future scenarios. The differences between the near future and distant future scenarios were lowest for RCP 2.6 and highest for RCP 8.5, with RCP 4.5 falling in the middle. Because this study used equations developed for the northeastern US, future research should focus on developing HWA mortality equations for Nova Scotia. Future studies should also consider more variables that have been linked to HWA population distributions.

Abbreviations and Glossary

Average daily mean winter temperature (ADMWT): The mean daily temperatures averaged for December through March.

Average monthly mean winter temperature (AMMWT): The mean monthly temperatures ([monthly high + monthly low] / 2) averaged for December through March (J. Steenberg, personal communication, March 1, 2019).

Canadian Food Inspection Agency (CFIA): The "lead agency responsible for preventing the entry and spread of invasive insect species" (Environment Canada, 2012, p. 4).

Hemlock woolly adelgid (HWA; *Adelges tsugae*): An insect that kills hemlock trees by injecting poison into their twigs as it feeds on sap (Cranshaw & Shetlar, 2017).

Non-indigenous invasive species (NIIS): Introduced species that change ecosystem dynamics, usually by outcompeting or preying on indigenous species (Chisholm, 2012).

Nova Scotia Department of Lands and Forestry (NSDLF): Formerly Nova Scotia Department of Natural Resources.

Nova Scotia Department of Natural Resources (NSDNR)

Hemlock: For the purposes of this paper, "hemlock" means eastern hemlock (*Tsuga canadensis*).

Acknowledgements

I would like to thank my supervisor, Peter Duinker, and my professors, Steven Mannell and Andrew Bergel, for their guidance. I would also like to thank James Steenberg for creating useful temperature datasets, and my classmates, friends, family, and partner for their emotional support.

Chapter 1: Introduction

Invasive Species

Humans introducing species to unfamiliar regions is as old as human migration (Mack et al., 2000; Chisholm, 2012), but increases in trade and transportation over the past 500 years, and even more so in the past 200 years, have intensified species introduction rates (di Castri, 1989). This has, in turn, increased the amount of non-indigenous invasive species (NIIS) worldwide, and it is estimated that about 1% of introduced, or naturalized, species become invasive (Chisholm, 2012). Without the coevolutionary checks and balances of their native habitats, NIIS change ecosystem dynamics, usually by outcompeting or preying on indigenous species (Chisholm, 2012).

By altering managed and natural ecosystems, invasive species cause numerous ecological and financial issues. It has been estimated that, in the United States, economic costs of NIIS recently amounted to $120 billion per year in losses, damages, and pest management (Pimentel, Zuniga & Morrison, 2004). This number does not even include external costs such as changes to ecosystem services (Pimentel et al., 2004). By changing the population dynamics of ecosystems, NIIS can alter a wide range of processes and systems. The focus of this study will be the hemlock woolly adelgid (HWA; *Adelges tsugae*), a NIIS from Asia (Cranshaw & Shetlar, 2017) that has drastically changed ecosystems by feeding on and killing eastern hemlock (*Tsuga canadensis*) and carolina hemlock (*Tsuga caroliniana*) trees, which are foundational in their ecosystems (Case, Buckley, Barker-Plotkin, Orwig, & Ellison, 2017; Orwig, Cobb, D'Amato, Kizlinski & Foster, 2008; Vose, Wear, Mayfield & Nelson, 2013).

Impacts of HWA

HWAs appear on tree branches as little white sacks, but beneath this cottony cover, the adelgids are black or red (Cranshaw & Shetlar, 2017). They kill hemlock trees by injecting poison into twigs as they feed on sap, which causes the hemlock leaves to drop (Cranshaw & Shetlar, 2017).

HWAs kill hemlock trees, but this is only the beginning of their impacts. Hemlocks across the eastern United States have been severely impacted by HWA infestations (Fitzpatrick, Preisser, Porter, Elkinton & Ellison, 2012; Vose et al., 2013). Hemlock wood is used in framing, roofing, boxes, and pallets in some areas (CABI, 2013), but hemlock is not an economically important species in Nova Scotia (P. Duinker, personal communication, February 14, 2019). Tea brewed from hemlock bark and needles has also been used by indigenous healers in North America (CABI, 2013). By killing this foundational species, HWAs also cause shifts in ecosystem dynamics. For example, as hemlocks slow soil nitrogen (N) cycling, HWA infestations have been correlated to increased N cycling in soils (Orwig et al., 2008; Jenkins, Aber & Canham, 1999). Nutrients are not expected to stay in soils, however; hemlock death is expected to increase the amount of nutrients in soil water (Yorks, Jenkins, Leopold, Raynall & Orwig, 2000). As hemlocks are often found in riparian zones, this means that increased fertilization of aquatic ecosystems is expected with hemlock death (Orwig et al., 2008). Algal blooms and eventual eutrophication are possible results of increased aquatic fertilization (Whyte, 2013). This is just one example of how an ecosystem can change as hemlocks are replaced by other species.

The Canadian Food Inspection Agency (CFIA; 2017) confirmed the HWA's presence in Nova Scotia in August of 2017. Although eastern hemlocks are of low commercial importance in Nova Scotia, this is a serious issue because they are essential for maintaining biodiversity in certain areas of the province. Hemlock is a defining species of one of the two dominant old-growth Acadian forest types: tolerant coniferous (Stewart, Neily, Quigley, Duke & Benjamin, 2003). Old-growth Acadian forests are no longer common in Nova Scotia due to aggressive timber harvests, but they are considered invaluable biodiversity hubs (Stewart et al., 2003). Biodiversity is vital for human sustainability, because it helps drive ecosystem services that people rely on, such as biomass production, nutrient cycling, and decomposition (Cardinale et al., 2012).

Natural Temperature Mitigation

The HWA's vulnerability to cold winter temperatures has been well studied (Paradis, Elkinton, Hayhoe & Buonaccorsi, 2008). In one laboratory study, cell damage was found in HWAs exposed to -20°C and -25°C, and -30°C exposure resulted in total HWA mortality (Gouli, Parker & Skinner, 2001). Paradis et al. (2008) fit HWA mortality data and eight different measures of winter temperature to a model to determine which measure best predicted mortality. Average daily mean winter temperature (ADMWT) was found to be the best predictor of HWA mortality in the study. Furthermore, the same study found that three consecutive years of ADMWTs below -5°C is expected to limit population expansion. Given the link between temperature and HWA mortality, climate change is expected to have a significant effect on the spread of HWA (Paradis et al., 2008).

Studies of potential HWA range and hemlock vulnerability have generally been limited to the eastern United States and, to a lesser extent, southern Ontario, where HWA infestations have been most pervasive (Paradis et al., 2008; Fitzpatrick et al., 2012; Jones, Song & Moody, 2015). The relationship between HWA mortality and winter temperatures in Nova Scotia has not been widely studied. McAvoy, Regniere, St-Amant, Schneeberger & Salom (2017) conducted a study on HWA mortality that considered Nova Scotia, but it was not the focus of the study. Nevertheless, the study posited that the average Nova Scotian winter temperature for the period 1981-2010 could have caused more than 91% HWA mortality in most areas of the province, but that, over time (predictions to 2100), percent mortality will drop below 91% across the province, with some areas decreasing more than others. As of fall 2018, I have been unable to find any published studies focusing on HWA in Nova Scotia.

Problem Statement

How HWA populations are likely to be influenced by Nova Scotia's current and future climates has not been well studied. Such studies are a vital pre-requisite for assessing potential impacts of HWA on the future populations of eastern hemlock in Nova Scotia.

Significance

Management of the HWA is possible. Benton et al. (2016) found that chemical imidacloprid basal soil drench treatments significantly mitigated HWA populations and related hemlock defoliation. Vose et al. (2013) also pointed to imidacloprid stem or soil injections and dinotefuran trunk spray as common chemical treatments in the southern Appalachians. Successful biological controls may also be possible with the release of various natural enemies working in tandem (Vose et al., 2013). HWA populations can be mitigated with good management, so it is useful to consider which hemlock populations are most vulnerable to the pest.

As winter temperature is an important controlling factor of natural HWA mortality (Paradis et al, 2008), it is worthwhile to consider how winter temperatures in Nova Scotia have changed and how they are expected to impact HWA mortality rates today and under future climate projections. With this information, management strategies can prioritize eastern hemlock forests that are expected to suffer the largest mortality rates due to HWA infestations. What HWA mortality may have looked like in the past, had it been introduced to Nova Scotia earlier, will also be considered in this study. This will give insight into how climate change has already influenced Nova Scotia's hemlock susceptibility to the pest.

Research Question

How will climate change affect the mortality of HWA in Nova Scotia, and by extension, its ability to proliferate throughout the province?

Hypothesis

With climate change, the potential for HWA mortality will decrease province-wide, increasing the insect's ability to proliferate throughout the province.

Study Design

In a study by Paradis et al. (2008), ADMWT is the best predictor of HWA mortality (p-value = 0.008; $R^2 = 0.43$). Projected daily mean temperatures were not available for use in this study, however. Projected and past monthly means were acquired through a data-sharing agreement with the Nova Scotia Department of Lands and Forestry (NSDLF; 2018). Projected monthly means for December through March were averaged to create a past winter climate normal (1981-2010) and future (2041-2070 and 2071-2100) winter warming scenarios for three representative concentration pathways (RCPs), RCP 2.6, RCP 4.5, and RCP 8.5. Average monthly mean winter temperature (AMMWT) was used in place of ADMWT in the equation from Paradis et al. (2008) to calculate theoretical HWA mortality for the past and future scenarios. The differences between temperatures calculated from AMMWTs and ADMWTs and the resulting mortalities are also considered here. A map of the differences is provided (Figure 1).

Hemlock presence in forest stands across Nova Scotia was determined using Nova Scotia Department of Natural Resources (NSDNR; 2017) public forest inventory data. Stands with hemlock present were added to all HWA mortality maps to depict at-risk areas.

Summary

Invasive species cause many ecological and economic issues, and the HWA's recently confirmed presence in Nova Scotia is expected to be no different. Winter temperature is widely understood to be a limiting factor of HWA spread due to its impact on mortality, but studies on actual and predicted HWA range have not generally extended as far north as Nova Scotia. Thus, the effects of past and future Nova Scotian winter temperatures on HWA mortality is the focus of this study. AMMWTs for the period 1981-2010 were retrieved, and then the temperatures were run through an equation developed by Paradis et al. (2008) to determine theoretical HWA mortality. Average theoretical HWA mortalities for the period 1981-2010 were then mapped with stands containing hemlock. Three temperature projections for each of the periods 2041-2070 and 2071-2100 were also considered. Predicted HWA mortality was calculated and mapped with stands containing hemlock for low-, middle-, and high-change scenarios (RCP 2.6, 4.5, and 8.5 respectively). Understanding the potential effects of Nova Scotia's past and future climates on HWA populations is an important step towards two goals: determining best practices for HWA management, and understanding hemlocks' HWA-related vulnerability to climate change.

Chapter 2: Literature Review

Hemlocks are invaluable for ecosystem processes and habitats (Sackett et al., 2011). As such, ecosystems are expected to be seriously altered by HWA infestations. Chemical and biological HWA controls have been developed, but they have not been perfected for use at the forest level (Vose et al., 2013). Climate is understood to control the range of many species (Hellmann, Byers, Bierwagen & Dukes, 2008), but the use of climatic envelope models, which use climate thresholds to determine the mortality of species, is debated among scientists (Pearson & Dawson, 2003). Generally, these types of models are best for studies of highly temperature-dependent subjects at coarse spatial levels, with (Pearson & Dawson, 2003). HWA is such a subject. High mortality of HWA has been correlated to low winter temperatures in many studies (Paradis et al., 2008; Cheah, 2017; McAvoy et al., 2017; Parker, Skinner, Gouli, Ashikaga & Teillon; 1999). Winter temperature is not the only controlling factor of HWA distribution, however (McClure, 1991; Trotter & Shields, 2009; Fitzpatrick et al., 2012).

Hemlocks and Ecosystems

Hemlocks are foundation species, which means they have many influences on the surrounding ecosystem (Sackett et al., 2011). For example, as described above, hemlocks slow nitrogen cycling (Ellison et al., 2005). This is especially important when they inhabit riparian zones, because less nitrogen is available to run off into streams and cause eutrophication (Ellison et al., 2005). Furthermore, certain species are linked to the unique environment created by hemlock forests. Snyder, Young, Lemarie & Smith (2011) found significantly more taxa of benthic macroinvertebrates (large, bottom-dwelling insects) in streams draining hemlock-dominant forests compared to mixed hardwood forests. They also found a strong association between some of these taxa and hemlock. In fact, there are records of over 400 hemlock-associated insect species in the southern Appalachians alone (Coons, Lambdin, Grant, Rhea & Mockford, 2012). Numerous bird species rely on hemlock trees for their habitat (Tingley, Orwig, Field & Motzkin, 2003). In southern New England, Tingley et al. (2002) found that two species of warbler and the Acadian flycatcher were particularly strongly associated with hemlock forests.

HWA Impacts

HWA infestations are expected to impact ecosystems and species composition in various ways. First, hemlock death is expected to increase rates of soil nitrogen cycling, likely causing eutrophication in surrounding water bodies (Orwig et al., 2008; Jenkins et al., 1999). Furthermore, benthic diversity is expected to decline with HWA-related hemlock death (Snyder et al., 2011). Similarly, Tingley et al. (2002) found that certain species of birds were sensitive to hemlock removal, but they also found that some bird species are expected to benefit from hemlock removal, particularly those that favour densely packed hardwood seedlings, which are expected to replace hemlocks in many cases. Although some species may be positively impacted by hemlock death in hemlock-dominant forests, species composition and some ecosystem dynamics are undoubtedly expected change with the introduction of HWA.

Hemlock death due to HWA infestations have been shown to change hydrological systems. However, the nature of these changes appears to be dependent on various factors, such as time and region. Transpirations rates are expected to change with HWA infestation, but the nature of this change is not expected to be consistent over time. Transpiration is expected to initially decrease due to hemlock death as leaf area decreases (Brantley, Ford & Vose, 2013; Kim et al., 2017). However, hemlocks have comparatively low transpiration rates, so, as hemlocks are replaced by species with higher transpiration rates, overall transpiration is expected to increase in

HWA-infested forests (Brantley et al., 2013; Ford & Vose, 2007; Daley, Phillips, Pettijohn & Hadley, 2007).

It has also been posited that impacts depend on regional factors. Kim et al. (2017) studied water yields over 10 years in two catchment areas in New England and found that, over this time, water yields in the HWA-infested catchment area increased more than those in the neighbouring catchment area with less hemlock. Brantley, Miniat, Elliott, Laseter & Vose (2015) considered a different region, the southern Appalachians, and found that water yields decreased with HWA infestations. Brantley et al. (2015) hypothesized a short-term increase in water yield due to hemlock death and attributed their finding to low hemlock density and quick replacement, which are regionally-dependent factors. Kim et al. (2017) also suggested that the discrepancy between the two findings indicates that the impacts of HWA infestations on the hydrological cycle depend on regional conditions, such as hemlock density, but they also pointed to climate as a potential regional factor.

Potential Management Treatments

As discussed above, chemical insecticide treatments have been shown to significantly limit HWA survival and spread, but this management option has notable limitations. Benton et al. (2016) found that four to seven years after imidacloprid basal drenching, HWA populations were low enough that there were no observable impacts on hemlock health. They also found more HWA on trees seven years post-treatment compared to four- and six-years post treatment. Cowles (2009) suggests that imidacloprid can have negative impacts on aquatic species, and it is expected to leach into these ecosystems if too much of the chemical is administered. Knoepp, Vose, Michael & Reynolds (2012) studied the movement of imidacloprid in soils in the southern Appalachians and found that vertical movement was rapid, but concentrations decreased with depth, and horizontal movement was limited. According to Vose et al. (2013), insecticides like imidacloprid are also costly, and they can only be applied on a tree-by-tree basis. Vose et al. (2013) also mention that the chemical dinotefuran can be used to manage HWA. Both chemicals have use restrictions around water in certain areas, however, due to potential leaching (Vose et al., 2013). Considering the limitations, Vose et al. (2013) determined that insecticides are an important part of HWA management but are not a practical long-term, broad-scale solution.

Biological controls are also an important aspect of HWA management, but it is not expected that any one species will be able to keep HWA populations under control. The need for multiple biological controls can be illustrated through the potential and downfalls of *Laricobius* species. Mausel, Salom, Kok & Fidgen (2008) released the HWA predator *Laricobius nigrinus* in study sites in Virginia and studied its impacts on HWA populations. They determined that the predator's impacts on HWA populations after two years made it an important potential biological control. *Laricobius* species do not feed on HWA year-round, however (Vose et al., 2013). Thus, Vose et al. (2013) determined that species active in *Laricobius'* off-seasons should also be used. Vose et al. (2013) concluded that, in general, a variety of biological controls is needed to sufficiently limit HWA populations.

Using Climate to Model the Future Spread of Species

Climate change is expected to alter environmental constraints and pathways that control species distributions (Hellmann et al., 2008). A review study by Hellmann et al. (2008) considered many studies of future species' ranges and determined that temperate zones, such as those in the northeastern United States, are particularly vulnerable to climate change, because species ranges tend to be determined by winter temperatures.

Modelling future ranges of invasive species using climate thresholds is common (McDowell, Benson & Byers, 2014), but this method is debated. After Paradis et al. (2008) came up with an equation that determined a mean winter temperature of -5°C was expected to keep HWA populations under control, they modelled the expected future spread of the species using this threshold. The study mapped -5°C isotherms from historical data and under projected warming scenarios. This is an example of what is termed a "bioclimatic envelope model" (Araújo & Peterson, 2012). That is, the model determines a climatic threshold below (and/or above) which a species cannot maintain a viable population (Araújo & Peterson, 2012).

Pearson & Dawson (2003) considered some shortcomings of these methods. For example, Pearson & Dawson (2003) point out that biotic interactions are important to consider when modelling future ranges of species, but these interactions are not captured in bioclimatic envelope models. A key finding of this review study was that spatial scale is important to consider when applying a bioclimatic envelope approach. Pearson & Dawson (2003) concluded that this type of modelling is useful for macro levels, but that, at more local levels, influences of other factors are more likely to be detected. An example of this is illustrated in a study by Pearson, Dawson, Berry & Harrison (2002) in which bioclimatic modelling of the distribution of plant species in Europe was more accurate than when the model was downscaled for Great Britain. Thus, Pearson & Dawson (2003) argue that a hierarchical model should be used, starting with bioclimatic models at synoptic levels and then considering other factors, such as topography, land use, soil type, and biotic interaction at finer levels. It is also mentioned that bioclimatic envelope models should only be used when temperature is known to have a significant effect on the species under consideration (Pearson & Dawson, 2003).

Temperature Controls HWA Distributions

Winter temperature is widely understood to be a controlling factor of HWA mortality and spread. Some studies have found that HWA mortality and temperature have an inverse, linear or non-linear (i.e. logistic) relationship (Paradis et al., 2008; Cheah, 2017; McAvoy et al., 2017) Furthermore, a study by Parker et al. (1999) did not include a regression analysis, but it did explain that a gradual decline in HWA populations was observed with decreasing temperatures in January and February. Interestingly, Trotter & Shields (2009) found inconsistent explanatory power of winter temperatures on HWA mortality in two years. In their study, winter temperature only explained <10% of the variation in HWA mortality in 2003, but over 47% in 2004. Thus, although there are some discrepancies, it is generally understood that decreases in winter temperatures increase HWA mortality.

Paradis et al. (2008) point out that 91% winter mortality is expected to stop HWA populations from spreading. A study by McAvoy et al. (2017) tested the 91% mortality threshold posited by Paradis et al. (2008) and determined that it is a good expansion predictor. Cheah (2017) used 90-99% as their highest winter mortality category, further reinforcing the idea that the lowest mortality to sufficiently limit HWA spread is approximately 90%. Thus, it is generally understood that winter temperature can limit the spread of HWA populations.

ADMWT is one predictor of HWA mortality that has been used. Paradis et al. (2008) determined that ADMWT was the best predictor of HWA mortality. They found that an ADMWT of -5°C was required for 91% to 100% overwintering mortality. Furthermore, of the eight temperature criteria considered by Paradis et al. (2008), only one resulted in a relationship with a p-value over 0.05, but ADMWT was the only criterion that gave a relationship with a p-value under 0.01. Fitzpatrick et al. (2012) used this ADMWT equation developed by Paradis et al. (2008) to model HWA range dynamics.

The use of this temperature criterion is debated, however. Cheah (2017) was concerned that daily mean winter temperature would not capture significant cold snaps that could have a sizeable effect on HWA populations. Cheah (2017) used a different temperature criterion that Paradis et al. (2008) found to be significant: minimum daily winter temperature. Other studies have also used minimum winter temperatures in their equations (Trotter & Shields, 2009; McAvoy et al., 2017). Paradis et al. (2008) found that a minimum daily winter temperature of -35°C was required for 91% overwintering mortality. Similarly, Parker et al. (1999) found that no HWAs survived temperatures of -35 and -40°C. Conversely, Cheah (2017) determined that minimum daily winter temperatures between -21.2 and -24°C, depending on the region, resulted in 90% HWA mortality. Furthermore, McAvoy et al. (2017) found that acclimation to cold temperatures and accumulation of winter temperatures were both significant determinants of HWA mortality.

Winter temperature is evidently an important HWA control, and it is well understood that winter temperatures can keep populations from spreading. Predictive models are still being developed, however. There is no agreed-upon best indicator or model. It should also be mentioned that McClure (1996) hypothesized that HWA would develop cold-hardiness over time, allowing it to spread northward because of the adelgid’s cold tolerance in its native Japanese habitat.

Although winter temperatures are most often studied in relation to HWA mortality, summer temperature mortality has also been reported. Mech, Tobin, Teskey, Rhea & Gandhi (2018) found that 100% HWA mortality occurred with exposure to 35 and 40°C for 48 hours.

Such temperatures are not common in the range of HWA, but the study also found that more common temperatures (20 and 25°C) for 192 hours caused some mortality, albeit minimal (<15%). These finding suggests that changes in summer temperatures should also be considered when predicting how climate change will affect HWA mortality (Mech et al., 2018). They are especially important because increased temperatures are generally expected to decrease mortality of invasive insects like HWA. Summer HWA mortality is beyond the scope of this study, but it is an important topic for future research.

Other Factors Control HWA Distributions

Studies have also found non-temperature determinants of HWA performance and distribution. McClure (1991) found that branch HWA density was significantly negatively correlated with the insect's performance. Also, Trotter & Shields (2009) completed a study at the landscape level and found a significant negative relationship between HWA density and survival. Trotter & Shields (2009) pointed out that the predictive power of the density-mortality relationship was weak, however. Moreover, including density in the temperature models did not increase the R^2 values significantly. Trotter & Shields (2009) also considered latitude and elevation as explanatory variables of HWA mortality in their study. Elevation alone did not account for much variation; however, latitude explained about half of the variation for each year (44% in 2003 and 54% in 2004). Latitude itself is not a restraining factor but may act as a useful proxy for biologically important factors, including temperature. As explained above, Trotter & Shields (2009) found that temperature only explained <10% of the variation in HWA mortality observed in 2003. The finding that latitude explained more variation in mortality than temperature alone in 2003 suggests that some other latitude-related factor was affecting HWA survival (Trotter & Shields, 2009). In a study by Fitzpatrick et al. (2012) that modelled HWA range dynamics, winter temperature and hemlock abundance were used to determine HWA population growth. Hemlock abundance determined whether HWA establishment would be possible in each region, and it also set the maximum population thresholds. The study suggests that hemlock abundance is an important factor that controls the distribution of HWA populations (Fitzpartick et al., 2012). Accurate hemlock mapping has also been an area of study in relation to HWA impacts. For example, Clark, Fei, Liang & Rieske (2012) compared classification techniques to determine how to best continuously map hemlock to determine HWA spread and management possibilities. Thus, non-temperature factors are expected to impact HWA distributions.

Summary

Although summer temperatures and other factors may influence HWA distributions and mortality, winter temperatures appear generally to be the best predictor. The use of climatic envelope models is debated, but HWA is heavily dependent on winter temperature and, therefore, is a good contender for a climatic envelope approach (Pearson & Dawson, 2003). Management efforts exists, but they are generally done on a tree-by-tree basis (Vose et al., 2013). Thus, it is important to understand how HWA populations are likely to respond to temperatures in Nova Scotia over time to target particularly vulnerable areas. Finally, if HWA populations cannot be kept under control, species diversity and ecosystem processes in hemlock-dominant forests are expected to be altered in a variety of ways.

Chapter 3: Methods

This study seeks insight into how Nova Scotia's changing climate is expected to alter winter-temperature-related HWA mortality and, by extension, proliferation. Mortality was calculated from historical and projected winter temperature raster data for three periods: the past (1981-2010), the near future (2041-2070), and the distant future (2071-2100). Locations of concern were displayed by overlaying stands with hemlock present onto the HWA mortality maps.

Temperature

Past and projected future temperature surfaces were created by James Steenberg and accessed through a data-sharing agreement with the (NSDLF, 2018). These data were "downscaled from the CanESM2 global climate model and spatially interpolated using thin plate smoothing splines as implemented in the ANUSPLIN climate modelling software" (NSDLF, 2018). For this dataset, Environment and Climate Change Canada data were used to interpolate the historical data. Three representative concentration pathway (RCP) scenarios created for the Intergovernmental Panel on Climate Change's Fifth Assessment Report were included: RCP 2.6, RCP 4.5, and RCP 8.5. The RCP 2.6 scenario assumes that radiative forcing will reach a peak of approximately 3 W/m^2 before 2100 and then decline. The RCP 4.5 scenario assumes that radiative forcing will stabilize around 4.5 W/m^2 by 2100. The RCP 8.5 scenario assumes that radiative forcing will rise to 8.5 W/m^2 by 2100 (NSDLF, 2018). In these data, monthly means were calculated by averaging the monthly maximum and minimum values (J. Steenberg, personal communication, March 1, 2019). The means were then averaged for December through March to create winter means.

As ADMWTs for December through March were used by Paradis et al. (2008) to create the predictive mortality equation that was used here, ADMWT would have been a more suitable predictor. ADMWTs for future warming scenarios were not available for use in this study, so AMMWTs were used instead. To depict the differences between the two calculation methods in a coarse way, ADMWTs for the period 1981-2010 were calculated using average daily temperature data from the Government of Canada (2018). In these data, daily mean temperatures are calculated as [daily maximum + daily minimum] / 2. It is unclear whether Paradis et al. (2008) used daily means calculated from daily maximum and minimum or hourly temperatures. A weather station was included if there were ten or more years of data available with more than one mean temperature reading for each month considered. Ultimately, data for 65 weather stations across Nova Scotia were collected. The weather station data were then interpolated using a regularized spline with 0.1 weight and 20 points. ANUSPLIN climate modelling software was not available for use in this study. A regularized spline was used because ANUSPLIN implements thin-plate smoothing splines.

Mortality

Paradis et al. (2008) found that ADMWT was the best predictor of HWA mortality in their study of Massachusetts and Connecticut. The model fitting this predictor to HWA mortality had a p-value of 0.008 and an R^2 of 0.43. The ADMWT equation developed by Paradis et al. (2008) has also been used in other regional contexts. For example, Fitzpatrick et al. (2012) used this equation to model HWA range dynamics in the eastern United States. The Paradis et al. (2008) equation used to determine HWA mortality in this study is

$$y = -0.078x + 0.507,$$

$$\text{if } y < 0, y \text{ is set} = 0.$$

where y is the proportion of HWA mortality and x is the ADMWT for a given year. Again, AMMWT is used here instead of ADMWT due to data availability. The AMMWTs for each station and year were run through this equation to determine the theoretical proportion of HWA mortality. Negative mortality is not possible, so if a negative number were to be calculated for HWA mortality, it would be changed to 0.

HWA mortality was calculated using Raster Calculator in ArcGIS. Each temperature layer was run through the equation above. The proportions were then labeled as percentages and categorized using 10%, or 0.1 proportion, intervals (e.g. 0-10%). Although only mortality greater than about 90% is expected to keep HWA populations from proliferating, higher mortality is expected to cause some reduction in the species' overall survival. A common defined interval was chosen to clearly depict change between past and projected climate normals. No one interval could align with every histogram, so an interval was chosen based on the projection that fell in the middle of the data considered (RCP 4.5 for the period 2041-2070). The mortality percentages were also turned into integers using the "int" tool in ArcGIS, and the cell counts were graphed. The mean mortality for the province was calculated from these integers. Finally, the proportion of Nova Scotian land that fell under each category was calculated.

Hemlock Distribution

A current hemlock distribution layer was then calculated from NSDNR (2017) forest inventory data. The forest inventory data define the top four species in each Nova Scotia stand and the relative abundance of each from 10% to 100%, 1-10 in the dataset (P. Duinker, personal communication, March 1, 2019). Stands with hemlock present were overlaid onto the HWA mortality layers to depict vulnerable areas. Relative abundance was not used in this study, but it could be used to create more quantitative risk maps in the future. The future hemlock distribution is not known, so the current hemlock distribution was used for all maps.

Chapter 4: Results

Differences in Daily and Monthly Means

As described above, monthly means were used to determine average winter temperatures in this study, but the HWA mortality equation used here calculated average winter temperatures with daily means. For ~90% of the province, the difference between these predictors is estimated to be less than ~1.1°C, and the difference is between -0.31 and 0.39°C for ~43% of the province (Figure 1). The ADMWTs were 1.75 to 3.50°C higher in ~3% of the province (mostly in southern Cape Breton), whereas the AMMWTs were 1.82 to 2.51°C higher in only ~0.12% of the province (Figure 1). The difference between the HWA mortality associated with these predictors was less than ~8.5% for ~89% of the province, and the difference was between -2.88 and 2.69 for ~40% of the province (Figure 1). AMMWTs were 30.79 to 14.05°C higher in ~3% of the province and ADMWTs were higher in 13.87 to 18.23°C higher in ~0.12% of the province (Figure 1).

Past and Future HWA Mortality

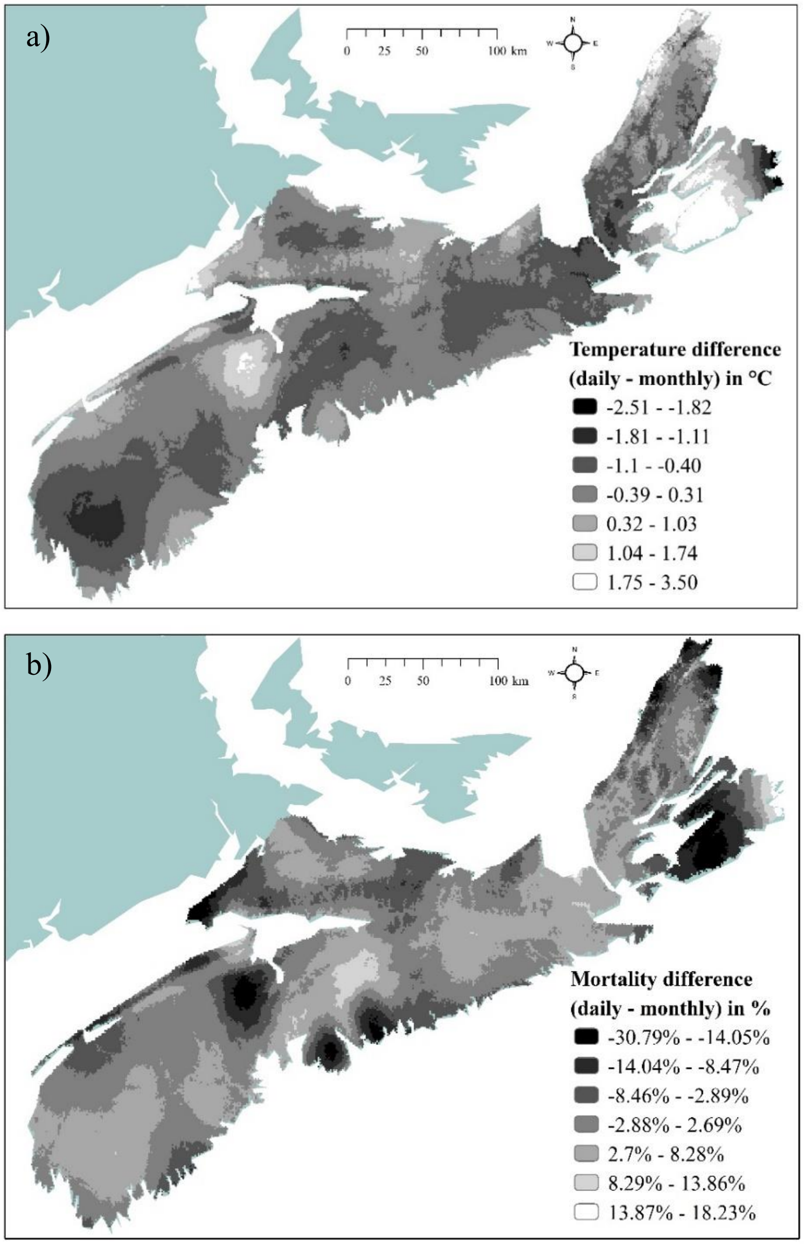
Based on past average winter temperatures in Nova Scotia, HWA populations would have experienced greater than 90% mortality in 4.76% of the province (Figure 2). It is expected that 34.47% of the province would have experienced > 80% and ≤ 90% HWA mortality, and 42.68% of the province would have been in the >70 to 80% HWA mortality range (Figure 2). The mean HWA mortality across the province for this period is 78% (Figure 2).

The 2041 to 2070 (near future) and 2071 to 2100 (distant future) projections are similar for RCP 2.6. In both cases, projected HWA mortality is in the >50 to 60% HWA mortality range for ~47% of the province and the highest HWA mortality class, >70 to 80%, is expected to occur in ~2% of the province (Figure 3; Figure 4). The proportion of the province that falls in the >60 to 70% HWA mortality range is also similar for these projections, at 25.55% for the near future scenario and 26.63% for the distant future scenario (Figure 3; Figure 4). These two projections also have the same mean HWA mortality, 56% (Figure 3; Figure 4).

For both the near future and distant future RCP 4.5 projections, the highest HWA mortality class is expected to be >60 to 70% (Figure 5; Figure 6). In the near future scenario, 11.94% of the province is expected to fall into this class, while in the distant future scenario, 4.47% is expected to fall into this class (Figure 5; Figure 6). The >50 to 60% and >40 to 50% HWA mortality ranges are expected to occur in most of the province in both these scenarios (Figure 5; Figure 6). The mean HWA mortality for these two scenarios is similar at 48% for the near future scenario and 49% for the distant future scenario (Figure 5; Figure 6).

The difference between the near future and distant future RCP 8.5 scenarios is the most pronounced of the three RCPs considered. The maximum mortality class for the near future scenario is >60 to 70%, while the maximum class for the distant future scenario is >40 to 50% mortality (Figure 7; Figure 8). Also, the minimum class for the near future scenario is >30 to 40% HWA mortality, and the minimum class for the distant future scenario is >10 to 20%. For the near future RCP 8.5 scenario, most of Nova Scotia is expected to experience >40 to 60% HWA mortality, whereas for the distant future RCP 8.5 scenario, most of Nova Scotia is expected to experience >20 to 40% HWA mortality (Figure 7; Figure 8). The mean HWA mortality is 49% for the near future RCP 8.5 scenario and 32% for the distant future scenario.

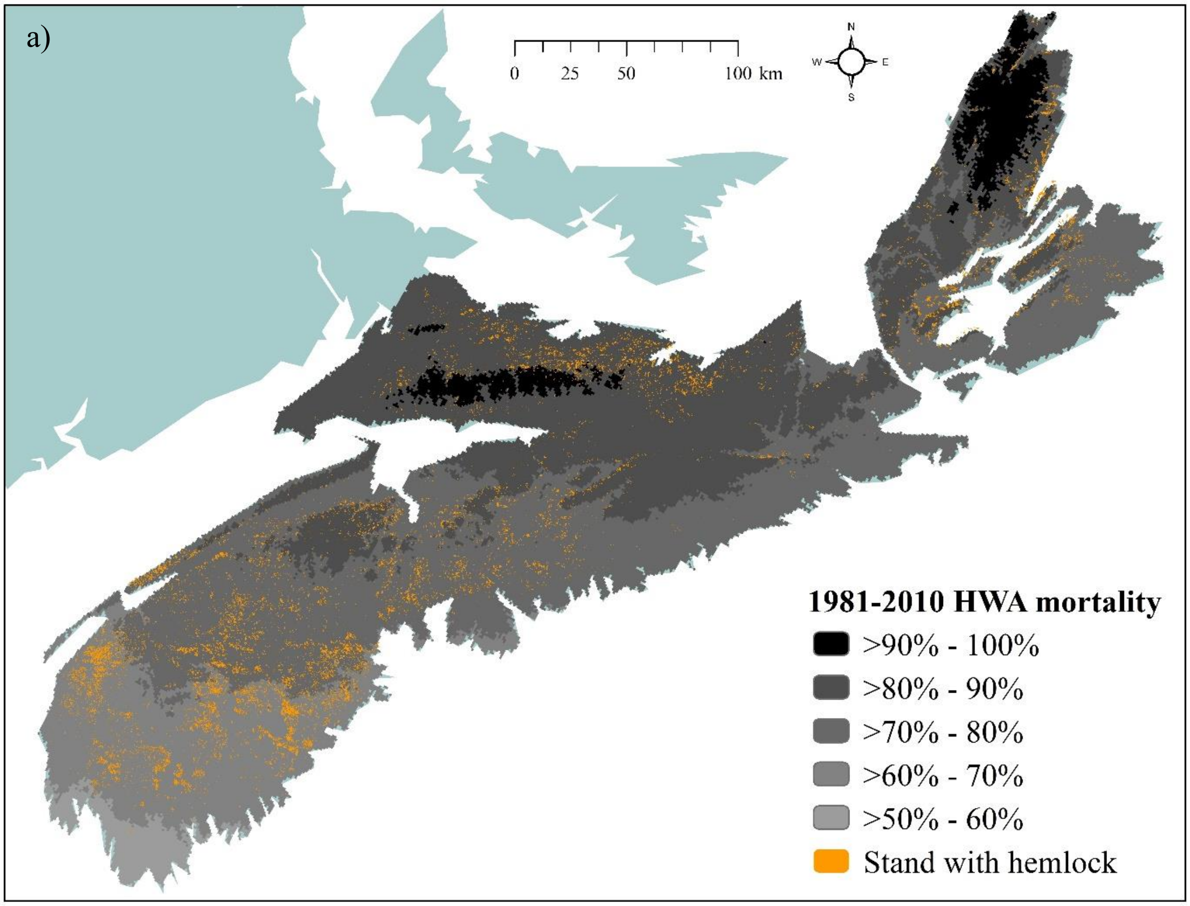
High and low temperatures are similarly distributed for all scenarios, with highest mortality occurring in northern, high elevation regions of the province and lowest mortality occurring in south-western regions (Figures 2-9). For all scenarios, there are few stands containing hemlock in areas that are expected to have the highest HWA mortality (Figures 2-8).



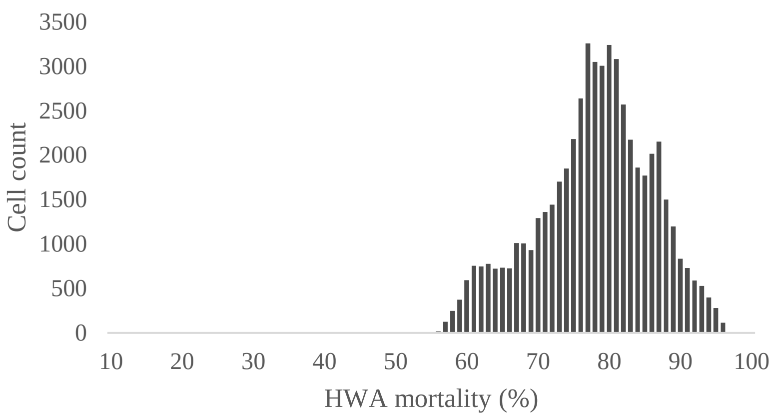
Change in Temperature (°C)	Area (%)
-2.51 - -1.82	0.12%
-1.81 - -1.11	2.44%
-1.1 - -0.4	30.27%
-0.39 - 0.31	43.22%
0.32 - 1.03	16.18%
1.04 - 1.74	4.79%
1.75 - 3.50	2.98%

Change in Mortality (%)	Area (%)
-30.79 - -14.05	2.91%
-14.04 - -8.47	6.10%
-8.46 - -2.89	16.01%
-2.88 - 2.69	39.93%
2.7 - 8.28	33.07%
8.29 - 13.86	1.87%
13.87 - 18.23	0.12%

Figure 1: Difference between past (1981-2010) (a) temperatures and (b) mortality calculated from Government of Canada (2018) daily means and interpolated using a regularized spline surface and temperatures calculated from NSDLF (2018) monthly means and interpolated using ANUSPLIN climate modelling software. The class break interval is one standard deviation, and the tables show the proportion of area for each class.



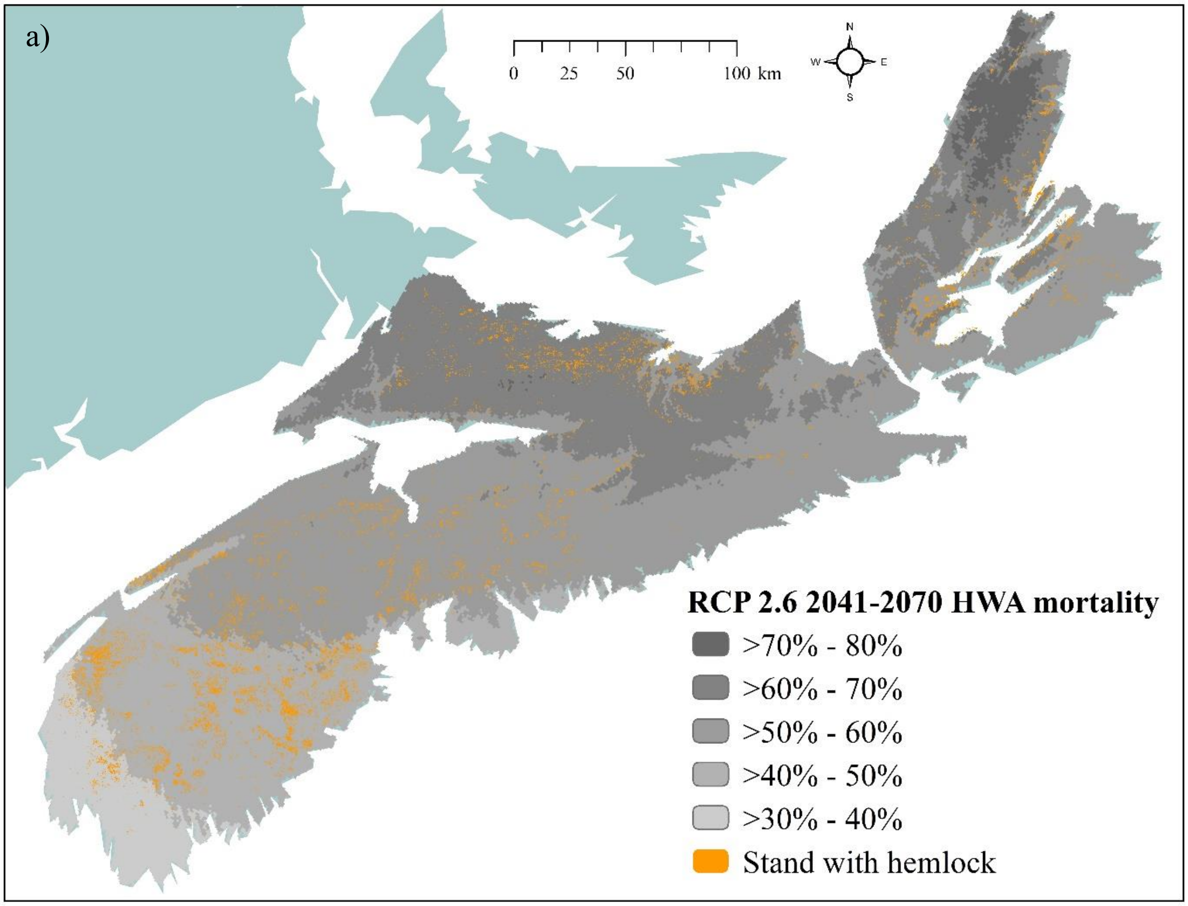
b)

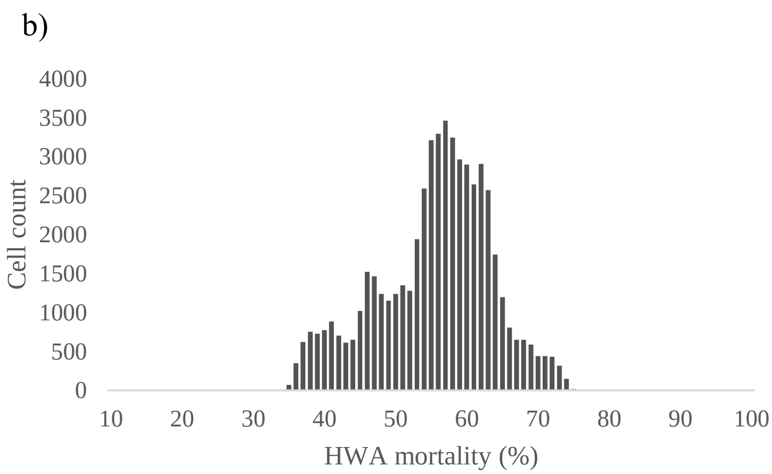


c)

Mortality (%)	Area (%)
>90 - 100	4.76%
>80 - 90	34.47%
>70 - 80	42.68%
>60 - 70	15.65%
>50 - 60	2.44%

Figure 2: a) Past (1981-2010) classified average HWA mortality and stands that contain hemlock. b) Past proportion of HWA mortality (%) by number of raster cells. Mean HWA mortality = 78%. c) The proportion of Nova Scotia associated with each HWA mortality class. Data are from NSDLF (2019) and NSDNR (2017).

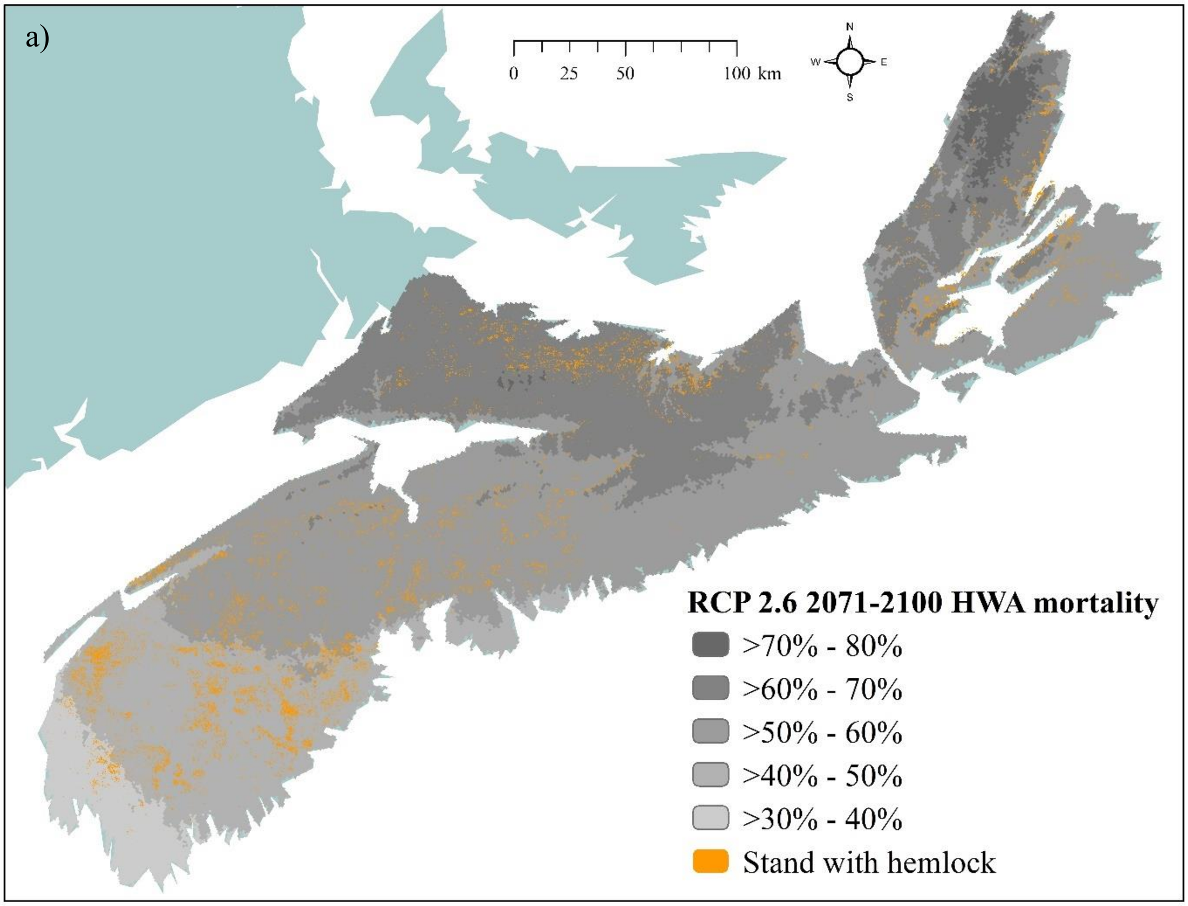




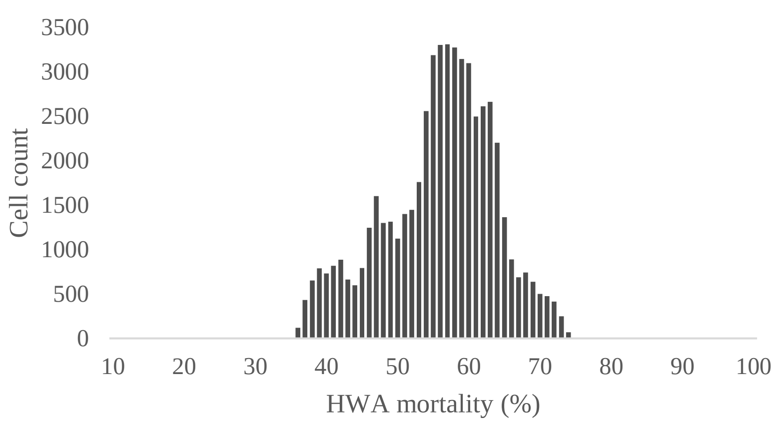
c)

Mortality (%)	Area (%)
>70 - 80	2.44%
>60 - 70	25.55%
>50 - 60	47.21%
>40 - 50	18.87%
>30 - 40	5.93%

Figure 3: a) Near future (2041-2070) RCP 2.6 average HWA mortality and stands that contain hemlock. b) Near future (2041-2070) RCP 2.6 proportion of HWA mortality (%) by number of raster cells. Mean HWA mortality = 56%. c) The proportion of Nova Scotia associated with each HWA mortality class. Data are from NSDLF (2019) and NSDNR (2017).



b)

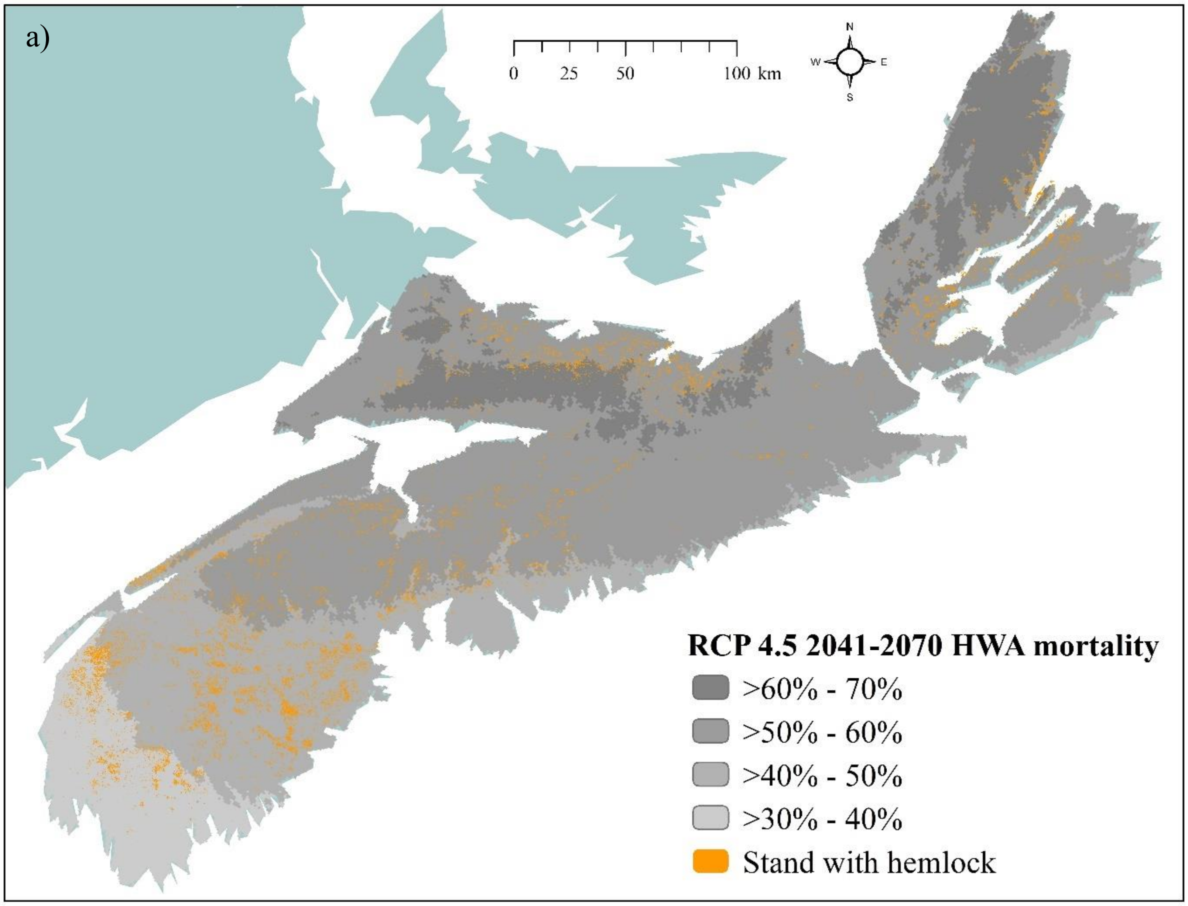


c)

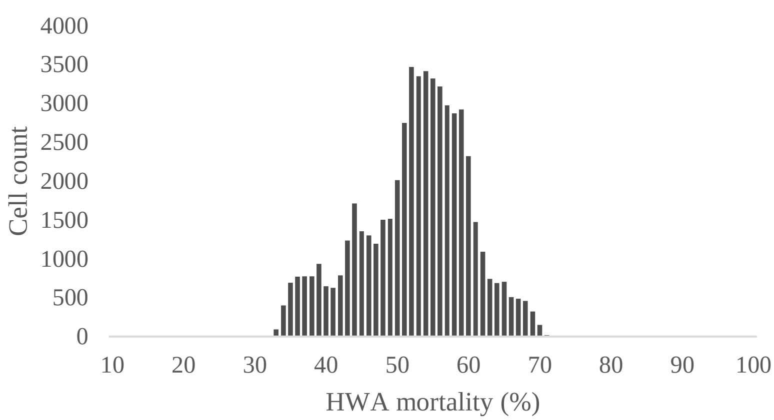
Mortality (%)	Area (%)
>70 - 80	2.18%
>60 - 70	26.63%
>50 - 60	47.66%
>40 - 50	18.62%
>30 - 40	4.91%

Figure 6: a) Distant future (2071-2100) RCP 2.6 average HWA mortality and stands that contain hemlock. b) Distant future (2071-2100) RCP 2.6 proportion of HWA mortality (%) by number of raster cells. Mean HWA mortality = 56%. c) The proportion of Nova Scotia associated with each HWA mortality class. Data are from NSDLF (2019) and NSDNR (2017).

a)



b)

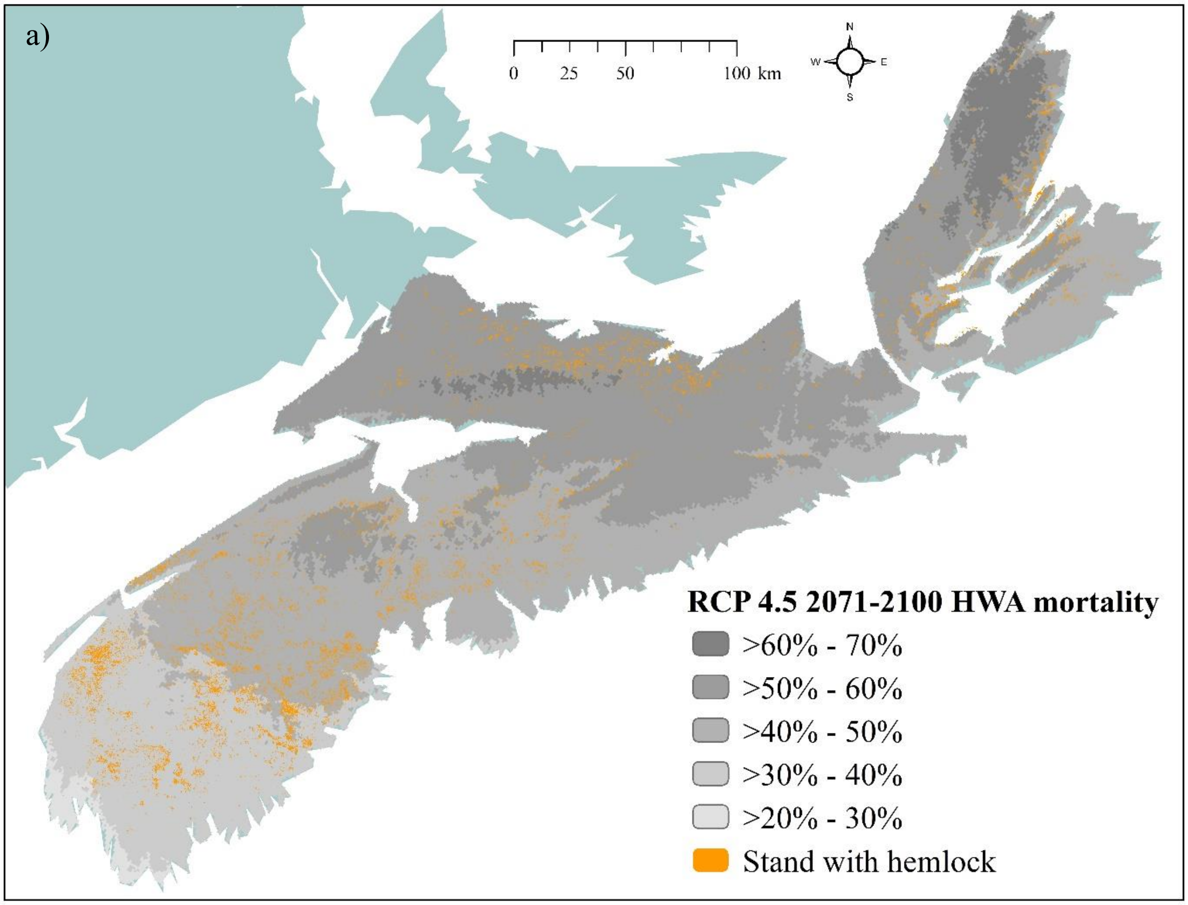


c)

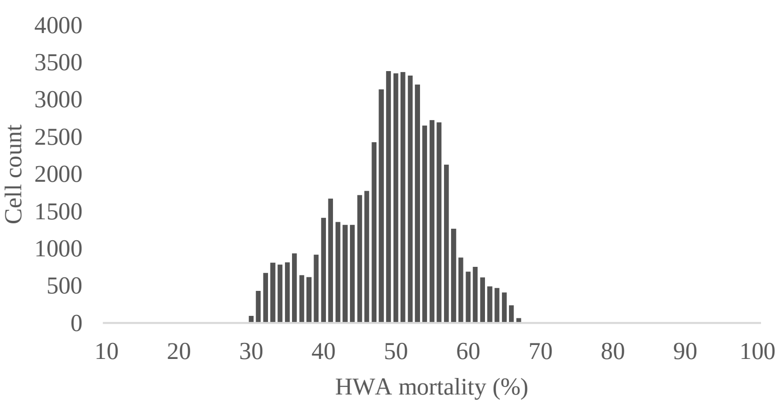
Mortality (%)	Area (%)
>60 - 70	11.94%
>50 - 60	55.08%
>40 - 50	23.83%
>30 - 40	9.16%

Figure 4: a) Near future (2041-2070) RCP 4.5 average HWA mortality and stands that contain hemlock. b) Near future (2041-2070) RCP 4.5 proportion of HWA mortality (%) by number of raster cells. Mean HWA mortality = 53%. c) The proportion of Nova Scotia associated with each HWA mortality class. Data are from NSDLF (2019) and NSDNR (2017).

a)



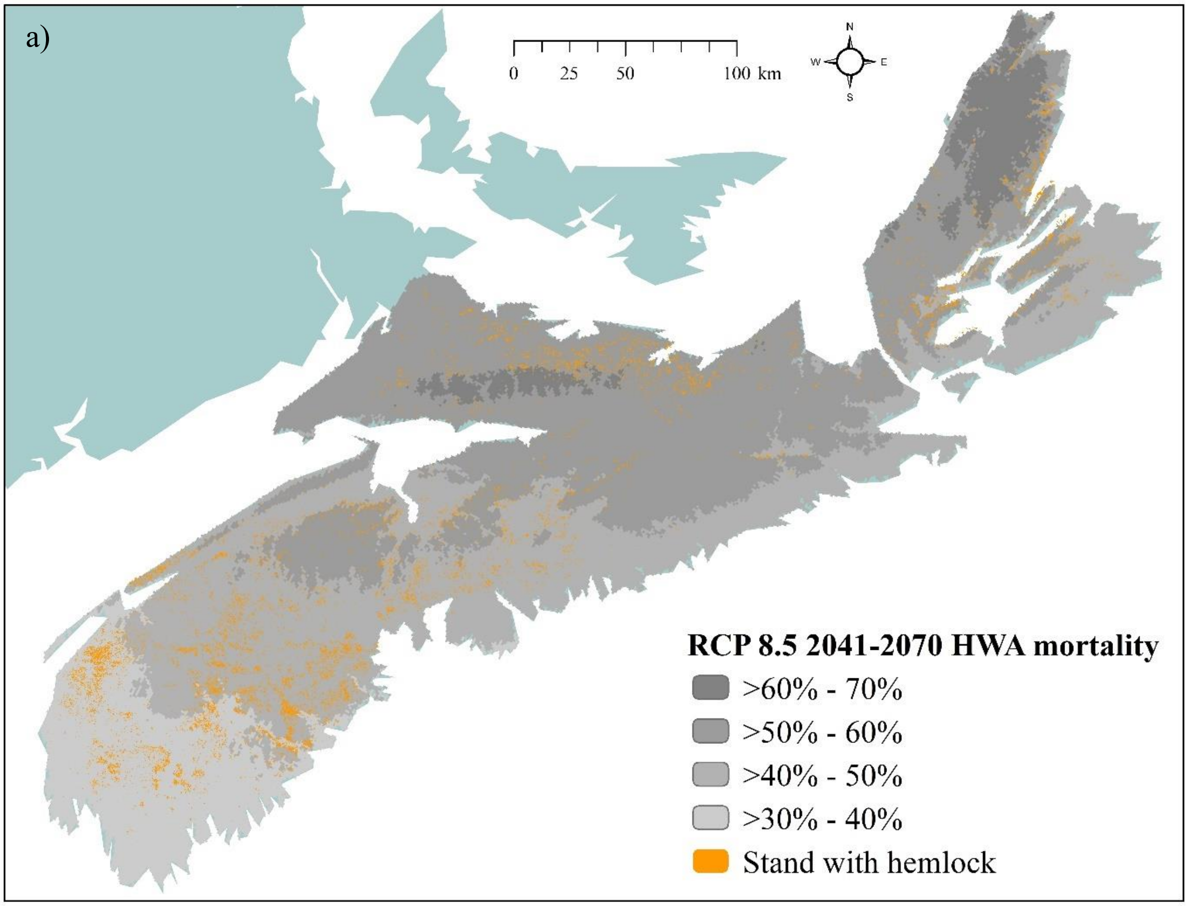
b)



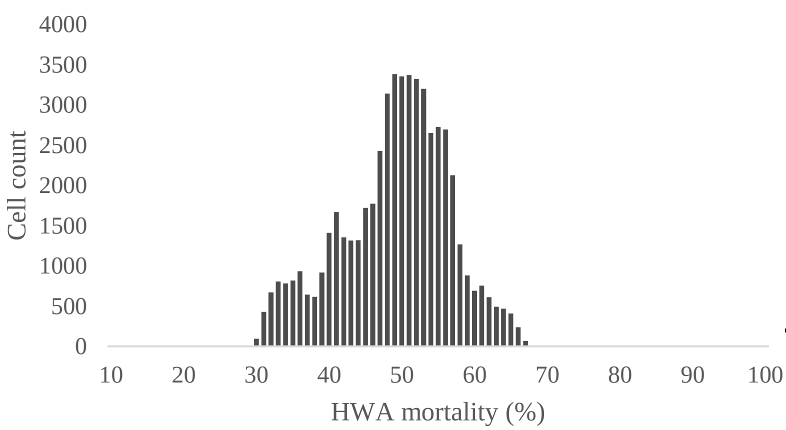
c)

Mortality (%)	Area (%)
>60 - 70	4.47%
>50 - 60	37.81%
>40 - 50	39.83%
>30 - 40	16.61%
>20 - 30	1.27%

Figure 7: a) Distant future (2071-2100) RCP 4.5 average HWA mortality and stands that contain hemlock. b) Distant future (2071-2100) RCP 4.5 proportion of HWA mortality (%) by number of raster cells. Mean HWA mortality = 48%.c) The proportion of Nova Scotia associated with each HWA mortality class. Data are from NSDLF (2019) and NSDNR (2017).



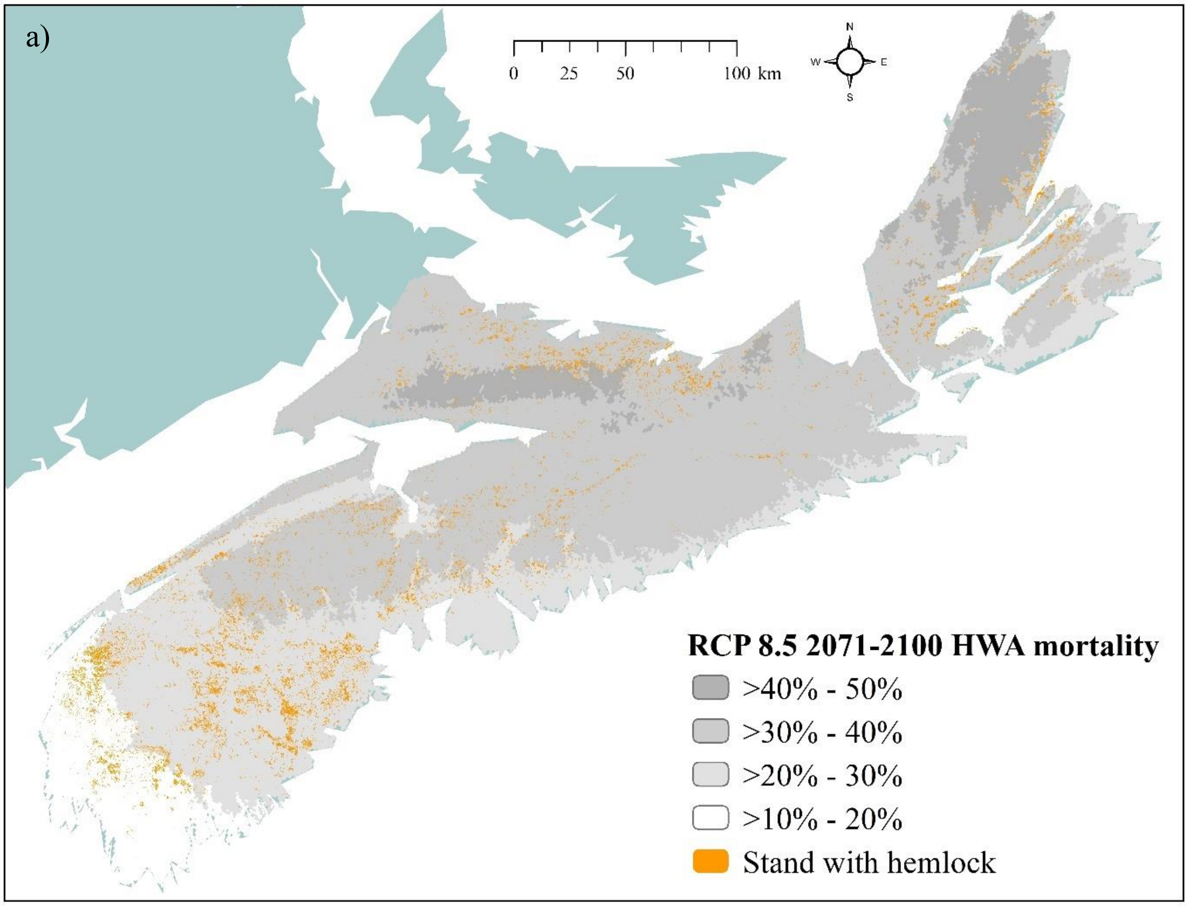
b)



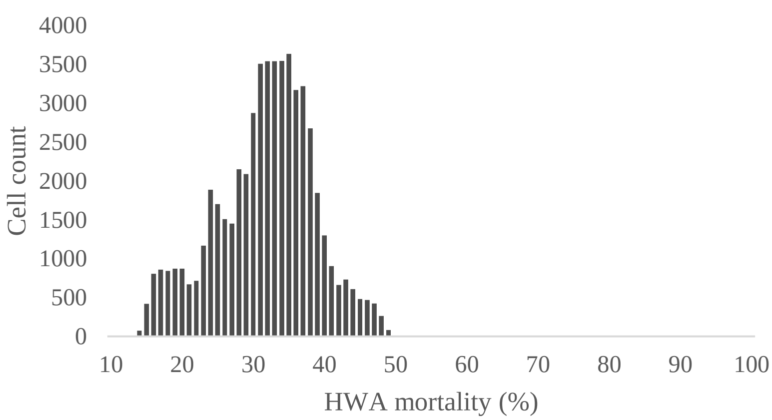
c)

Mortality (%)	Area (%)
>60 - 70	5.48%
>50 - 60	41.27%
>40 - 50	38.62%
>30 - 40	14.62%

Figure 5: a) Near future (2041-2070) RCP 8.5 average HWA mortality and stands that contain hemlock. b) Near future (2041-2070) RCP 8.5 proportion of HWA mortality (%) by number of raster cells. Mean HWA mortality = 49%. c) The proportion of Nova Scotia associated with each HWA mortality class. Data are from NSDLF (2019) and NSDNR (2017).



b)



c)

Mortality (%)	Area (%)
>40 - 50	8.33%
>30 - 40	53.95%
>20 - 30	29.19%
>10 - 20	8.53%

Figure 8: a) Distant future (2071-2100) RCP 8.5 average HWA mortality and stands that contain hemlock. b) Distant future (2071-2100) RCP 8.5 proportion of HWA mortality (%) by number of raster cells. Mean HWA mortality = 32%. c) The proportion of Nova Scotia associated with each HWA mortality class. Data are from NSDLF (2019) and NSDNR (2017).

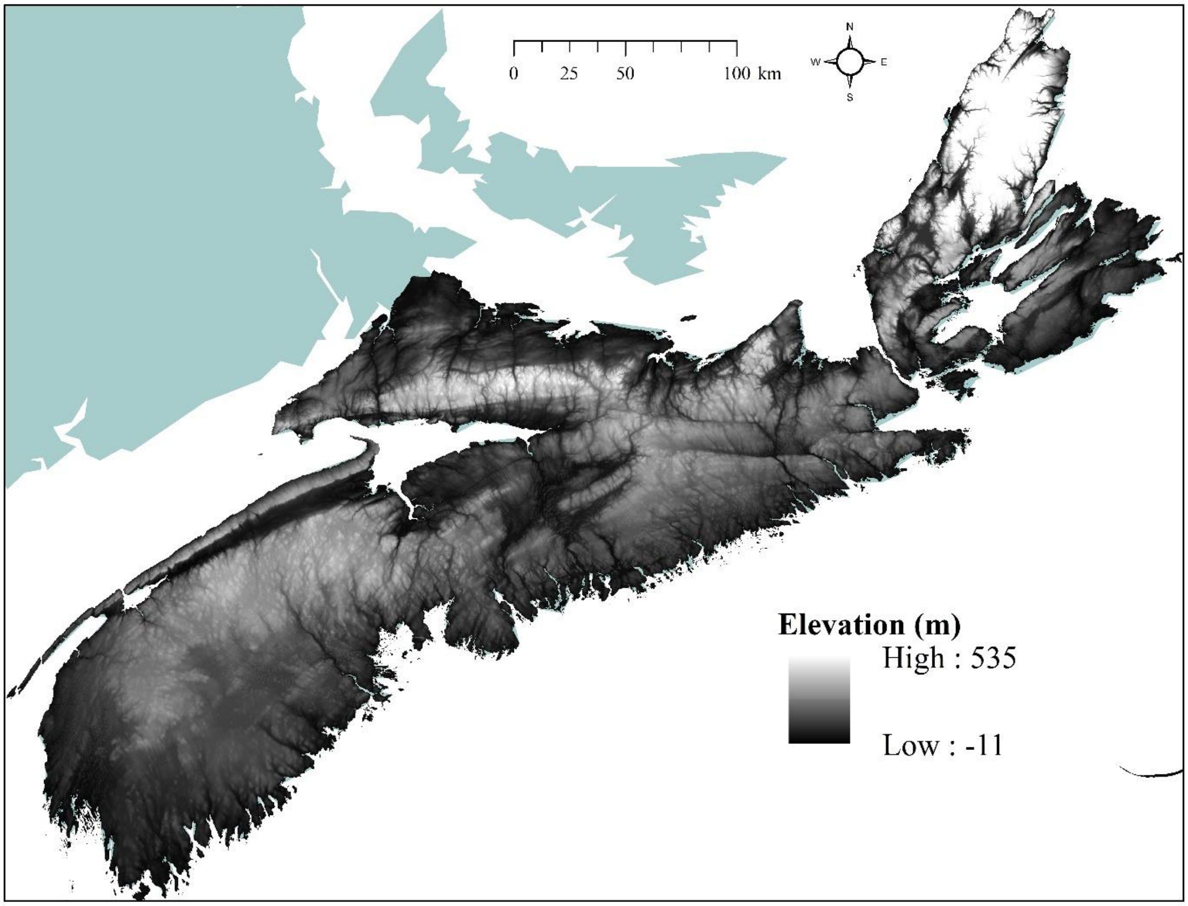


Figure 9: Digital elevation model of Nova Scotia (NSDNR, 2013).

Chapter 5: Discussion

Other Insects and Climate Change

Many insects are expected to be affected by a changing climate (Prather et al., 2013). For example, the range of the mountain pine beetle (MPB) has expanded largely due to climate change (Stahl, Moore & McKendry, 2006). MPBs kill pine trees to reproduce successfully (Logan & Powell, 2001). Synchrony is important for MPB reproduction because many individual MPBs must attack a pine tree at once to overcome the tree's defensive chemistry (Logan & Powell, 2001). Thus, many beetle individuals are required for successful reproduction (Logan & Powell, 2001). Considering timing and synchrony in relation to climate change, Logan & Powell (2001) expected an increase in the range of the MPB further north. An outbreak of MPB in British Columbia was also linked to fewer extreme cold spells, which were expected to cause increased mortality (Stahl et al., 2006).

Higher winter temperatures will not necessarily lead to reduced mortality and increased proliferation, however. The forest tent caterpillar (FTC), for instance, may experience increased mortality due to climate change (Dukes et al., 2009). A sequence of warm days decreases the cold tolerance of the FTC, causing increased susceptibility to sudden transitions between extreme warm and cold temperatures in winter months (Dukes et al., 2009). Thus, an increase in overall winter temperatures with climate change may cause increased mortality if it is paired with short cold snaps (Dukes et al., 2009). Reduced freezing temperatures during the transition between winter and spring may cause decreased mortality, however, so it is unclear how FTC will respond to climate change. Many insect pests, pathogens, and invasive plants are expected to be influenced by climate change, although complex ecosystem dynamics make the true impact of climate change on many of these species difficult to predict (Dukes et al., 2009).

Indirect effects of climate change, such as changing nutrient concentrations in plants and changing enemy and symbiont dynamics, are also expected to affect the proliferation of insects (Dukes et al., 2009). A particularly well-studied example is interactions between plants and invertebrates (Dukes et al., 2009). Invertebrate population size, life history traits, and behaviour will likely be affected with plant quality variations expected to occur with a changing climate (Dukes et al., 2009). Changing enemy and mutualist dynamics are also expected to affect insect proliferation (Dukes et al., 2009). Similarly, non-native invasive species will continue to be introduced to new locations, changing ecosystem dynamics and putting new stressors and subsidies on existing species.

Discussion of Findings

This study suggests that, had HWA been present in Nova Scotia from 1981 to 2010, winter temperatures would have limited the spread (>90% mortality), on average, in some regions, especially those with comparatively high elevations. These are regions that do not have many stands containing hemlock trees, however, so HWA would not have been a considerable issue in these areas. The reason the tree inventory contains few stands containing hemlock in high elevation regions of Nova Scotia is unknown, but it may be due to high winds (P. Duinker, personal communication, March 15, 2019).

This study also posits that climate change will alter HWA's ability to proliferate throughout the province, with lower mortality levels associated with all future temperature predictions, and HWA mortality decreasing over time. It is not surprising that similar mortality was found for the periods 2041-2070 (near future) and 2071-2100 (distant future) under RCP 2.6, as radiative forcing under this projection is expected to plateau well before 2100. In contrast, steeper radiative forcing curves for RCP 4.5 and 8.5 are responsible for the finding of more pronounced changes in mortality between the near future and distant future projections, with the two RCP 4.5 scenarios being moderately different and the RCP 8.5 scenarios being the most different.

The differences between mortality associated with ADMWTs and AMMWTs is considerable in much of Nova Scotia. Although these differences cannot solely be attributed to the temperature predictors themselves, as different interpolation methods were used to create the two datasets, the notable differences bring an important point to light: small changes in mean temperature calculations cause considerable changes to mortality predictions. This is an issue for the past winter temperature predictor, and with the uncertainty of climate change futures, the validity of these predictions is also called into question.

A study by McAvoy et al. (2017) that considered HWA mortality in Nova Scotia included predictors related to extreme temperatures and changes in cold-hardiness. McAvoy et al. (2017) related HWA mortality observed in the eastern United States to the lowest minimum temperature before the mortality was assessed, the number of days before the extreme minimum date with mean temperatures <−1 °C, and the mean temperature for the three days leading up to the extreme minimum. Respectively, these predictors accounted for extreme temperatures, cumulative effects, and acclimation (McAvoy et al., 2017). These predictors were all found to be significant.

Compared to the study at hand, McAvoy et al. (2017) found higher HWA mortality in their past scenario (1981-2010), with most of the province being associated with >91% mortality. The future scenarios considered by McAvoy et al (2017), RCP 4.5 for the periods 2041-2070 and 2071-2100, modelled similar distributions of high and low mortality as the RCP 4.5 future scenarios modelled here, but McAvoy et al. (2017) found notably higher mortality overall.

McAvoy et al. (2017) pointed out that projected HWA mortality values for Nova Scotia may decrease more than their model suggested due to “the warming effects of offshore currents” (pp. 507). This higher HWA mortality in past and future scenarios found by McAvoy et al. (2017) is likely mainly due to the application of a different model, however. It should also be noted that, because their mortality predictors depended on daily temperatures, McAvoy et al. (2017) disaggregated predicted future monthly temperature data to get daily temperatures.

Issues with Averages

There are issues with using averages when studying temperature-driven processes. Paradis et al. (2008) found ADMWT to be the best predictor of HWA mortality, but inter- and intra-year temperature variations are indistinguishable with the averages presented here, which causes interpretation issues. Extreme high and low values within the winter season are not evident when temperatures are averaged out to create a winter mean. A winter with extreme values may have the same mean as a winter that does not reach extreme highs or lows. This is true whether daily means or monthly means are used. As HWA has been shown to respond to extreme temperatures in a laboratory setting (Gouli et al., 2001), and their cold-hardiness has been shown to change as the winter progresses (Skinner, Parker, Gouli & Ashikaga, 2003; McAvoy et al., 2017), this is an inherent issue. The significance of the cumulative effects, and acclimation predictors in the HWA mortality equation used by McAvoy et al. (2017), is also evidence that intra-winter temperature variation affects HWA populations. Similarly, the distribution of years that are particularly cold or warm is not clear. One very cold winter may significantly limit HWA proliferation, and this may cause reduced proliferation in several subsequent years. These year-to-year relationships are not captured in these mean values.

Future Studies

Both the study at hand and the study by McAvoy et al. (2017) use HWA mortality equations that were developed based on mortality in the eastern United States. It is important for future studies to assess mortality in Nova Scotia, because there is evidence to suggest that HWA mortality depends on regionally dependent climatic factors. Skinner et al. (2003) found that HWA in central and southern sites lost their cold-hardiness earlier in the winter season compared to HWA in northern sites. This finding suggests that northern HWA may be hardier than HWA in more southern regions. Furthermore, McClure & Cheah (2002) have suggested that snow on hemlock branches may insulate HWA from cold air, increasing survival, and Brantley et al. (2017) suggested that higher levels of sunlight reduce HWA density. McClure & Cheah (2002) also noted that the impacts of wind and rain on HWA were not well studied and suggested that this warranted investigation. To date, this relationship does not appear to have been studied in any meaningful way. Because of the potential importance of these other climatic factors, geographically specific models that account for more variables are likely important.

Nova Scotia's unique geography affects its climate, further reinforcing the need for models to be developed for the region. For example, Nova Scotia is surrounded by water. Cool winds coming off the sea delay the arrival of spring and extend the duration of fall in the province (Davis & Browne, 1998). Furthermore, the climates of various regions of Nova Scotia are influenced by their geographic features. Cold waters in the bay of Fundy keep this area cool, while the North Mountain keeps the Annapolis Valley warm by interrupting the flow of cold air (Davis & Browne, 1998). There are also notable micro-climates throughout the province (Davis & Browne, 1998), and coastal areas are expected to experience less warming than the interior of the province (Natural Resources Canada, 2015). These region-specific climatic factors may impact HWA in the province, but they are not accounted for in models created for other regions.

Furthermore, hemlock abundance in Nova Scotia will likely change with a changing climate. Steenberg, Duinker & Bush (2011) studied the interactions between forest management and climate change in central Nova Scotia. They modeled futures considering three adaptation treatments, including permutations of multiple treatments. The harvesting treatments considered by Steenberg et al. (2011) were based on the size of canopy-opening cuts, the ages of trees removed, and the composition of the species removed. For most of the scenarios considered, hemlock was expected to have more presence in the landscape in 2300 compared to 2000. The only scenarios that predicted less presence were the control, age, and age-composition scenarios. These scenarios predicted presence loss of 2 or 4%. The other scenarios predicted increases of 18 to 27%. Perhaps changes in hemlock presence and distribution should be considered in future climate-change-related HWA mortality modeling and risk-analysis studies.

Chapter 6: Conclusions

This study suggests that the degree to which climate change might lift HWA-population-limiting winter temperatures depends on the location of a specific site of interest (meaning location in all three dimensions of space) as well as the specific climate-change scenario chosen for analysis. In any plausible scenario of future climate change, HWA will increasingly proliferate across Nova Scotia. The finding that even near-future winter temperatures will relax constraints on HWA proliferation suggests that management interventions for ecologically important hemlock trees, such as those in old-growth Acadian forests, should be designed and implemented in a timely manner. Management methods like imidacloprid basal drenching and biological controls may help keep HWA populations from destroying these trees. In other, less ecologically important areas, it is likely worthwhile for woodlot owners and municipal, provincial, and federal foresters to begin planning for the demise of eastern hemlock in the province, especially by refraining from planting the species. As chemical controls are expensive and may have negative effects (e.g. chemical leaching into waterways; Vose et al., 2013), this management method should be reserved for stands that are considered invaluable.

It is necessary to reinforce that this is a preliminary study based on readily available data. The averages used here do not consider intra- or inter-winter variations that will likely affect HWA proliferation. Cold-hardiness of HWA is expected to change as winter weather continues to change (Skinner et al., 2003; McAvoy et al., 2017), which means that intra-winter variation is likely important. Furthermore, consideration of inter-year variation is advisable, because a significant winter HWA die-off in one year will likely affect proliferation in following years. The HWA mortality values calculated using winter temperature averages are also vulnerable to relatively small changes (Figure 1).

In the future, it is suggested that region-specific studies considering many variables be conducted to determine how HWA is expected to be affected by climate change in Nova Scotia. As HWA has only recently been found in Nova Scotia (CFIA, 2017), studies have not yet assessed actual winter HWA mortality in the province. This is an important next step, as it has been suggested that HWA mortality is somewhat controlled by region-specific factors (Skinner et al., 2003). Furthermore, factors other than winter temperatures are likely important to consider. For example, branch HWA density (McClure, 1991), hemlock abundance (Fitzpatrick et al., 2012), and summer temperatures (Mech et al., 2018) have all been linked to the distribution of HWA populations. All of these will likely be directly altered by a changing climate.

This study gives a broad idea of how HWA mortality may be affected by a changing climate in Nova Scotia, but the many direct and indirect effects of climate change create a complicated web of interactions that this study only begins to unravel. Many more studies are required to unpack the complicated relationships between not only winter-temperature-HWA-mortality interactions, but also other direct and indirect effects of climate change that may be expected to affect the proliferation of HWA in Nova Scotia.

References

Araújo, M. B. & Peterson, A. T. (2012). Uses and misuses of bioclimatic envelope modeling. *Ecology, 97*(7), 1527-1539. doi:10.1890/11-1930.1.

Benton, E. P., Grant, J. F., Webster, R. J., Cowles, R. S., Lagalante, A. F., Saxton, A. M., … Coots, C. I. (2016). Hemlock woolly adelgid (*Hemiptera: Adelgidae*) abundance and hemlock canopy health numerous years after imidacloprid basal drench treatments: Implications for management programs. *Journal of Economic Entomology, 109*(5), 2125-2136. doi:10.1093/jee/tow160.

Brantley, S. T., Ford, C. R., & Vose, J. M. (2013). Future species composition will affect forest water use after loss of eastern hemlock from southern Appalachian forests. *Ecological Applications, 23*(4), 777-790. doi:10.1890/12-0616.1.

Brantley, S. T., Miniat, C. F., Elliott, K. J., Laseter, S. H., & Vose, J. M. (2015). Changes to southern Appalachian water yield and stormflow after loss of a foundation species. *Ecohydrology, 8*(3), 518-528. doi:10.1002/eco.1521.

Brantley, S. T., Mayfield, A. E., Jetton, R. M., Miniata, C. F., Zietlowa, D. R., Browna, C. L., & Rhead, J. R. (2017). Elevated light levels reduce hemlock woolly adelgid infestation and improve carbon balance of infested eastern hemlock seedlings. *Forest Ecology and Management, 385*, 150-160. doi:10.1016/j.foreco.2016.11.028.

CABI (Ed.). (2013). *Tsuga canadensis*. In, *The CABI encyclopedia of forest trees*. Oxford, UK: CABI. Retrieved from http://ezproxy.library.dal.ca/login?qurl=https%3A%2F%2Fsearch.credoreference.com%2Fcontent%2Fentry%2Fcabicabi%2Ftsuga_canadensis%2F0%3FinstitutionId%3D365

Cranshaw, W., & Shetlar, D. (Eds.). (2017). Adelgids that develop on twigs and terminals of conifers. In, *Garden insects of North America: the ultimate guide to backyard bugs (2nd ed.)*. Princeton, NJ: Princeton University Press.

Canadian Food Inspection Agency. (2017, August 3). *Hemlock Woolly Adelgid confirmed in Nova Scotia* [Press release]. Retrieved from https://www.canada.ca/en/food-inspection-agency/news/2017/08/hemlock_woolly_adelgidconfirmedinnovascotia.html#benefits.

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., … Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature, 486*(7401). 59-67. doi:10.1038/nature11148.

Case, B. S., Buckley, H. L., Barker-Plotkin, A. A., Orwig, D. A., & Ellison, A. M. (2017). When a foundation crumbles: forecasting forest dynamics following the decline of the foundation species *Tsuga canadensis*. *Ecosphere, 8*(7): e01893. doi:10.1002/ecs2.1893.

Cheah, C. A. S. J. (2017). Predicting hemlock woolly adelgid winter mortality in Connecticut forests by climate divisions. *Northeastern Naturalist, 24*(7), B90-B118. doi:10.1656/045.024.s713.

Chisholm, R. (2012). The ecology, economics, and management of alien invasive species. In S. A. Levin, S. R. Carpenter, & H. C. J. Godfray (Eds.), The Princeton Guide to ecology. Princeton, NJ: Princeton University Press.

Clark, J. T., Fei, S., Liang, L., Rieske, L. K. (2012). Mapping eastern hemlock: Comparing classification techniques to evaluate susceptibility of a fragmented and valued resource to an exotic invader, the hemlock woolly adelgid. *Forest Ecology and Management, 266*, 216-222. doi:10.1016/j.foreco.2011.11.030.

Cowles, R. S. (2009). Optimizing dosage and preventing leaching of imidacloprid for management of hemlock woolly adelgid in forests. *Forest Ecology and Management, 257*(3), 1026-1033. doi:10.1016/j.foreco.2008.11.005.

Daley, M. J., Phillips, N. G., Pettijohn, C., & Hadley, J. L. (2007). *Canadian Journal of Forest Research, 37*(10), 2031-2040. doi:10.1139/X07-045.

Davis, D. & Browne, S. (Eds.). (1998). *Natural history of Nova Scotia, vol. 1: Topics and habitats*. Halifax, NS: Nimbus Publishing.

di Castri, F. 1989. History of biological invasions with emphasis on the Old World. In J. Drake, F. di Castri, R. Groves, F. Kruger, H. A. Mooney, M. Rejmanek, and M. Williamson (Ed.), *Biological invasions: a global perspective* (pp.1-30). New York: Wiley.

Dukes, J. S., Pontius, J., Orwig, D., Garnas, J. R., Rodgers, V. L., Brazee, N., … Ayres, M. (2009). Responses of insect pests, pathogens, and invasive plant species to climate change in the forests of northeastern North America: What can we predict? *Canadian Journal of Forestry Research, 39*(2), 231-248. doi:10.1139/X08-171.

Ellison, A. M., Bank, M. S., Clinton, B. D. Colburn, E. A., Elliott, K., Ford, C. R., … Webster, J. R. (2005). Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Frontiers in Ecology and the Environment, 3*(9), 479-486. doi:10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2.

Environment Canada. (2012). *Invasive alien species partnership program: 2005–2010 report.* Retrieved from http://www.publications.gc.ca/site/eng/9.506824/publication.html.

Fitzpatrick, M. C., Preisser, E. L., Porter, A., Elkinton, J., & Ellison, A. M. (2012). Modeling range dynamics in heterogeneous landscapes: invasion of the hemlock woolly adelgid in eastern North America. *Ecological Applications, 22*(2), 472-486. doi:10.1890/11-0009.1.

Ford, C. R. & Vose, J. M. (2007). *Tsuga Canadensis* (L.) Carr. mortality will impact hydrological processes in southern Appalachian forest ecosystems. *Ecological Applications, 17*(4), 1156-1167. doi:10.1890/06-0027.

Gouli, V., Parker, B. L., Skinner M. (2001). Haemocytes of the hemlock woolly adelgid *Adelges tsugae Annand* (*Hom., Adelgidae*) and changes after exposure to low temperatures. *Journal of Applied Entomology, 124*(3-4), 201-206. doi:10.1046/j.1439-0418.2000.00436.x.

The Government of Canada. (2018). *Past weather and climate: Historical data*. Retrieved from http://climate.weather.gc.ca/historical_data/search_historic_data_e.html.

Hellmann, J. J., Byers, J. E., Bierwagen, B. G., & Dukes, J. S. (2008). Five potential consequences of climate change for invasive species. *Conservation biology, 22*(3), 534-543. doi:10.1111/j.1523-1739.2008.00951.x.

Jenkins, J.C., Aber, J.D., & Canham, C.D. (1999). Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. The Canadian *Journal of Forest Research, 29*(5), 630-645. doi:10.1139/x99-034.

Jones, C., Song, C., Moody, A. (2015). Where's woolly? An integrative use of remote sensing to improve predictions of the spatial distribution of an invasive forest pest the hemlock woolly adelgid. *Forest Ecology and Management, 358*, 222-229. doi:10.1016/j.foreco.2015.09.013.

Kim, J., Hwang, T., Schaaf, C. L., Orwig, D. A., Boose, E., & Munger, J. W. (2017). Increased water yield due to the hemlock woolly adelgid infestation in New England. *Geophysical Research Letters, 44*(5), 2327-2335. doi:10.1002/2016GL072327.

Knoepp, J. D., Vose, J. M., Michael, J. L., & Reynolds, B. C. (2012). Imidacloprid movement in soils and impacts on soil microarthropods in southern Appalachian eastern hemlock stands. *Journal of Environmental Quality, 41*(2), 469-478. doi:10.2134/jeq2011.0306.

Logan, J. & Powell, J. (2001). Ghost forests, global warming, and the mountain pine beetle (*Coleoptera: Scolytidae*). *American Entomologist, 47*(3), 160-173. doi:10.1093/ae/47.3.160.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., & Bazzaz, F. A. (2000). Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications, 10*(3): 689-710. doi:10.1890/1051-0761(2000)010[0689:BICEGC]2.0.CO;2.

Mausel, D. L., Salom, S. M., Kok, L. T., & Fidgen, J. G. (2008). Propagation, synchrony, and impact of introduced and native *Laricobius* spp. (*Coleoptera: Derodontidae*) on hemlock woolly adelgid in Virginia. *Environmental Entomology, 37*(6), 1498-1507. doi:10.1603/0046-225X-37.6.1498.

McAvoy, T. J., Regniere, J., St-Amant, R., Schneeberger, N. F., Salom, S. M. (2017). Mortality and recovery of hemlock woolly adelgid (*Adelges tsugae*) in response to winter temperatures and predictions for the future. *Forests, 8*(12), 497-517. doi:10.3390/f8120497.

McClure, M. S. & Cheah, C. A. S. J. (2002). Important mortality factors in the life cycle of hemlock woolly adelgid (*Homoptera: Adelgidae*) in the northeastern United States. In R. C. Reardon, B.P. Onken & J. Lashomb (Eds.), *Proceedings: Hemlock Woolly Adelgid in the Eastern United States Symposium*, *New Brunswick, N.J* (pp. 13-22). New Brunswick, N.J., USA: New Jersey Agricultural Experiment Station.

McClure, M. S. (1996). Biology of *Adelges tsugae* and its potential for spread in the northeastern United States [Abstract]. *Proceedings of the First Hemlock Woolly Adelgid Review, USA, 17,* 16–25. Retrieved from https://www.cabdirect.org/cabdirect/abstract/19970600316.

McClure, M. S. (1991). Density-dependent feedback and population cycles in *Adelges tsugae* (*Homoptera: Adelgidae*) on *Tsuga canadensis*. *Environmental Entomology, 20*(1), 258–264, doi:10.1093/ee/20.1.258.

McDowell, W. G., Benson, A. J., & Byers, J. E. (2014). Climate controls the distribution of a widespread invasive species: implications for future range expansion. *Freshwater Biology, 59*(4), 847-857. doi:10.1111/fwb.12308.

Mech, A. M., Tobin, P. C., Teskey, R. O., Rhea, R. J., & Gandhi, K. J. K. (2018). Increases in summer temperatures decrease the survival of an invasive forest insect. *Biological Invasions, 20*(2), 365-374. doi:10.1007/s10530-017-1537-7.

Natural Resources Canada. (2015). *Climate and climate-related trends and projections*. Retrieved from https://www.nrcan.gc.ca/environment/resources/publications/impacts-adaptation/reports/assessments/2008/10261#box2.

Nova Scotia Department of Lands and Forestry. (2018). *Climate data* [raster digital data]. Truro, NS: Nova Scotia Department of Lands and Forestry, Forestry Division.

Nova Scotia Department of Natural Resources. (2017). *2016, forest inventory, Nova Scotia, Canada* (version 3) [digital shapefile]. Retrieved from https://novascotia.ca/natr/forestry/gis/dl_forestry.asp.

Nova Scotia Department of Natural Resources. (2013). *DP ME 55, 2006, enhanced digital elevation model, Nova Scotia, Canada* (version 2) [raster digital data]. Retrieved from http://www.gov.ns.ca/natr/meb/download/dp055.asp.

Orwig, D.A., Cobb, R.C., D'Amato, A.W., Kizlinski, M.L., & Foster, D.R. (2008). Multi-year ecosystem response to hemlock woolly adelgid infestation in southern New England forests. *The Canadian Journal of Forest Research, 38*, 834-843. doi:10.1139/X07-196.

Paradis, A., Elkinton, J., Hayhoe, K., & Buonaccorsi, J. (2008). Role of winter temperature and climate change on the survival and future range expansion of the hemlock woolly adelgid (*Adelges tsugae*) in eastern North America. *Mitigation and Adaptation Strategies for Global Change, 13*(5), 541-554. doi:10.1007/s11027-007-9127-0.

Parker, B. L., Skinner, M., Gouli, S., Ashikaga T. H., & Teillon, B. (1999). Low lethal temperature for hemlock woolly adelgid (*Homoptera: Adelgidae*). *Environmental Entomology, 28*(6), 1085–1091. doi:10.1093/ee/28.6.1085.

Pearson, R. G. & Dawson, T. P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography, 12*(5), 361-371. doi:10.1046/j.1466-822X.2003.00042.x.

Pearson, R. G., Dawson, T. P., Berry, P. M., & Harrison, P. A. (2002). SPECIES: a spatial evaluation of climate impact on the envelope of species. *Ecological modelling, 145*(3), 289-300. doi:10.1016/S0304-3800(02)00056-X.

Pimentel, D., Zuniga, R., & Morrison, D. (2004). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, *52*(3), 273-288. doi:10.1016/j.ecolecon.2004.10.002.

Prather, C. M., Pelini, S. L., Laws, A., Rivest, E., Woltz, M., Bloch, C. P., … Joern, A. (2013). Invertebrates, ecosystem services, and climate change. *Biological Reviews, 88*, 327-348. doi:10.1111/brv.12002.

Sackett, T. E., Record, S., Bewick, S., Baiser, B., Sanders, N. J., & Ellison, A. M. (2011). Responses of microarthropod assemblages to the loss of hemlock (*Tsuga canadensis*), a foundation species. *Ecosphere, 2*(7), 1-16. doi:10.1890/ES11-00155.1.

Skinner, M., Parker, B. L., Gouli, S. & Ashikaga, T. (2003). Regional Responses of hemlock woolly adelgid (*Homoptera: Adelgidae*). *Environmental Entomology, 32*(3), 523-528. doi:10.1603/0046-225X-32.3.523.

Snyder, C. D., Young, J. A., Lemarie, D. P., & Smith, D. R. (2011). Influence of eastern hemlock (*Tsuga canadensis*) forests on aquatic invertebrate assemblages in headwater streams. *Canadian Journal of Fisheries and Aquatic Sciences, 59*(2), 262-275. doi:10.1139/f02-003.

Stahl, K., Moore, R. D., & McKendry, I. G. (2006). Climatology of winter cold spells in relation to mountain pine beetle mortality in British Columbia, Canada. *Climate Research, 32*, 13-23. doi:10.3354/cr032013.

Stewart, B. J., Neily, P. D., Quigley, E. J., Duke, A. P., & Benjamin, L. K. (2003). Selected Nova Scotia old-growth forests: Age, ecology, structure, scoring. *The Forestry Chronicle, 79*(3), 632-644. doi:10.5558/tfc79632-3.

Steenberg, J. W. N., Duinker, P. N., & Bush, P. G. (2011). Exploring adaptation to climate change in the forests of central Nova Scotia, Canada. *Forest Ecology and Management, 262*, 2316-2327. doi:10.1016/j.foreco.2011.08.027.

Tingley, M. W., Orwig, D. A., Field, R., & Motzkin, G. (2002). Avian response to removal of a forest dominant: consequences of hemlock woolly adelgid infestations. *Journal of Biogeography, 29*(10-11), 1505-1516. doi:10.1046/j.1365-2699.2002.00789.x.

Trotter, R. T. & Shields, K. S. (2009). Variation in winter survival of the invasive hemlock woolly adelgid (*Hemiptera: Adelgidae*) across the eastern United States. *Environmental Entomology, 38*(3), 577–587, doi:10.1603/022.038.0309.

Vose, J. M., Wear, D. N., Mayfield, A. E., & Nelson, D. C. (2013). Hemlock woolly adelgid in the southern Appalachians: Control strategies, ecological impacts, and potential management responses, *Forest Ecology and Management, 291*, 200-219. doi:10.1016/j.foreco.2012.11.002.

Whyte, I. (2013). Eutrophication. In *Environmental history and global change series, v. 2: A dictionary of environmental history*. London: IB Tauris.

Yorks, T. E., Jenkins, J. C., Leopold, D. J., Raynall, D. J., & Orwig, D. A. (2000). Influences of Eastern Hemlock mortality on nutrient cycling. In K. A. McManus, K. S Shields, & D. R. Souto (Eds.), *Proceedings: Symposium on sustainable management of hemlock ecosystems in eastern North America. Gen. Tech. Rep. NE-267* (pp. 126-133). Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station.