MODELING THE IMPACT OF HEMLOCK WOOLLY ADELGID UNDER SEVERAL CLIMATE CHANGE SCENARIOS

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LAKEHEAD UNIVERSITY

THUNDER BAY, ONTARIO

April 2023

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An Undergraduate Thesis Submitted in partial Fulfillment of the Requirements for the Degree of the Honours Bachelor of Science in Forestry

Faculty of Natural Resources Management

Lakehead University

April 2023

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Major Advisor	Second Reader

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ABSTRACT

Cornelsen, C. 2023. Modeling the impact of hemlock woolly adelgid under several climate change scenarios. 48 pp.

The hemlock woolly adelgid (*Adelges tsugae*), or HWA, is a species of insect invasive to eastern North America that has caused significant mortality amongst its hemlock (*Tsuga* spp.) hosts. Survivorship and subsequent population expansion of the HWA is theorized to be limited primarily by minimum winter temperatures. As climate change reduces the severity and cold periods of winter, the potential for a northward expansion of the HWA is introduced. This study utilized maximum entropy modeling (MaxEnt) in conjunction with an iNaturalist citizen-science occurrence dataset via the Global Biodiversity Information Facility (GBIF) and WorldClim (HadGEM3) downscaled climate projection data to model habitat suitability for the HWA throughout eastern hemlock's (*Tsuga canadensis*) range. In addition to a historic conditions baseline, species distribution models were generated using SSP 126, SSP 245, and SSP 585 emissions scenarios for mid-century (2041-2060) and late-century (2081-2100) climate change scenarios. The results showed that under a low emissions SSP 126 scenario, the HWA will be capable of inhabiting almost the entirety of the eastern hemlock's current range by the end of the century. More extreme SSP 245 and SSP 585 warming scenarios resulted in a more rapid northwards shift in suitable habitat, encompassing the entire range of eastern hemlock by the middle of the century. The consequences for eastern hemlock are significant, with HWA infestations likely to become more widespread and severe due to climate change.

Keywords: *Adelges tsugae*, Citizen Science Data, Eastern Hemlock, iNaturalist, Invasive insect, MaxEnt, Pest, Species Distribution Modeling

ACKNOWLEDGEMENTS

I would like to recognize the contributions of my thesis supervisor, Dr. Seung-Il Lee, for his guidance and input in this undergraduate thesis. Additionally, I would like to recognize my second reader, Dr. Jian Wang, for his contributions. I would also like to recognize Dr. Christian MacQuarrie of Natural Resources Canada for his invaluable advice in the preparation of this study. Additionally, I acknowledge the contributions of Lakehead University Ph.D. candidate Vianney Janice Cupiche Herrera, who provided me with invaluable technical assistance with the QGIS and MaxEnt programs. As well, I acknowledge the World Climate Research Programme, which coordinated and promoted CMIP6 through its Working Group on Coupled Modelling. I thank these climate modeling groups for producing and making available their model outputs and the Earth System Grid Federation (ESGF) for archiving this data and providing access. I also thank the multiple funding agencies who support the CMIP6 and the ESGF. Finally, I would like to recognize the GBIF for making occurrence data from the iNaturalist project available for download and use in this project.

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INTRODUCTION

Adelges tsugae Annand, commonly called hemlock woolly adelgid (HWA), is a species of invasive insect first introduced to eastern North America from southern Japan sometime in the early 1950s (Havill *et al.* 2016). HWA parasitizes both eastern hemlock (*Tsuga canadensis* (L.) Carrière), which is distributed widely in eastern North America, and Carolina hemlock (*Tsuga caroliniana* Engelmann), which is isolated in the southern Appalachian Mountains. The HWA feeds on the ray parenchyma cells of host trees, extracting the sap from the host and reducing their available nutrients (Orwig and Foster, 1998). The feeding activity of HWA is also believed to cause a hypersensitive response that restricts water transport through the hosts' xylem (Havill et al. 2016). Therefore, hemlocks infested with the HWA subsequently suffer from decline and mortality four to ten years after initial infestation (Orwig *et al.* 2003).

Eastern hemlock is a significant climax species throughout the forests of southeastern Canada and the northeastern United States, with a range that extends from the Canadian Maritimes in the northeast, west through the Great Lakes – St. Lawrence region, and south throughout the Appalachian Mountains to northern Georgia and Alabama (McClure *et al.* 1996). Eastern hemlock is a long-lived species, with some individuals reaching more than 800 years old (Ward *et al.* 2004). The tree is also impressively large, reaching heights up to 175ft tall and 6ft in diameter. Eastern hemlock also exhibits among the highest shade tolerance of any species in eastern North America and can grow in forest ecosystems with as little as 5% full light penetration (Godman and Lancaster 1990). This allows hemlock to frequently form pure stands with very dense canopies that create cool and shady understories. The tree is of significant value to wildlife because it provides excellent cover from extreme temperatures to several species of birds and mammals, as well as forage for more than 80 species of birds (Ward *et al.* 2004). Eastern hemlock is also a key component of many riparian ecosystems where the deep shade created by the thick canopy helps to cool water temperatures. It is especially important in riparian areas of southern hardwood forests where as one of the few evergreen species it is an important driver of transpiration during winter leaf-off (Ford and Vose 2007). Although not as commercially valuable as other softwood species, hemlock is still utilized somewhat extensively in the pulp and paper industry, as a building material, and has seen particular success as a landscape and ornamental tree (Ward *et al.* 2004; McClure *et al.* 1996; Godman and Lancaster 1990).

HWA has spread throughout approximately half the range of eastern hemlock (Havill *et al*. 2016), extending from the Appalachian Mountains in the south (Paradis *et al.* 2008), northwards along the US east coast to the southwestern corner of Nova Scotia, where it was identified as established in 2017 (Muise *et al.* 2020). The impact of HWA on hemlock stands has been severe but is not constant across its entire range. Paradis *et al*. (2008) observed that several hemlock had remained uninfected in some northern and western regions of Massachusetts despite a 17-year regional infestation. In the southern extent of its range, the spread of HWA and subsequent mortality of hemlock trees has been most severe due to warm minimum winter temperatures reducing HWA mortality (Ford and Vose 2007). Cold winter temperatures are believed to be the primary limiting factor in the northern limit of HWA range expansion, and a key regulator of outbreak severity (McAvoy *et al.* 2017). Winter temperatures lower than negative 25 degrees Celsius begin to cause increased HWA mortality, with temperatures lower than negative

30 to 35 degrees Celsius resulting in near-complete or total mortality (Costa *et al.* 2004). Skinner *et al*. (2003) found that less than 3 percent of HWA taken from USDA growing zones 5a through 6b survived under January and February temperatures lower than negative 30 to 35 degrees Celsius. A greater cold tolerance exhibited by HWA taken from colder growing zones does, however, indicate the species is adapting a genetically increased cold tolerance (Skinner *et al.* 2003). This was further proven by a common garden study from Butin *et al*. (2005), which determined that the HWA population was sufficiently genetically diverse to allow for selection driven mutation towards a greater genetic tolerance to cold.

Ontario currently lies primarily to the north and west of the current range of HWA, although it is increasingly at risk of infestation. The first two infestations of HWA in Ontario were detected in Etobicoke in 2012 and Niagara Gorge in 2013, both of which had intensive sanitation measures taken to irradicate the infestations (Fidgen *et al.* 2014). Several subsequent infestations have been detected in Ontario since 2019, most of which have been located throughout the Niagara region around the towns of Niagara Falls (2019), Wainfleet (2019), and Pelham (2022); although as of 2022 an infestation has been recorded north of Lake Ontario around the community of Grafton (CFIA 2022). Climate change introduces the potential for the further northward expansion of HWA as minimum winter temperatures increase (McAvoy *et al.* 2017).

OBJECTIVES

This thesis will seek to model the growth potential of hemlock woolly adelgid populations across the range of eastern hemlock under several climate change scenarios using citizen science data on the current distribution of HWA. This study will explore if warming winter temperatures as a result of climate change will allow the HWA to spread throughout the range of its eastern hemlock host. This study will also explore potential habitat suitability for the HWA throughout the range of eastern hemlock, and how this may affect hemlock survivorship in the future using the Maximum Entropy (MaxEnt) model and citizen science data from the iNaturalist project.

HYPOTHESIS

As minimum winter temperatures rise throughout the northern portions of the eastern hemlock's range, favourable environmental conditions for HWA population establishment will be created. It is predicted maximum entropy modeling would reveal that 1) climate change allows the northward expansion of HWA, and 2) warmer climate scenarios will create the capacity for larger populations of HWA in northern regions of the eastern hemlock's range.

LITERATURE REVIEW

HEMLOCK WOOLLY ADELGID (HWA)

The hemlock woolly adelgid (HWA), named *Adelges tsugae* Annand in binomial nomenclature, belongs to the family Adelgidae in the order Hemiptera (Havill and Foottit 2007). The HWA is a small ovular insect with a waxy coating that closely resembles many species of aphids (CFIA 2021). Adult HWA sistens (Figure 1) are a mere 1.41mm long and 1.05mm wide on average. The HWA feeds on the sap of host hemlocks with the use of four specialized sucking mouthparts called stylets which are arranged in a stylet bundle (Young *et al.* 1995). The HWA feeds by attaching to the base of hemlock needles where the cuticle is thinnest (Figure 2), then penetrating through the epidermal tissue of the host with its stylet to access the sap-rich parenchyma cells contained in the xylem rays of the underlying vascular tissue (Havill *et al.* 2016). The HWA feeds on the sap of hemlocks throughout every instar stage of its development, reinserting its stylet after each time it is forced to molt. This gradually diminishes the sugar reserves of the hosts' parenchyma cells. The native range of HWA encompasses the distribution of several species of hemlock (*Tsuga* spp.) throughout mainland China, Taiwan, and Japan, as well as a distinct lineage found in western North America (Havill *et al.* 2016).

The HWA has a one-year polymorphic lifecycle during which it undergoes four distinct instar stages; although the first three stages of instar development are nearly indistinguishable from one another (McClure 1989). The lifecycle of the HWA begins in early spring, with adult HWA sistens laying a single mass of up to 300 eggs in characteristic white woolly structures known as ovisacs (Figure 3) (McClure *et al.*

1996). In the early to mid-spring, two types of HWA hatch from the ovisacs; asexual non-winged individuals referred to as progrediens, and less numerous sexual winged individuals referred to as sexuparae (Figure 4) (McClure *et al.* 1996; McClure 1989). After rapidly maturing in less than three months, mature progrediens produce 20-75 eggs each, which give rise to a longer-lived progeny referred to as sistens (USDA 2005; CFIA 2021). In early summer the 1st instar nymph sistens (Figure 5) hatch and immediately move to the base of available hemlock needles, attach via their stylets, and enter a state of dormancy throughout the summer called aestivation (Foley *et al.* 2022). As temperatures cool in the early to mid-fall, the nymphs emerge from their dormancy and rapidly mature through the four instars of development throughout the late fall and early winter before entering yet another dormancy (McClure *et al.* 1996; Foley *et al.* 2022; Havill *et al.* 2011). Adult sistens finally emerge from dormancy in the late winter or early spring, complete development if they have not already, and lay asexually produced eggs in early spring. The exact timing of the HWA lifecycle is largely dependent on the climate in which they are present, with development being more accelerated in cooler northern and high-elevation climates, and extended in the more temperate southern reaches of its ranges (McClure *et al.* 1996: Havill *et al.* 2011).

Unlike the unwinged progrediens, upon hatching, the generation of winged sexuparae immediately disperse in search of alternative spruce (*Picea* spp.) hosts on which they can lay their eggs (Elkinton *et al.* 2011). In the presence of suitable spruce primary hosts, a generation of sistens capable of sexual reproduction is produced (CFIA, 2021; Havill *et al.* 2011). Not all spruce are suitable primary hosts, however, and in the case of HWA lineages that originated from southern Japan only tigertail spruce (*Picea* *torano* (K. Koch) Koehne) is suitable. HWA populations in western North America have been found to lack a suitable *Picea* spp. host for sexual reproduction, and subsequently maintain entirely asexual populations (McClure 1989; Havill *et al.* 2011; Foley *et al.* 2022).

Within its native range across Japan, China, and western North America, the HWA is largely non-problematic and can only build to significant populations on trees that are already severely stressed or in decline (McClure *et al.* 1996). This is attributed to the resistance of host trees to the insect, in addition to the presence of natural predators such as *Leucopis* spp. in western North America (CFIA 2021; Motley *et al.* 2017).

Figure 1. Adult HWA sisten. Image via Nathan Havill, USDA Forest Service.

Figure 2. HWA nymph sistens feeding at the base of hemlock needles. The stylet bundle is marked with a white arrow. Image via Nathan Havill, USDA Forest Service.

Figure 3. HWA ovisac dissected to display the eggs contained within. Image via Lorraine Graney, Bartlett Tree Experts.

Figure 4. Adult HWA sexuparae. Image via Michael Montgomery, USDA Forest Service, Bugwood.org

Figure 5. HWA 1st instar nymph sisten. Image via Kelly Oten, North Carolina State University, Bugwood.org

CURRENT IMPACT OF HWA IN NORTH AMERICA

Although it is believed to be native to Western North America, the HWA does not naturally occur on the eastern side of the continent (McClure and Cheah 1999). Introduced HWA was first discovered in eastern North America in 1951, and was determined to have originated from the island of Honshu, Japan (Fidgen *et al.* 2014;

McClure and Cheah 1999). The lineage of HWA introduced to North America naturally alternates between southern Japanese hemlock (*Thuja sieboldii* Carrière) and its primary host, tigertail spruce (*Picea torano* (Siebold ex K.Koch) Koehne), (Onken and Reardon 2011). The introduced HWA has been able to feed successfully on hemlock hosts in Eastern North America, but in the absence of tigertail spruce, it is unable to reproduce sexually. Therefore, much like the population in Western North America, HWA in Eastern North America is entirely reliant on asexual propagation (Onken and Reardon 2011).

The eastern hemlock and Carolina hemlock, both native to eastern North America, exhibit virtually no tolerance to feeding damage by the introduced HWA. Coupled with the lack of natural predators to control establishment, HWA populations in eastern North America are frequently able to build to levels that cause serious deleterious effects for host trees (Havill *et al.* 2016). Extensive HWA feeding not only causes the depletion of the host's energy reserves but has also been linked to a hypersensitive response that restricts water transport throughout the host tree's xylem and leads to further decline (Havill *et al.* 2016). The mortality of eastern hemlocks that experience infestation by HWA is therefore very high, and articles published by Natural Resources Canada and the United States Department of Agriculture both claim that in the eastern US mortality of hemlocks infected with HWA has significantly exceeded 90% (Fidgen *et al.* 2014; Ward *et al.* 2004). Mortality of the host tree takes between four and ten years, with climate, host size, and host vigour being the largest factors in determining the duration of infestation (Orwig and Foster, 1998).

Since its introduction, the HWA has spread rapidly throughout the range of hemlocks in eastern North America, with nearly 50% of the eastern hemlock's range now threatened with infestation (Havill *et al.* 2016; Emilson *et al.* 2018). The HWA has been shown to spread at a rate of between 12.5 and 20.8 km/yr, with the rate of spread largely determined by the favourability of the habitat into which the HWA is expanding (Evans and Gregoire 2007). Given the inability of winged progeny to successfully reproduce in North America the independent movement of HWA is very slow, but wind, birds, mammals, and humans have all helped to facilitate the rapid spread of the insect (McClure 1990). HWA has now established itself throughout the majority of hemlocks' native ranges in the US, with areas in the extreme west and northeast of eastern hemlock's range being the only notable exception. However, some isolated pockets of uninfected refugia still do exist in the southern Appalachian Mountains. HWA was also found to have established itself in more than 5 counties in southwestern Nova Scotia as of 2017 (Emilson *et al.* 2018). Ontario, historically to the west and north of HWA's range, has also begun to experience some limited infestations in the extreme southeast of the province (Fidgen *et al.* 2014). Two populations were identified in 2013 and 2014, the first of which was in Etobicoke, and the second in Niagara Falls, respectively. Extensive eradication efforts were made to control the infestation through the sanitation (burning and removal) of all infected trees, and eradication efforts appeared to have been successful (Fidgen *et al.* 2014). However, since 2019, further infestations have been reported in the province (CFIA 2022). Most of these infestations are located throughout the Niagara region, including 2019 infestations in Niagara Falls and Wainfleet, as well as 2021 and 2022 detections in Fort Erie and Pelham, respectively. Notably, a further infestation was also located on the north shore of Lake Ontario around the community of Grafton as of 2022 (CFIA 2022).

HWA AND CLIMATE CHANGE

An increasingly large body of academic literature has established a correlation between the survival of HWA in eastern North America and winter temperatures (Trotter, III, and Shields 2009; Paradis *et al.* 2008; Evans and Gregoire 2007; Parker *et al*. 1999). HWA is particularly susceptible to winter mortality, largely as a result of its feeding activity occurring in both early and late winter (McAvoy *et al*. 2017). Across its range, winter mortality of the HWA is subsequently higher in the northern components of its distribution, where average winter temperatures are coldest (Trotter III and Shields 2009).

The ability of HWA to expand its range is reliant on overwintering mortality of less than 91%, after which the fecundity of the population is reduced sufficiently to result in population decline (Paradis *et al*. 2008). Minimum winter temperature has been correlated with HWA survivorship, with colder temperatures resulting in increased mortality (Parker *et al*. 1999; Skinner *et al*. 2003). For HWA taken from plant hardiness zone 5a, the coldest zone in which HWA is present, temperatures below negative 30 degrees result in fewer than 3 percent HWA survivorship, with temperatures lower than negative 35 resulting in complete mortality of the insect (Skinner *et al*. 2003; Parker *et al*. 1999). Differences in cold tolerance, however, have been found based on location and the time of year. Skinner *et al*. (2003) found that HWA taken from growing zones 6a and 6b experienced complete mortality when exposed to temperatures lower than negative 30 degrees, which is unlike the aforementioned HWA taken from zone 5a. The study also found that from January to March the percentage of HWA survivorship following exposure to negative 15 degrees Celsius temperatures degraded 50 to 60 percent for HWA from growing zones 6a and 6b. This was further supported by Parker *et al*. (1999), who found that at negative 25 degrees Celsius the proportion of HWA survivorship fell from 14-22 percent in January, to 8-12 percent in February, and just 0-4 percent in March.

Negative 25 degrees Celsius was subsequently identified as a significant threshold temperature by Skinner *et al*. (2003), who found that HWA survivorship dipped below 10 percent regardless of the time of year or growing zone. This was supported by Cheah (2017), who found that minimum winter temperatures of negative 24 degrees Celsius or below resulted in greater than 90 percent mortality of HWA in northwestern Connecticut. This is unlike Parker *et al*.'s aforementioned findings, which still found an overwintering HWA survivorship rate of up to 12 percent following negative 25 degree temperatures in February. The amount of time that HWA is exposed to cold temperatures is also significant. Paradis *et al*. (2008) estimated that a mean winter temperature of less than negative 5 degrees Celsius, or more than 79 days below negative 10 degrees Celsius, is sufficient to reduce HWA survivorship below the 91 percent minimum required for population expansion. HWA has historically been limited to regions no colder than USDA plant hardiness zone 5a (Skinner *et al*. 2003), where the average winter minimum temperature ranges from negative 26.1 to negative 28.9 degrees Celsius (USDA, 2012). As temperatures warm globally as a result of climate change, the impact of HWA is likely to become more severe in infested regions, and its distribution will likely expand into regions previously too cold for population establishment (Paradis *et al*. 2008; McAvoy *et al*. 2017; Kantola *et al*. 2019).

It is of note that there are observed variances in cold tolerance through the range of HWA (Skinner *et al*. 2003; Cheah 2008). Individuals along the northern extreme of the range exhibiting higher colder tolerance indicates the ability of the species to adapt to colder winter temperatures (Skinner *et al*. 2003). Butin *et al*. (2005) conducted a common garden experiment with HWA taken from both the southern and northern components of its range to test for adaptation to cold. The study found that despite being limited to parthenogenic reproduction, the genetic diversity of the HWA population was sufficiently large such that selection and mutation have allowed for the insect to develop greater genetic cold tolerance along the northern fringes of its range.

MODELING THE SPREAD OF HWA

Predicting the spread of invasive forest insects through population modeling has become increasingly utilized in the scientific community. Species distribution models, which predict geographic habitat suitability for a given species based on biologically significant climatic factors, are among the most widely utilized (Jeshchke and Strayer 2008). Although the potential for predicting population responses to climatic with species distribution models has been increasingly recognized (Chiou *et al*. 2015; Bryn *et al.* 2021), there are fundamental assumptions made by these models that must be recognized (Jeshchke and Strayer 2008). One such assumption is that the biotic interactions of a species are constant over geographic and temporal scales, and are subsequently not significant in influencing or determining its geographic range. SDMs also assume that the genotypic and phenotypic expression of the species is geographically and temporally constant, and that there is no variation in habitat preference/tolerance within the species. Finally, these models assume that there are no biotic or abiotic limitations to the dispersal of the species other than climate (Jeshchke and Strayer 2008).

Maximum entropy modeling, or MaxEnt (Phillips *et al.* 2006), is a widely used species distribution model which predicts the geographic presence of a species based on known occurrence points and their relationship with bioclimatic data (Lissovsky and Dudov 2021). One of the key features of MaxEnt is that it is able to generate species distribution models without the need for absence points, locations in which the species is known not to occur. This allows for the utilization of presence-only occurrence datasets (Phillips *et al.* 2006). MaxEnt has been demonstrated as capable of exhibiting a high degree of accuracy comparative to other high-performance species distribution models (Elith *et al*. 2006). There are, however, two primary limitations with presence-only species distribution modeling; the inability to generate the probability of species occurrence, and the increased influence of sample selection bias (Elith *et al*. 2010). Unlike most other presence-absence methods of species distribution modeling, which can predict the probability of a species occurrence over a geographic area, presence-only MaxEnt modeling is unable to do this and instead generates a map of habitat suitability. This can make the intercomparison with the results of other species distribution models more difficult. Sample selection bias, where some geographic regions are samples more intensely than others, also has a significantly stronger effect on presence-only models than their presence-absence counterparts (Phillips *et al*. 2009). This source of error can, however, be reduced through the elimination of occurrence point aggregations at a scale selected based on the resolution of the bioclimatic data being utilized (Lissovsky and Dudov 2021).

CLIMATE DATA

As early as the 1960s and 70s there was an increasingly large body of scientific literature that linked human industrial activities with altered climatic conditions; namely that global temperatures were warming as a result of greenhouse gas emissions into the atmosphere (Peterson *et al.* 2008). However, agreement amongst the scientific community about human-caused warming of global temperatures was far from unanimous, and some literature even argued that the increased contribution of atmospheric aerosols through industrial activity would result in the Earth cooling rather than heating (Rasool and Schneider 1971). Since the controversial claims made by early literature on climate change, there has been an increasingly large consensus reached amongst the scientific community that anthropogenic actions are exceedingly likely to be causing a warming of the global climate (Wuebbles *et al.* 2017). As of 2021, two separate reviews of scientific consensus have concluded that there is a minimum of 99 percent agreement amongst peer-reviewed literature that global warming is at least partially a result of anthropogenic influences (Myers *et al.* 2021; Lynas *et al.* 2021).

The emission of greenhouse gases through human activities is predicted with very high confidence to be the primary cause of current trends in global warming (Eyring and Gillet *et al.* 2021). Numerous climatic models have been developed to both establish the link between climate change and human activity, as well as to predict the extent to which future warming will occur (Eyring and Gillet *et al.* 2021; Wuebbles *et al.* 2017). The construction of climatic models generally requires the input of emissions scenarios that predict future greenhouse gas inputs and their cumulative effect on radiative forcing (Nakicenovic and Swart 2000). Radiative forcing, for reference, is any factor such as greenhouse gases that results in an alteration of the Earth's radiative energy budget and subsequently its climatic processes (Ramaswamy *et al.* 2018). One such set of radiative forcing-based emissions scenarios is the representative concentration pathways (RCPs) developed for the 5th Intergovernmental Panel on Climate Change (IPCC) (Moss *et al*. 2010). The RCP scenarios were developed to cover the possible range of radiative forcing that could occur by 2100 (measured in W/m^2 of solar radiation). Based on academic literature chosen by the IPCC, four RCP pathways were developed that lead to 2.6, 4.5, 6, and 8.5 W/m^2 of radiative forcing by 2100 respectively (Van Vuuren *et al.* 2011). The RCP pathways were chosen to represent the widest realistic range of radiative forcing presented in the scientific literature (Moss *et al*. 2010; Van Vuuren *et al.* 2011). RCP8.5 represents very high emissions scenarios above the 90th percentile of radiative forcing scenarios, and RCP2.6 represents very low radiative forcing established below the 10th percentile of emission mitigation scenarios. RCP4.5 and RCP6.0, meanwhile, are designed to represent medium emissions scenarios (Moss *et al*. 2010; Van Vuuren *et al.* 2011).

The Shared Socioeconomic Pathways (SSPs) are a series of socioeconomic climate change scenarios developed by the climate research community in parallel with the RCP radiative forcing scenarios (Riahi *et al*. 2017). These scenarios predict the impact of climate change on future societal conditions, examining impacts, mitigation, and adaptation globally. The scenarios were constructed from the effects of broader political, social, demographic, technological, environmental, and economic trends (O'Neill *et al*. 2017). Five such SSP scenarios were developed by O'Neill *et al*. (2017), with narratives constructed to represent a range of reasonable mitigation and adaptation possibilities. The scenarios are numbered numerically one to five, with SSP1 representing a global shift towards environmental sustainability, with low challenges to both climate change adaptation and mitigation. SSP2 represents a median scenario in which broader economic, social, and technological developments do not stray considerably from the trends of the past century. In this scenario, there are moderate challenges for both global climate change adaptation and mitigation. The SSP3 scenario assumes a negative change to global cooperation on climate change mitigation, with a high degree of global challenges to both the adaptation to, and mitigation of, climate change. The SSP4 and SSP5 scenarios provide examples of an uneven approach to climate change adaptation and mitigation. SSP4 predicted a low level of challenge to mitigation, with a high amount of challenges to adaption due to increasing levels of economic and technological inequality globally. SSP5 is the inverse, with a high number of challenges to climate change mitigation, and a low amount of challenges to adaptation as a result of increasing (and more equal) global technological and societal advancements, at the cost of increased fossil fuel utilization.

The Coupled Model Intercomparison Project (CMIP) is an intercomparison project that provides a framework for the construction of multiple-model datasets to determine the factors affecting past, present, and future climatic changes (Eyring *et al.*

2016). As a component of the Scenario Model Intercomparison Project for CMIP Phase 6 (CMIP6) multi-model climate projections of future climate change scenarios were produced using the SSP socioeconomic and RCP radiative forcing scenarios (O'Neill *et al*. 2016). O'Neill *et al*. (2016) constructed several key future climate scenarios using the SSP scenarios, with radiative forcing values derived from the most appropriate corresponding RCP scenario. SSP5-8.5 (SSP585) represents a severe or high-emissions climate change scenario, and is a combination of the SSP5 scenario and RCP8.5 radiative forcing values. SSP2-4.5 (SSP245) represents a median or moderate-emissions climate change scenario, and is a combination of the SSP2 scenario and RCP4.5 radiative forcing values. SSP1-2.6 (SSP126) is a mild or low-emissions climate change scenario, and combines the SSP1 scenario with RCP 2.6 radiative forcing values.

CITIZEN SCIENCE DATA

Citizen science refers to data that is collected by the general public, which is often done voluntarily and by a wide array of individuals, many of whom have little or no scientific training (Bonney *et al.* 2014). The key benefit provided by citizen science is that an extensive amount of data can be collected affordably, and can therefore provide researchers with a large volume of data that would otherwise be unattainable (Tulloch *et al*. 2013). The usefulness of citizen data to research varies widely depending on the type of information that is being collected, how it is gathered, and how it is presented (Sullivan *et al.* 2014). Additionally, concerns have been raised about the accuracy of citizen science data (Falk *et al.* 2019). In some cases, advancements in the utilization of technology have allowed for more continuous interaction between experts and the public, as well as the presentation of data in an organized and accessible manner. This has greatly increased the potential reliability and scientific application of many citizen science projects. One such example cited by Sullivan and his colleagues in 2014 is eBird, a web application that has fostered the collaboration of expert and amateur bird researchers to create an objectively comprehensive and reliable database that contains extensive data on the range and abundance of numerous bird species.

Several other internet-based citizen science projects have since been developed, and these databases have been identified as useful tools by several ecological researchers (Wilson *et al.* 2020). One such online database, iNaturalist, was developed in 2008 by Ken-ichi Ueda, Nate Agrin, and Jessica Kline as a master's project for the University of California Berkley's School of Information (Ueda 2022). The program has since evolved to become an initiative of the California Academy of Sciences in 2014, and a joint initiative of the National Geographic Society in 2017. iNaturalist allows the public to record sightings of fungi, flora, and fauna through the use of an application or website (Mugford 2021). Using the iNaturalist program, the public can report the location of species sightings, with an option to upload images for verification. These images are reviewed by other app users through a voting system that is meant to achieve a higher accuracy amongst the citizen data. Additionally, these images give researchers the ability to visually verify the identity of the observed species (Wilson *et al.* 2020). One key limitation identified with the iNaturalist system is that it is difficult for researchers to identify whether alterations in species abundance are the result of actual ecological changes to species abundance or the inconsistency of data collection (Mugford 2021).

MATERIALS AND METHODS

STUDY AREA

In this study, climatically suitable habitat for the hemlock woolly adelgid was modeled throughout the temperate zone of eastern North America under several potential climate change scenarios. The range of the HWA's only host species native to Ontario, the eastern hemlock, is therefore a key consideration when examining the potential future range of species. It is predicted that under one or more future climate scenarios the climatically suitable range of HWA will likely exceed the current distribution of eastern hemlock. Modeling by Natural Resources Canada has shown that the ideal climatic range of eastern hemlock will also shift north under several global warming scenarios (NRCAN 2022). However, several studies have found that the northward migration of species is limited by not only the climate but non-climatic factors as well, such as soil composition and existing species composition (Carterton *et al.* 2020; Putnam and Reich 2016; Van Der Veken *et al.* 2007). Therefore, any potential changes in the range of eastern hemlock are difficult to accurately predict. As a result, this study will assume that the range of eastern hemlock will remain constant throughout the study period until 2100.

The current range of eastern hemlock is available from several government inventories. For this study, a shapefile of Elbert Little's 1971 map of the preindustrial range of eastern hemlock from the *Atlas of United States trees volume 1 Conifers and important hardwoods* (Map 91-E) was utilized. This map was utilized for illustration purposes, as well as served as the geographic extent of modeling. As seen in Figure 6, Little's map was combined with a jurisdictional map of North America published by the

U.S. Geological Survey as part of the National Atlas of the United States of America, 1997 – 2014 (INEGI *et al*. 2004). A shapefile of the North American Great Lakes was also accessed from the Great Lakes Commission GIS database for use in the presentation of MaxEnt models and Little's eastern hemlock range map as pictured in Figure 6 (GLC 2022).

In addition to Little's range data, a published range of eastern hemlock is also available from Natural Resources Canada's *Trees, insects and diseases of Canada's forests* database (NRCAN 2015). Unlike Little's range map, the NRCAN range map focuses only on the northern components of the range of eastern hemlock. Subsequently, this study utilized Little's maps for use in modeling. However, the NRCAN map served as a valuable reference to ensure the accuracy of Little's older range estimations in key regions around central and southern Ontario. NRCAN's map is presented below in Figure 7 for reference.

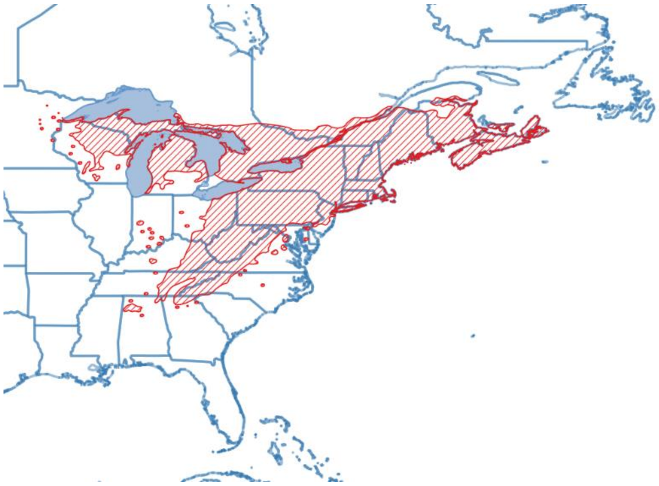

Figure 6. Range of eastern hemlock in Ontario based on Little's 1971 range maps. The range of eastern hemlock appears in hashed red over USGS political boundaries and the GLC Great Lakes shapefile.

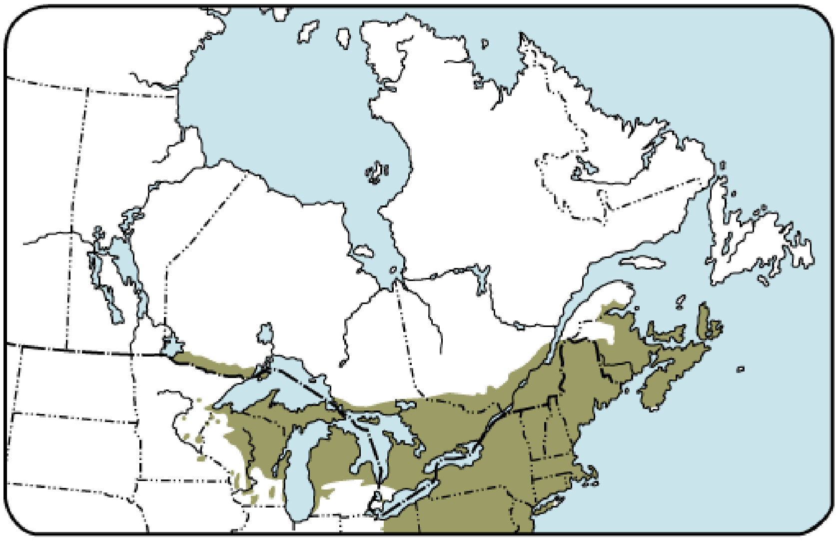

Figure 7. The range of eastern hemlock (green) throughout Canada as presented by Natural Resources Canada.

DATA SOURCE

Two primary datasets were utilized for this study, hemlock woolly adelgid occurrence data, and bioclimatic data for present and future climatic conditions. An occurrence dataset of “research-grade” iNaturalist observations was accessed via the Global Biodiversity Information Facility (GBIF) archive (GBIF 2022). This simple archive dataset included the date, coordinate location, and occurrence of HWA for each observation (datapoint) globally. For this study, which focused on HWA as an invasive pest in eastern North America, the dataset was modified to only include occurrences within the approximate native range of eastern hemlock. The HWA occurrence dataset was also cleaned to avoid selection bias for use in MaxEnt. Aggregated points closer than 1 km to each other were removed. This resolution was chosen based on the 30 second resolution of the climate data, which represents approximately 1 km at the equator.

Climatic data for this study was accessed via the WorldClim.org website, which hosts both historic climate data as well as projected datasets of future climate change scenarios (WorldClim 2022a, 2022b). Climate data from the WorldClim database is delineated into separate bioclimatic variables which are attained from monthly temperature and precipitation values, and represent biologically significant variables that are useful in the creation of species distribution models (WorldClim 2022a). Based on findings in previous literature, which link minimum winter temperatures to HWA mortality and range limitation (Parker *et al*. 1999; Skinner *et al*. 2003; Paradis *et al*. 2008; Cheah 2017; McAvoy *et al*. 2017; Kantola *et al*. 2019), five climatic variables were ultimately chosen for this model. These variables were the monthly average minimum temperature of January (Tn1), February (Tn2), and March (Tn3), as well as the minimum temperature of the coldest month (Bio6) and the mean temperature of the coldest quarter (Bio11). WorldClim datasets are available in several spatial resolutions, expressed as minutes of a degree of latitude and longitude (WorldClim 2022a). For this study, a 30 second resolution was chosen as it was the highest resolution available, and subsequently afforded the highest level of accuracy.

Climate data is available for a historical (near current) period of 1970 to 2000 and was developed by Fick and Hijmans for WorldClim version 2.1, which was released in January 2020 (Fick and Hijmans, 2017). In addition to its direct use in this study, this historical data acts as a baseline for the downscaling, calibration, and bias reduction of future climate datasets. The future climate datasets available on WorldClim are downscaled future climate projections from several global climate models generated as part of the IPCC's CMIP6 (O'Neil *et a*l. 2016). For this study, downscaled climate data projections from the Met Office Hadley Center HadGEM3-GC31-LL (2016) global climatic model were utilized, which, again, were developed as a component of the CMIP6 coupled model intercomparison project (Ridley *et al*. 2019).

WorldClim projected future climate variables are delineated into 20-year periods from 2021 to 2100 (WorldClim 2022b). For this study, 2041 to 2060 and 2081 to 2100 time periods were used to represent mid-century and late-century climatic effects. WorldClim future projection datasets are available for the SSP 126, 245, 370, and 585 emissions scenarios (WorldClim 2022b). For this study, datasets derived from SSP 126, 245, and 585 were utilized. These pathways were chosen to represent a wide range of potential future emissions pathways, presenting minimal, moderate, and severe global warming scenarios. A summary of the selected emissions pathways and time periods (Table 1) as well as the selected bioclimatic variables used in this study (Table 2) are displayed below.

Table 1. Summary of SSP emissions pathways and time periods used in this study.

Historical (1970-2000)	Mid Century (2041-2060)	Late Century (2081-2100)
-	SSP 126	SSP 126
-	SSP 245	SSP 245
-	SSP 585	SSP 585

Table 2. Summary of climate variables used in this study.

Climate Variable	Definition
Tn1	Average minimum monthly temperature - January
Tn2	Average minimum monthly temperature - February
Tn3	Average minimum monthly temperature - March
Bio6	Minimum temperature of the coldest month
Bio11	Mean temperature of the coldest quarter

DATA ANALYSIS

Analysis of HWA's range under the aforementioned climate change scenarios was conducted through the use of entropy modeling. For this purpose, the Maximum Entropy (MaxEnt) model version 3.4.4 was chosen (Phillips *et al.* 2022). DIVA-GIS (Hijmans *et al.* 2022) was used in conjunction with the HWA dataset obtained from iNaturalist (GBIF 2022) and Little's 1971 eastern hemlock range map to prepare a cleaned occurrence dataset reduced to the desired extent. The cleaned occurrence dataset was then utilized in conjunction with the selected historical WorldClim climate variables in MaxEnt to generate a historical species distribution model. To predict changes in HWA's range under future climate scenarios, the selected downscaled HadGEM3 climate projection datasets were then applied to the aforementioned historical species distribution model in MaxEnt. As was previously stated, SSP 126, SSP 245, and SSP 585 emissions scenarios were generated for both the 2041-2060 and 2081-2100 time periods, resulting in a total of 7 species distribution models including the base model generated with near-present (historical) climate conditions.

In the species distribution models (SDMs) a red hue was used to indicate habitat suitability. Areas with a darker red to near black hue indicate higher potential suitability (trending towards 100% habitat suitability), whereas areas with a lighter red to near white hue indicate a lower potential suitability (trending towards 0% habitat suitability). The current range of eastern hemlock is outlined in green. Additionally, occurrence points used for model training were highlighted in purple for the present conditions SDM. These points are for illustrative purposes only, and several occurrence points around the margins of the shapefile, specifically in southern Ontario and Michigan, were not visible.

RESULTS

Throughout the species distribution models MaxEnt's machine learning algorithm calculated an area under curve (AUC) value of 0.872. As seen in Table 3, when the relative contribution of a variable to the modeling processes was expressed as a percent, the most important climatic variable was Bio11, followed by Tn3, Bio6, Tn2, and Tn1. These variables had a percent contribution of 44.8, 21.1, 18.6, 11.1, and 4.4 respectively. When measured by permutation importance, the decrease in model score when the values of a variable are shuffled, Bio11 was once again the most significant variable with a permutation importance of 54. Tn2 had the second highest permutation score of 21.5, followed by Tn3 and Bio6 with scores of 14.8 and 9.8 respectively. Tn1 once again had the least significant model impact with a permutation score of 0.

Table 3. Percent contribution and permutation importance of climate variable used in the species distribution models.

Variable	Percent contribution	Permutation importance
Bio11	44.8	54.0
Tn3	21.1	14.8
Bio6	18.6	9.8
Tn2	11.1	21.5
Tn1	4.4	0

Note: Bio6, minimum temperature of the coldest month; Bio11, mean temperature of the coldest quarter; Tn1, average minimum temperature of January; Tn2, average minimum temperature of February; Tn3, average minimum temperature of March.

The near-present SDM closely resembled the current northern margins of HWA's range (Figure 8). This included at least marginal habitat suitability throughout southwestern Nova Scotia, as well as much of southeastern Ontario (especially the Niagara region), and a small area along the north shore of Lake Ontario. The SSP 126 emissions scenario resulted in a northern expansion in the suitable range of the HWA, as well as greater climatic suitability in the present extent of the infestation (Figures 9 and

10). From 2041-2060 the entirety of Michigan's lower peninsula, much of the upper peninsula, and most of eastern hemlock's range in Ontario became highly suitable for the HWA (Figure 9). This is with the exception of areas in the Algonquin highlands and the easternmost regions of southern Quebec, which retain only limited or marginal suitability for the HWA. From 2081-2100, however, almost the entirety of eastern hemlock's range displayed relatively high suitability for the HWA, with the most hostile northern areas for HWA population growth, far eastern New Brunswick and the western part of Michigan's upper peninsula, still indicating at least marginal suitability (Figure 10).

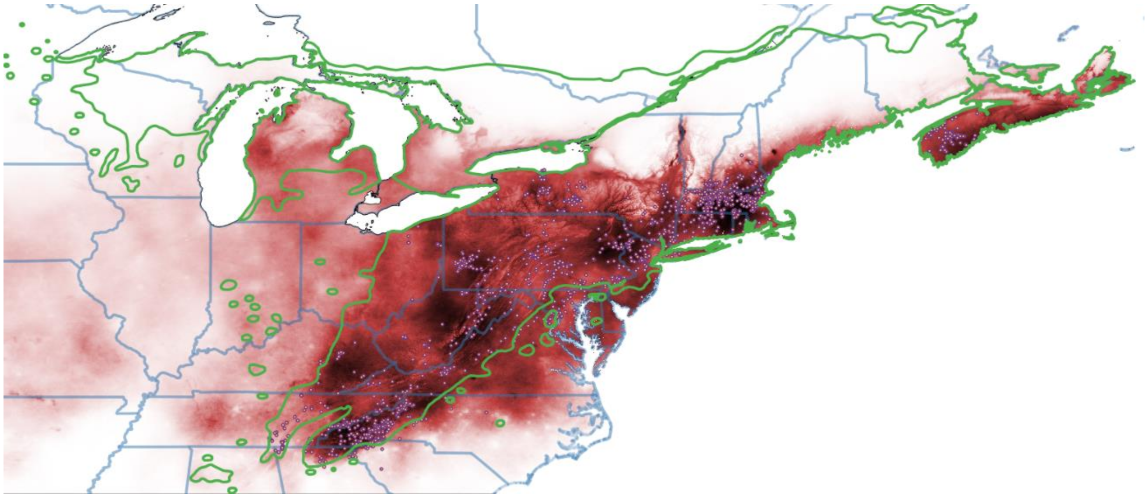

Figure 8. Species distribution map of the hemlock woolly adelgid based on historic (1970-2000) climate data. The range of eastern hemlock is outlined in green. Purple dots represent HWA occurrence points used for model training. Dark and light red colours indicate high and low habitat suitability for HWA respectively. White colouration indicates no predicted suitability for HWA.

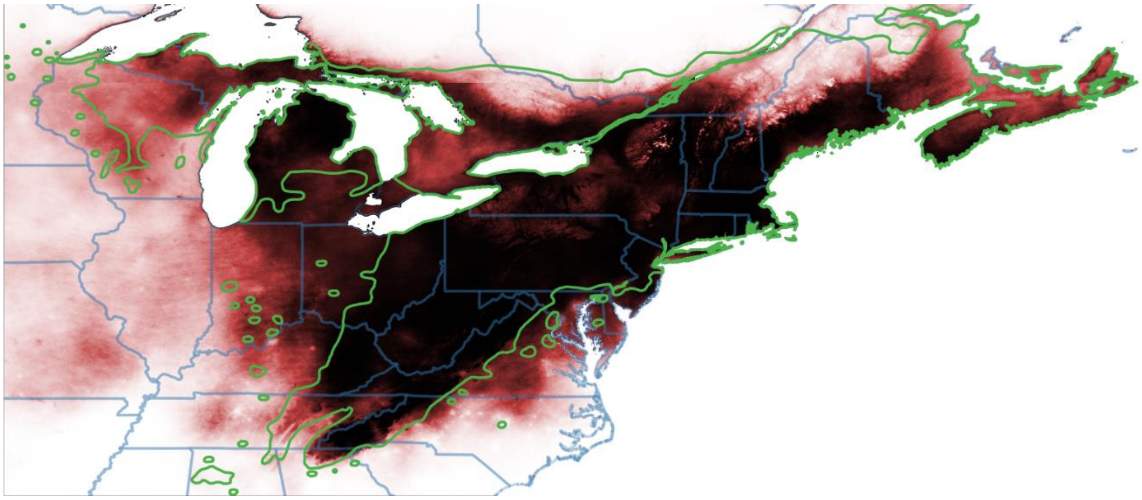

Figure 9. Future distribution map of the hemlock woolly adelgid in 2041-2060 based on downscaled climate data from the HadGEM3 SSP 126 scenario. The range of eastern hemlock is outlined in green. Dark and light red colours indicate high and low habitat suitability for HWA respectively. White colouration indicates no predicted suitability for HWA.

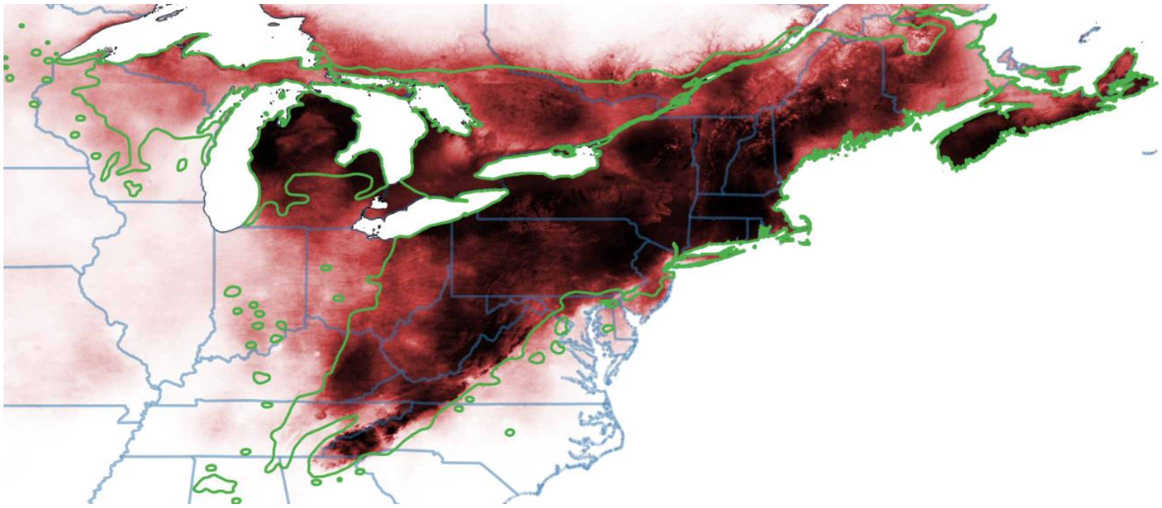

Figure 10. Future distribution map of the hemlock woolly adelgid in 2081-2100 based on downscaled climate data from the HadGEM3 SSP 126 emissions scenario. The range of eastern hemlock is outlined in green. Dark and light red colours indicate high and low habitat suitability for HWA respectively. White colouration indicates no predicted suitability for HWA.

Compared to the SSP 126 pathway, the higher radiative forcing SSP 245 emissions scenario SDMs resulted in an accelerated northwards shift in suitable habitat for the HWA (Figures 11 and 12). In the 2041-2060 timeframe, nearly the entirety of the eastern hemlock's range is predicted to be highly suitable for the HWA (Figure 11). This is once again with exceptions in the far west of Michigan's upper peninsula, and the extreme northeastern coast of New Brunswick, which still displayed moderate suitability. In the 2081-2100 time period, the SSP245 SDM predicted high suitability for the HWA extending far north of the current range of eastern hemlock (Figure 12). The model also predicted at least moderate habitat suitability extending well into northeastern Ontario and northwestern Quebec. However, in the southern extent of the HWA's present range, the predicted habitat suitability for the HWA was reduced. This is seen in the extreme south of the eastern hemlock's range, where the model predicts little to no suitability for the HWA despite its present existence in the region.

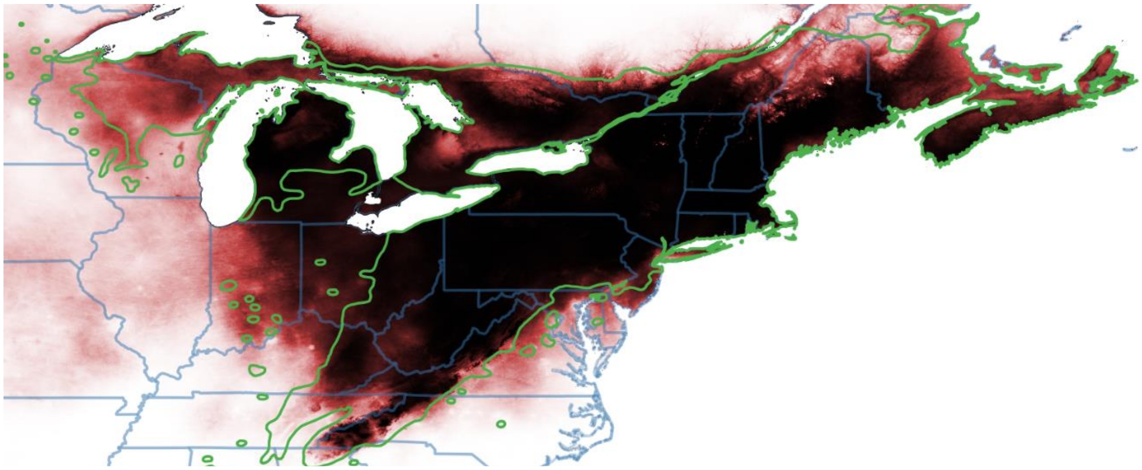

Figure 11. Future distribution map of the hemlock woolly adelgid in 2041-2060 based on downscaled climate data from the HadGEM3 SSP 245 emissions scenario. The range of eastern hemlock is outlined in green. Dark and light red colours indicate high and low habitat suitability for HWA respectively. White colouration indicates no predicted suitability for HWA.

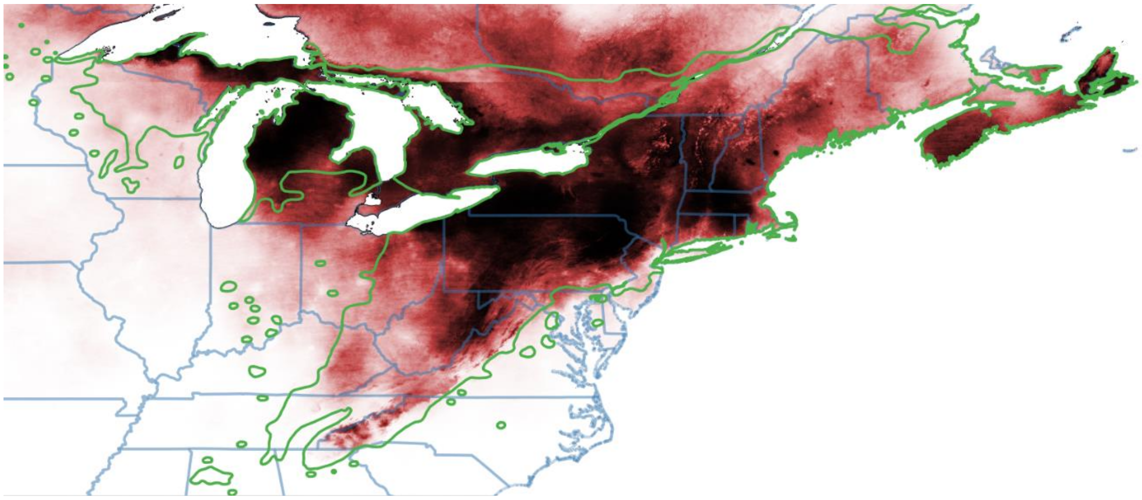

Figure 12. Future distribution map of the hemlock woolly adelgid in 2081-2100 based on downscaled climate data from the HadGEM3 SSP 245 emissions scenario. The range of eastern hemlock is outlined in green. Dark and light red colours indicate high and low habitat suitability for HWA respectively. White colouration indicates no predicted suitability for HWA.

SDMs generated from the highest radiative forcing SSP 585 emissions scenario predicted the largest northwards shift in the HWA's suitable habitat (Figures 13 and 14). In the 2041-2060 time period the model predicted high habitat suitability for the HWA extending northwards of the current northern limit of the eastern hemlocks range (Figure 13). Like in the SSP 245 end-of-century model, the habitat suitability of the far southern extent of the HWA's current infestation was significantly reduced. In the 2081-2100 end-of-century model, the SDM displayed extremely high HWA habitat suitability extending well beyond the current range of eastern hemlock (Figure 14). In contrast to the northern expansion of HWA, a large part of the HWA's current range throughout the continental United States was predicted to have low or very low habitat suitability (Figure 14).

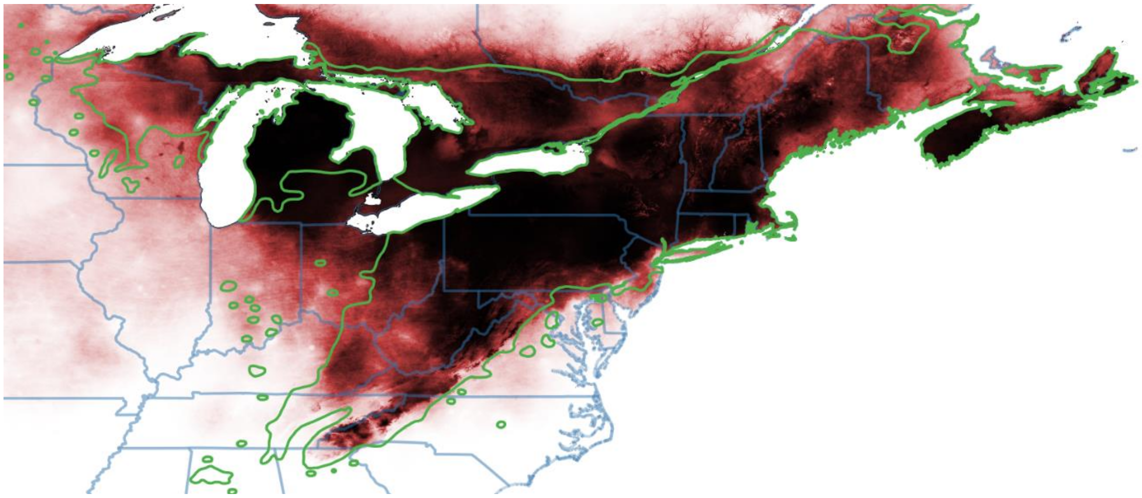

Figure 13. Future distribution map of the hemlock woolly adelgid in 2041-2060 based on downscaled climate data from the HadGEM3 SSP 585 emissions scenario. The range of eastern hemlock is outlined in green. Dark and light red colours indicate high and low habitat suitability for HWA respectively. White colouration indicates no predicted suitability for HWA.

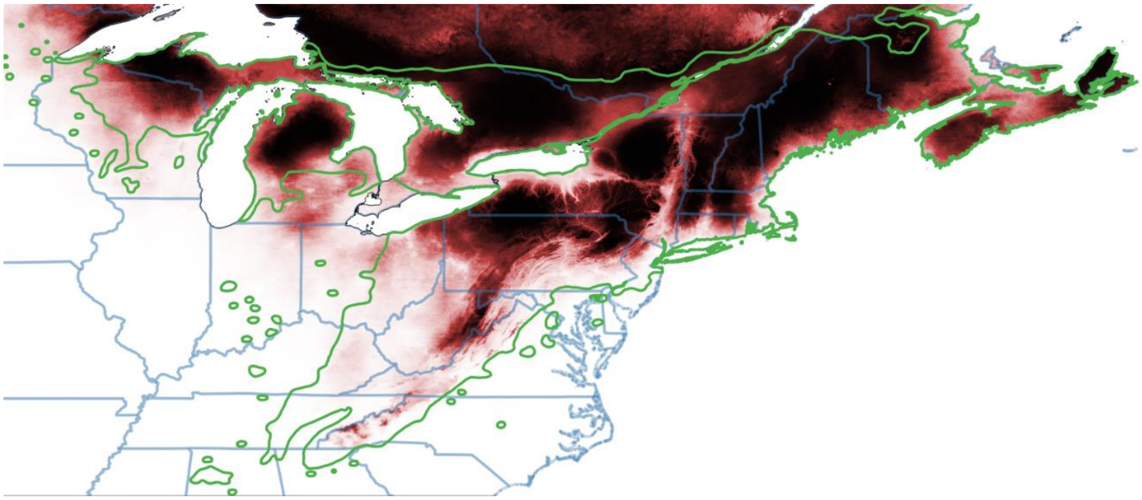

Figure 14. Future distribution map of the hemlock woolly adelgid in 2081-2100 based on downscaled climate data from the HadGEM3 SSP 585 emissions scenario. The range of eastern hemlock is outlined in green. Dark and light red colours indicate high and low habitat suitability for HWA respectively. White colouration indicates no predicted suitability for HWA.

DISCUSSION

The findings of this study indicate that under future climate change scenarios there will be a significant northwards shift in the range of the HWA. The SDMs showed that even under a low-emissions SSP 126 global warming scenario the majority of eastern hemlocks' current range could become highly suitable for HWA infestation by the middle of the century, with the entirety of eastern hemlocks current range placed at high risk of infestation by 2100. This trend was amplified in more extreme emissions scenarios, with the climatically suitable habitat of the HWA extending far north of the current distribution of eastern hemlock by the end of the century in the SSP 245 and 585 emissions scenarios.

This study also demonstrates that the mortality of eastern hemlock will be significantly increased throughout much of its range currently infested with the HWA. The findings of Paradis *et al*. (2008), Ford and Vose (2007), and McAvoy *et al.* (2017) indicated that as winter temperatures warm and habitat suitability for the HWA increases, the rate and extent of eastern hemlock infestations will most likely increase, and the duration of infestation until host mortality occurs will be reduced. These findings support the conclusions that warmer winter temperatures resulting from climate change will facilitate the northward migration of the HWA in eastern North America (Kantola *et al*. 2019).

The extent to which this will occur varies between publications, and is not always consistent with the findings of the models generated in this study. Paradis *et al*. (2008) concluded that by the end of the century under a high-emissions scenario the HWA could encompass almost the entirety of the northeastern U.S. This finding is supported by the SDMs in this study, which under a high-emissions end-of-century scenario predict high habitat suitability for the HWA throughout almost the entire extent of the eastern hemlock's native range. However, under a low-emissions scenario Paradis *et al.* (2008) concluded that some isolated areas of upper-state New York, Vermont, New Hampshire, and the northern half of Maine would likely remain unsuitable for HWA infestation. This is not supported by the current study, which indicated that even under a low-emissions SSP 126 warming scenario the suitable range of the HWA would extend throughout virtually the entirety of the northeastern United States by the end of the century. The difference in conclusions between these two studies may be the result of several factors. One such factor is that Paradis *et al.* (2008) did not utilize a SDM for their study, and instead identified an average winter temperature of negative five degrees Celsius as the threshold for HWA expansion. Subsequently, in conjunction with MaxEnt's machine learning algorithm, recent occurrence points along the northernmost margins of the HWA's range may explain the more pessimistic findings of this study. The climatic data utilized by Paradis *et al.* (2008) was also simulated with the IPCC's older Special Report on Emission Scenarios (SRES), which were originally published in the year 2000 (Nakicenovic and Swart 2000). Instead, this study utilized the IPCC's newer SSP scenarios generated for CMIP6 (O'Neill *et al*. 2016). This newer climate data may further account for the difference in conclusions between this study and Paradis *et al*. (2008).

A more accurate comparison to this study is likely that of Kantola *et al*. (2019), which also utilized MaxEnt to model shifts in HWA suitability under climate change. The findings of Kantola *et al*. (2019) were once again more optimistic than this study, although predicted a larger northwards range shift under a high-emissions end-of-century scenario than Paradis *et al*. (2008). Unlike the current study, Kantola *et al*. (2019) chose to utilize a wider range of environmental variables, including climate, topography, and soil characteristics. This may explain some of the difference in results, as this study constrained HWA dispersion based entirely on climatic variables correlated to minimum winter temperature. Kantola *et al*. (2019) also gathered occurrence data from several sources. Some GBIF and iNaturalist occurrence data was included, but the study gathered the majority of their research data via scientists and forest managers. This is unlike the current study, which accessed occurrence data entirely from the GBIF's iNaturalist dataset. The iNaturalist occurrence data utilized in this study is also more recent than that used by Kantola *et al.* in 2019, but the omission of other datasets in this study may have reduced the number of HWA occurrences in some key regions, including southern Michigan.

The use of citizen science data in invasive species modeling highlights many of the key benefits, but also limitations of these datasets. One of the most apparent advantages of these citizen science datasets is their ease of accessibility. While other occurrence datasets are frequently controlled by groups, organizations, or individuals, citizen science datasets are most often publicly available and subsequently efficient and affordable for researchers to access. Additionally, the ease of addition to citizen science databases such as iNaturalist also allows for these datasets to be continuously updated. This creates an up-to-date dataset that researchers can access without the need to continuously rely on fieldwork or other expensive data collection methods to collect relevant data. There are, however, some key limitations to citizen science data. One of which is the potential for mistakes in data collection, including the misidentification of species or incorrect recording of locations. Some citizen science datasets such as iNaturalist attempt to counteract this through its “research-grade” moniker, which are occurrences verified via image by at least one other user, and that have a minimum of 50% consensus on the species’ identification (Mugford 2021). Despite this, the potential for inaccuracies in data collection remains. Another significant drawback of utilizing citizen science data for species distribution modeling is the potential for selection bias amongst the data. Citizen science data is likely to result in unequal regional sampling, with accessible and frequently traveled areas being more intensely sampled than areas with remote or difficult terrain. The accuracy of species distribution models is negatively impacted by selection bias within data (Elith *et al*. 2010), and the accuracy of occurrence-only models (such as MaxEnt) are particularly sensitive to selection bias (Phillips *et al*. 2009). Corrections can be made during data cleaning, but the potential for decreased model accuracy is likely to persist.

The AUC value generated by MaxEnt’s machine learning algorithm is an indication of model quality (Lissovsky and Dudov 2021). An AUC value of 0.5 indicates that outputs are completely random, with values closer to one indicating higher model performance (Philips *et al.* 2006). The AUC value of 0.872 generated in this study indicates that the models showed relatively high performance, and did not suffer from overfitting. During the modeling process, the incorporation of a wider range of downscaled climate variables, including values of average annual precipitation and maximum monthly temperature, yielded significantly higher AUC values surpassing 0.9. However, there is limited literature to support the effect of these climate variables on

HWA habitat suitability (Chandler *et al*. 2022; Mech *et al.* 2017). As was previously referenced, SDMs assume that the population of a target species is limited only by climate and no other abiotic or biotic influences (Jeshchke and Strayer 2008). Without a sufficient body of literature to support the connection between HWA habitat suitability and monthly precipitation or maximum summer temperature, it is difficult to conclude if SDM predictions are the result of a positive correlation between habitat suitability and these variables, or another environmental variable or selection bias.

A larger sample set of occurrence data, specifically around the margins of the HWA's expanding range, would also likely help to improve the quality of future models. Additionally, the collection of presence-absence datasets would allow for alternative SDM approaches to be utilized in conjunction with MaxEnt modeling. This could be an effective means of eliminating some of the identified sources of error and further increasing model confidence.

The effect of climatic variables other than minimum winter temperatures on HWA survivorship should also be explored further. The SDMs in this study predict that under mid and high emissions scenarios by the end of the century habitat suitability in the southern extent of the HWA's current range will be significantly reduced. This is a result of the MaxEnt machine learning algorithm and does not necessarily indicate that by the end of the century there will be a northwards retraction in the suitable range of the HWA. However, research has begun to indicate a correlation between high summer temperatures and HWA mortality (Mech *et al*. 2018), potentially demonstrating a climate-change-driven decline in HWA survivorship in the current southern extent of its range. Another study by Chandler *et al.* (2022) identified that high autumn precipitation indirectly resulted in increased mortality of HWA due to elevated growth of fungal pathogens. Further studies of the relationship between high temperatures, precipitation, and HWA survivorship should be conducted to improve the understanding of the HWA’s overall climatic tolerances. Such information is vital for the effective management of the HWA, and the preservation of eastern hemlock.

CONCLUSION

Using iNaturalist citizen-science data from a GBIF occurrence database, MaxEnt species distribution modeling of the HWA under several future climate change scenarios revealed that the suitable habitat of the species is likely to shift significantly farther northwards over the coming century. This will subsequently put nearly the entirety of eastern hemlock's range at risk of infestation. Additionally, greater habitat suitability is likely to accelerate the spread and impact of the HWA on its range of hemlock hosts. Projects to collect presence-absence data along the northern fringes of the HWA's current range will expand the opportunity for concurrent modeling projects. Moreover, further study should be carried out into the relationship between HWA survivorship and climatic variables other than minimum winter temperatures, such as maximum summer temperature and precipitation. This would allow for further assessment of the potential long-term range extent and host impact of the HWA in eastern North America, including in the southern portions of its range. As the HWA infestation continues to expand over the coming century, further study must be done to give managers and policymakers the necessary tools to combat this invasive pest.

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