Canadian Science Publishing | Canadian Journal of Forest Research

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Journal:	*Canadian Journal of Forest Research*
Manuscript ID	cjfr-2023-0275.R2
Manuscript Type:	Research Article
Date Submitted by the Author:	12-Jul-2024
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Is the manuscript for consideration in a Special Issue or Collection?:	Not applicable (regular submission)
Keyword:	Adelges tsugae, Citizen Science Data, Eastern Hemlock, Species Distribution Modeling, MaxEnt

Modeling the distribution of hemlock woolly adelgid under several climate change scenarios

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Abstract

The hemlock woolly adelgid (HWA), *Adelges tsugae* Annand, has invaded eastern North America and caused significant mortality to eastern hemlock, *Tsuga canadensis* (L.) Carrière. In eastern North America, HWA's range is theorized to be limited by minimum winter temperatures. As climate change reduces the severity of winter, the risk of northward expansion of HWA increases. This study used maximum entropy species distribution modeling in conjunction with HWA occurrence records and future climate projections to model habitat suitability for HWA throughout the range of eastern hemlock. Species distribution models were created for present and future climatic conditions using both historical climatic data and future climatic emissions scenarios for mid- and late-century. In addition, present climatic condition reference models for western North America and Asia were generated for comparison with HWA's current range and earlier predictions of the potential range in eastern North America. Under a low emissions scenario, HWA will be capable of invading almost the entire range of eastern hemlock by the end of the century. More extreme warming scenarios result in a more rapid northwards shift by mid-century. The consequences for eastern hemlock are significant, with 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

Introduction

Adelges tsugae Annand, the hemlock woolly adelgid (HWA), is an invasive insect first discovered in eastern North America in the early 1950s, and is believed to originate from southern Japan (Havill *et al.* 2016b). In eastern North America, HWA feeds on both eastern hemlock (*Tsuga canadensis* (L.) Carrière), which is distributed widely throughout the eastern temperate forests, and Carolina hemlock (*Tsuga caroliniana* Engelmann), which is isolated in the southern Appalachian Mountains. A separate native lineage of HWA exists in western North America, where a combination of host resistance and natural predators restrict populations to largely non-damaging levels (Havill *et al.* 2011). 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 (Radville et al. 2011). Therefore, hemlocks infested with the HWA subsequently suffer from decline and mortality four to ten years after initial infestation (Orwig *et al.* 2002), although extreme southern infestations may succumb more rapidly (Ford *et al.* 2011). 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). In addition to its significant ecological value as a source of both food and cover for dozens of species of birds and mammals (Ward *et al*. 2004), as well as its role as an important driver of winter transpiration in southern hardwood forests (Ford and Vose 2007), the eastern hemlock is a popular ornamental and landscape tree.

Hemlock woolly adelgid has spread throughout approximately half the range of eastern hemlock (USDA and Purdue 2022), extending from the Appalachian Mountains in the south northwards along the US east coast to southern Nova Scotia, where it was identified as established in 2017 (CFIA 2023). 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 hemlocks had remained uninfested 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 -30 ℃ to -35 ℃ have been identified as an absolute threshold for HWA establishment, resulting in near-complete or total mortality (Costa *et al.* 2005). Laboratory studies of HWA cold tolerance found that less than 3 percent of HWA sourced from USDA growing zones 5a through 6b survived under January and February temperatures lower than -30 ℃ to -35 ℃ (Skinner *et al*. 2003). A greater cold tolerance exhibited by HWA taken from colder growing zones, however, may indicate adaptation in HWA towards increased cold tolerance (Butin *et al*. 2003; Skinner *et al.* 2003), although the variation in cold tolerance may be the result of selection for cold-tolerant individuals from amongst the existing population; rather than selection-driven changes to the genetic structure of the population (Lombardo and Elkinton, 2017). The timing of cold-weather events and seasonality also influences HWA mortality. March temperatures as warm as -15 ℃ resulted in greater than 85% mortality of northern HWA populations (Skinner *et al*. 2003). Later, Elkinton *et al.* (2017) hypothesized that extreme cold weather events preceded by extended stretches of warm weather cause higher mortality than events that are preceded by extended low winter temperatures. This hypothesis was supported by the finding that HWA has yearly and seasonal variation in their supercooling points (Elkinton *et al.* 2017).

The hemlock distribution in the province of Ontario currently lies primarily to the north and west of the core invaded range of HWA. The province has been subject to HWA invasion and, as of 2023, hosts a number of known, small populations. The first two HWA infestations in Ontario were detected in Etobicoke in 2012 and the Niagara Gorge in 2013, both of which were eradicated (Fidgen *et al.* 2014). Several subsequent infestations have been detected in Ontario since 2019, most of which have been located in the Niagara region around the towns of Niagara Falls (2019), Wainfleet (2019), and Pelham (2022) but extending as far north as Hamilton's Royal Botanical Gardens and west to Haldimand County (2023); and in 2022 an infestation was recorded north of Lake Ontario near the community of Grafton (CFIA 2023). The current distribution of infestations in the province is consistent with the predictions from McAvoy *et al.* (2017); that is, suitable climate for HWA exists throughout Ontario's Niagara region and along the western and northern shoreline of Lake Ontario.

Our goal is to predict the future suitable range of HWA in eastern North America under several climate change scenarios through a lens of minimum winter temperatures as the key determining factor in habitat suitability. To do this, we chose climatic variables related to minimum winter temperature to evaluate the hypothesis that cold temperatures are a significant determining factor in HWA habitat suitability (Paradis *et al.* 2008; Cheah 2017; McAvoy *et al*. 2017; Ellison *et al*. 2018) and employed Maximum Entropy (MaxEnt) species distribution modeling based on observations of HWA occurrences for eastern North America, where it is an invasive pest, and western North America and Asia, where HWA is native. These species distribution models utilized historic climate data to map HWA's present climatically suitable habitat in all three regions. The species distribution models were then used to map middle and end-of-century habitat predictions under low, mid, and high-emission climate change scenarios for HWA in eastern North America. Our models show that under even low emission climate change scenarios there is high predicted HWA habitat suitability throughout almost the entirety of eastern hemlock's range by the end of the century. Under mid and high emission climate scenarios this trend was accelerated, with our models predicting high HWA habitat suitability throughout the present range of eastern hemlock by the middle of the century. These species distribution models provide a tool for forest managers and landowners to identify the risk posed to hemlock resources by HWA infestation, and prepare for the resulting impacts on economic and ecological objectives.

Methods

Data

Hemlock woolly adelgid occurrence records were assembled from a number of sources. The primary occurrence dataset utilized for eastern North America were records from iNaturalist (www.iNaturalist.org) obtained from the Global Biodiversity Information Facility (GBIF). This archive dataset included the date and geographic coordinates (latitude, longitude) for each observation of HWA as of June 2023. To better represent the current extreme margins of HWA's range, we supplemented the GBIF iNaturalist dataset with additional occurrence points from the iMapInvasives project (https://ibol.org), which was also accessed via the GBIF, and US county-level occurrence data obtained from the USDA and Purdue University's Alien Forest Pest Explorer (USDA and Purdue 2022). We converted the county-level data to geographic point data

by selecting the approximate centers of all counties in which HWA was detected and using those coordinates as the location of the species in that county. We then assembled a second dataset for the native range of HWA for both western North America and Asia. Data for the western United States was accessed via the GBIF's iNaturalist and International Barcode of Life (iBOL) databases, as well as from Havill *et al.* (2016a). An additional occurrence dataset for British Columbia was obtained from the Canadian Forest Insect and Disease Survey (FIDS) records held within the Forest Invasive Alien Species Document library (NRCan 2023). These FIDS records are observations of insects or damage reported as part of annual forest health surveys done in Canadian forests by the Canadian Forest Service (CFS) from 1936-1994, and additional records from earlier surveys conducted by the Canadian government prior to 1936. (see Van Sickle et al 2001). Data for Asia was also accessed from Havill *et al.* (2016a) and the GBIF's iBOL dataset. The number of occurrences within each dataset varied (Table 1).

For our subsequent modelling we restricted the native and invasive HWA occurrence datasets to include only records from within the approximate range of relevant hemlock host species for each region. We also removed extreme outlying points and those with poor spatial resolution. This included removing points which were located over the oceans, Great Lakes, and other bodies of water. Occurrence points from the iNaturalist database located along the range-edge of HWA infestation were also independently verified using the accompanying images on the iNaturalist website to ensure their accuracy. Finally, we reduced the HWA occurrence datasets to avoid selection bias for use in MaxEnt by removing points that were closer than 1 km to each other. This resolution was chosen based on the 30-second resolution of the climate data, which represents approximately 1 km at the equator.

We obtained historic and projected climate data from the WorldClim database (WorldClim 2022a, 2022b). Climate data from the WorldClim database is delineated into separate bioclimatic variables which are attained from monthly temperature and precipitation values (WorldClim 2022a). We used a literature-based approach to climatic variable selection based on studies that linked minimum winter temperatures to HWA mortality and range limits (Parker *et al*. 1999; Skinner *et al*. 2003; Paradis *et al*. 2008; Cheah 2017; McAvoy *et al*. 2017; Kantola *et al*. 2019). We selected five climatic variables to model the relationship between winter temperature and HWA habitat suitability: monthly average minimum temperature of January (Tm1), February

(Tm2), and March (Tm3), the minimum temperature of the coldest month (Bio6) and the mean temperature of the coldest quarter (Bio11). Climate data for a historical period of 1970 to 2000 was accessed from WorldClim version 2.1 (Fick and Hijmans, 2017). Downscaled future climate projections from the Met Office Hadley Center HadGEM3-GC31-LL (2016) global climatic model (Ridley *et al*. 2019), a component of IPCC's CMIP6 (O'Neil *et a*l. 2016), were utilized.

For this study, 2041 to 2060 and 2081 to 2100 time periods were selected to represent mid-century and late-century climatic effects. These time ranges were used in conjunction with datasets derived from Shared Socioeconomic Pathway (SSP) 126, 245, and 585 emissions scenarios. These scenarios consider possible social and economic pathways that may lead to varying levels of radiative forcing by the year 2100 (O'Neil *et al*. 2017), which is the change in the Earth's radiative energy budget measured in W/m^2. These pathways were chosen to represent a wide range of potential future emissions, presenting minimal, moderate, and severe global warming scenarios: SSP 126 represents a low-emissions scenario, in which total global greenhouse gas emissions are reduced through a global focus on sustainability, and there is 2.6 W/m^2 of radiative forcing in 2100; SSP 245 represents a mid-emissions scenario, in which total global greenhouse gas emissions largely follow present trends, resulting in 4.5 W/m^2 of radiative forcing in 2100; SSP 585 represents a high-emissions scenario, in which global industrialization results in an increase in fossil fuel use and 8.5 W/m^2 of radiative forcing in 2100 (O'Neil *et al.* 2017). Subsequently, the SSP585 scenario represents a more than three-fold greater level of radiative forcing by 2100 compared to the SSP126 scenario.

Data analysis

To create suitable habitat maps for HWA infestation, we generated species distribution models (SDM) for HWA using MaxEnt version 3.4.4 (Phillips *et al.* 2022). MaxEnt's integrated analysis suite was also used to generate the model's performance statistics, variable permutation importance, and perform jackknife analysis of variable contribution for each of the models. We first generated a reference SDM for eastern North America using historic (near present) climatic conditions which were then tested for model performance, variable effectiveness, variable contribution, and overfitting. We used the area under the receiver operating characteristic curve (AUC) as the primary indicator of model performance. An AUC value of close to 0.5 indicates that modeling is completely random, with values closer to 1 indicating improved model fitting

(Phillips *et al.* 2006). Given the geographic scale and complexity of the occurrence datasets utilized in this study, a standard regularization multiplier of '1.0' was selected to reduce overfitting while limiting AUC loss, which was observed with over regularization of the model (Dudík *et al*. 2004). An AUC of 0.8 was selected as the minimum target for model performance (Swets 1988), and so all models with an AUC > 0.8 were considered as accurate and included in our results.

We used permutation importance to test for variable contribution. Permutation importance is measured as the decrease in AUC when the values of a variable are shuffled, and variables with higher permutation importance contribute more to the prediction of habitat suitability. However, as all of the pre-selected variables are highly related to one another, the omission (or low performance) of one variable does not necessarily indicate that it is not relevant to habitat suitability. Jackknife analyses display the change in regularized training gain of the model (the improvement or degradation of model performance adjusted for the regularization multiplier) when the model training is performed with an individual variable, the remaining variables, or with all variables together (Phillips 2017). These analyses were subsequently run to ensure that each variable was not excessively correlated, as over-correlation of climatic variables can result in model distortion (Lissovsky and Dudov 2021). The percent contribution of each variable, a measure of model gain as each variable is introduced, was also generated by MaxEnt. Unlike permutation importance, this value is a heuristic and can vary depending on the algorithm employed during the machine learning process (Phillips 2017). The percent contribution is also susceptible to influence by correlated values and was subsequently only included as additional reference for the more robust permutation importance values.

Once we determined a present climatic condition model for eastern North America, we generated additional reference models for western North America and Asia. Our goals in developing the present-condition reference models were to demonstrate the accuracy of our future-condition eastern North American models through comparison to the known extent of HWA and its hosts, and to compare to other relevant modeling studies. Subsequently, these present condition reference models were compared to the current recorded range of HWA. Specific attention was given to the range-edge occurrences of HWA, which should correlate with the margins of predicted habitat suitability. The western North American model was important in this regard, as

the long-term infestation of the region should theoretically allow HWA to approach the limits of its possible climatic niche. A correlation between predicted habitat suitability and realized HWA occurrences indicates that the models are accurate and do not suffer from over or under fitting. The eastern North American model was subsequently applied to the downscaled future climate change predictions in MaxEnt to generate future climate change models using the same methods of model analysis.

Results

Our present climatic condition eastern North American SDM suggests a potential HWA distribution that exceeds the current northern margins of HWA's range (Figure 1). This model indicates there is moderate climatic suitability for HWA throughout central and eastern Nova Scotia, Southwestern Ontario (including the Bruce Peninsula, which extends northwards into Lake Huron), and much of the eastern shoreline of Michigan's Lower Peninsula. Our western North American SDM displayed a similar fit to HWA's known range in the region, with high habitat suitability along the Pacific coast, declining eastward with the more continental climates (Figure 2). This is a strong indicator of good model fit and increases confidence for the present and future models of eastern North America, where the climatic limits of HWA's range may not be fully realized. The Asian SDM displayed high suitability throughout the HWA's native range in Japan (Figure 3). Likewise, habitat suitability was expectedly high throughout the mountainous regions of the Himalayas, mainland China, Taiwan, and South Korea. The extent to which this represents HWA's actual range in the region is hampered by a lack of available literature on HWA's exact extent in mainland Asia, as well as the limited dataset used in this study (Table 1).

All the models exhibited AUC values above the target performance of 0.8 and identified one or more variables with a significant impact on model performance (Table 2). Jackknife analysis of each of the 'present condition' models also displayed that each variable contributed to an increase in regularized training gain when run in isolation (Figure 4). All variables were subsequently shown to contribute to model fit. Additionally, no single variable resulted in an exceptional increased in regularized training gain, indicating that the models did not suffer from variable over correlation. The variable with the largest contribution, when measured by permutation importance, differed among models (Table 2). The eastern North American model

was most affected by the random shuffling of the variable representing the mean temperature of the coldest quarter (Bio11) but was least affected by the average minimum temperature in January (Tm1). The model of western North America was instead most affected by the variable for average minimum temperature in February (Tm2) and was not affected by the average minimum temperature of either January or March (Tm1 and Tm3). It is of note that when measured by percent contribution the minimum temperature of the coldest month (Bio6) was the most important variable. This was contrary to permutation importance value, and was also not supported by the Jackknife analysis, which, except for the minimum temperature of the coldest quarter (Bio11), displayed a relatively even regularized training gain when each variable was run in isolation (Figure 4B). Lastly, the Asian model was most affected when the variable for minimum temperature of the coldest month (Bio6) was randomly shuffled and was not affected by the average minimum temperature of February (Tm2) (Table 2).

When we applied the low emissions scenario (SSP 126) to our present condition SDM, it resulted in a northern expansion in the suitable range of the HWA. This likely occurred because of greater climatic suitability throughout eastern hemlock's range. From 2041-2060 all of Michigan's lower peninsula, much of the upper peninsula, and most of eastern hemlock's range in Ontario is predicted to become highly suitable for the HWA (Figure 5A). The only areas not predicted to be suitable are in the Algonquin highlands of Ontario and the easternmost regions of southern Quebec. These areas maintained their limited or marginal suitability for the HWA. From 2081-2100, however, almost the entirety of eastern hemlock's range shows relatively high suitability for the HWA, with the most climatically hostile northern areas for HWA population growth, northwestern New Brunswick, the northern reaches of the Appalachian Mountains, and northern Wisconsin, still indicating at least marginal suitability (Figure 5D).

The SDMs generated with the mid-emissions scenario (SSP 245) resulted in an accelerated northwards shift in suitable habitat for the HWA. Under this scenario in the 2041-2060 timeframe, nearly the entirety of the eastern hemlock's range is predicted to be highly suitable for the HWA (Figure 5B). This is once again with exceptions in the northern reaches of the Appalachian Mountains including the extreme northwestern region of New Brunswick and northern Wisconsin, which still displayed moderate suitability. In the 2081-2100 period the mid-emissions scenario predicted high suitability for the HWA extending far north of the current

range of eastern hemlock (Figure 5E). The model also predicted at least moderate habitat suitability extending well into northeastern Ontario and northwestern Quebec. However, the predicted habitat suitability for the HWA was reduced in the southern extent of the HWA's present range. In the extreme south of the eastern hemlock's range, the model predicts a contraction in the southern range of HWA, with little to no suitability in the region.

Species distribution models generated from the high-emissions scenario (SSP 585) predicted the largest northwards shift of the HWA's suitable habitat. In the 2041-2060 timeframe the model predicted high habitat suitability for the HWA extending northwards of the current range of the eastern hemlocks (Figure 5C). This SDM also displayed that habitat suitability in the far southern extent of the HWA's current infestation was significantly reduced. In the 2081-2100 period, our high emissions scenario SDM predicted high HWA habitat suitability extending well beyond the current northern range limit of eastern hemlock, highlighting extreme habitat suitability in northeastern Ontario and northwestern Quebec as well as northeastern Wisconsin, northern Michigan, and majority of northeastern United States (Figure 5F). However, a large component of HWA's current range throughout the continental United States was predicted to have low or very low habitat suitability.

Discussion

We showed that climate change will likely allow for a significant northward shift in the range of HWA. The species distribution models illustrated that even under a low-emissions global warming scenario most of eastern hemlock's current range could become highly suitable for HWA infestation by the middle of the century, with the entirety of eastern hemlock's 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 mid- and high-emissions scenarios. However, the ideal climatic range of eastern hemlock is also predicted to shift north under several global warming scenarios (NRCan 2022) though the northward migration of species is limited by other factors, such as soil characteristics, interspecific competition, and barriers to seed dispersal (Van Der Veken *et al.* 2007; Carterton *et al.* 2020). Therefore, any potential changes in the range of eastern hemlock are difficult to accurately predict but will likely occur at a far more gradual rate than HWA dispersion.

In addition to allowing for the more northward expansion of HWA, warmer winter temperatures resulting from climate change will likely have significant consequences for how HWA interacts with host trees. As is demonstrated in the southern Appalachian Mountains, warmer and drier temperatures result in more rapid mortality of infested hemlocks through reduced host vigour, increased HWA survivorship, and accelerated HWA fecundity (Ford *et al*. 2011; Krapfl *et al.* 2011; Paradis *et al*. 2008). This indicates that climate change may drive an increase in hemlock mortality through the extent of the current invasion as conditions become increasingly favourable for HWA survivorship and feeding behaviour.

Our results support the hypothesis that warming winter temperatures will facilitate the northward movement of HWA in eastern North America (McAvoy *et al*. 2017, Ellison *et al.* 2018, Kantola *et al.* 2019). However, the predicted extant and rate at which this northward migration of HWA will occur varies among those studies and is not always consistent with the findings of our models. Paradis *et al*. (2008) concluded that by the end of the century under a high-emissions scenario, the HWA could encompass almost all 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 our models, which indicated that even under a low-emissions 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. Paradis *et al.* (2008) did not use an SDM for their study, but instead used the average winter temperature of -5 ℃ as the threshold for HWA expansion which appears to have underestimated the potential range. Over the past 15 years the range of HWA has expanded beyond the range predicted by Paradis *et al*. (2008) and beyond the -5 ℃ isotherm. This expanded range, which we included in the modeling efforts of our study, may explain the more pessimistic findings of Paradis *et al.* (2008). Paradis *et al.* (2008) also based their predictions on the older emissions scenario (Nakicenovic and Swart 2000), compared to those used in our study (i.e., CMIP6, O'Neil *et al*. 2016) which could also account for some of the differences we observed. Ellison *et al.* (2018) also developed range predictions under climate

change using a model from Fitzpatrick *et al.* (2012) and overwintering temperature predictions with similar results to both ours and Paradis *et al.* (2008). Those models made somewhat reasonable predictions for the spread of HWA into southern Ontario but failed to predict expansion into Nova Scotia.

More recently, Kantola *et al*. (2019) also used a MaxEnt approach to model shifts in HWA suitability under climate change. Their findings were also more optimistic than our study, although they predicted a greater northwards range shift under a high-emissions end-of-century scenario than Paradis *et al*. (2008). Kantola *et al*. (2019) used more environmental variables in their models than we did, including climate, topography, and soil characteristics. As well they used a modeling-based approach to variable selection in which the best-performing variables were selected from a far larger initial pool. We used a hypothesis-based approach to variable selection. Modeling-based approaches to variable selection are statistically robust and allow for the optimization of model performance as a function of AUC. Modeling-based approaches also support the mitigation of common modeling shortcomings such as overfitting and distortion due to correlated variables (Lissovsky and Dudov 2021). There is, however, the possibility of negating key climatic factors in model creation. For example, Orwig *et al*. (2002) found only weak effects of stand topography on HWA infestation in Connecticut and concluded that latitude, as a function of climate, was the most important factor in determining the severity and rate of HWA infestation in hemlock stands across the state. Kantola *et al*. (2019) did not incorporate variables related to minimum winter temperature in their models and instead identified slope as a key variable. This is not to say that modeling-based approaches of variable selection are inaccurate for predicting species distributions, but it does not facilitate the testing of hypotheses related to specific relevant variables that have been identified by other means.

Despite differences in our variable-selection processes, both ours and Kantola *et al*.'s (2019) models displayed similar trends for HWA habitat suitability in western North America. Both studies predict high habitat suitability for HWA along the Pacific coast of western North America. We, however, incorporated more data on the range of HWA in British Columbia than Kantola *et al*. (2019) by including historical observations from the province. We argue that this provides a more accurate depiction of the northern and eastern extent of HWA's range in western North America. One consequence of this additional data is that we predict a higher habitat

suitability along the northern coast of British Columbia, extending to Moresby Island, as well as marginally higher habitat suitability in the northern Rocky Mountains (Figure 2). This indicates that although climate is already likely a limiting factor for HWA in the interior regions of western North America, the HWA may exhibit higher cold tolerance in the Canadian Rocky Mountains than previously believed.

Unlike western North America, our model of the current HWA habitat suitability in Asia differed from that of Kantola *et al.* (2019). Both studies predicted high HWA suitability in the Himalayan mountains and throughout southern and central Japan. However, we predicted high HWA suitability throughout the northern Hokkaido region of Japan where Kantola e*t al.* (2019) did not. We also predicted little to no habitat suitability for HWA throughout the lowland areas of Taiwan, the south of mainland China, the northern interior of the Korean peninsula, or any of Myanmar. Kantola *et al.* (2019), however, predicted that these regions are suitable habitat for HWA. We attribute some of these differences to our literature-based approach to variable selection, which prioritized minimum winter temperatures, and generally predicted a more northwards distribution of HWA than the multi-variable approach utilized by Kantola *et al*. (2019).

Our models predict that by the end of the century, under mid and high emissions scenarios, habitat suitability in the southern extent of the HWA's current range in eastern North America will be significantly reduced. There is a correlation between high summer temperatures and HWA mortality (Sussky and Elkinton 2015; Mech *et al*. 2018), which suggests the potential for a climate-change-driven decline in HWA survivorship in the south of its eastern North American range. Chandler *et al.* (2022) also identified that high autumn precipitation indirectly resulted in increased mortality of HWA due to elevated growth of fungal pathogens. These observations of heat- and precipitation-caused mortality suggest that the effect of climatic variables other than minimum winter temperatures on HWA survivorship should be further explored to improve the understanding of the HWA's overall climatic tolerances.

An additional consideration when modeling future HWA fecundity is the potential for a climate change induced increase in the frequency of stochastic weather events, notably extreme winter weather. Several studies have proposed a link between warming arctic temperatures and extreme winter cold events in the temperate mid-latitudes of the northern hemisphere (Overland *et al.*

2011; Cohen *et al*. 2013; Cohen *et al*. 2018). This is highly relevant for HWA survivorship as extreme stochastic cold events (cold waves) and significant reductions in winter temperature preceded by extended stretches of mild weather can cause significant HWA mortality (Elkinton *et al.* 2017; Tobin *et al*. 2017). This has led to the hypothesis that climate change-driven stochastic cold weather events may limit HWA expansion in eastern North America despite a general warming trend under climate change (Mayfield *et al.* 2023). This hypothesis is not well supported, though, by observations in the northern range of the insect. An infestation of HWA on the north shore of Lake Ontario was able to recover from near complete mortality following an extreme weather event in early February of 2023 which saw temperatures dip to -26.7 ^{o}C, and populations in Nova Scotia were not substantially impacted by the same event even though temperatures reached record lows (MacQuarrie et al 2024). Populations of the insect also exist in northern lower Michigan along the Lake Michigan coastline and in the interior of the state. The survival and persistence of these populations are likely a result of HWA's high fecundity and parthenogenic reproduction, which allows recovery of populations from a single surviving crawler (Tobin *et al.* 2013). Cold wave events also can vary in their timing, location, intensity and persistence resulting in wide variation in survival over a given area (MacQuarrie *et al*. 2019, MacQuarrie *et al.* 2024). Given the proximity of these infestations to the limit of HWA's predicted range in our present climatic-condition model of eastern North America, such extreme weather events may be adequately captured by the algorithm's existing climatic parameters. However, the exact influence of these stochastic extreme weather events on HWA's theoretical climatic envelope in eastern North America is a notable area for further investigation.

Despite its undeniable usefulness in modeling the distribution of species without the need for costly fieldwork, the use of citizen science data in this study highlights some key considerations that must be made when working with these kinds of datasets. This includes the potential mistakes in data collection, including the misidentification of species or incorrect recording of locations. Data-gathering initiatives that rely on unconfirmed reports may attempt to counteract this through having reports verified by at least one other user. For instance, iNaturalist records that have a minimum of two-thirds consensus on species' identification from at least two other users are assigned a "research-grade" rating (GBIF 2023c). However, in our study, we still detected some erroneous reports of HWA with research-grade ratings and therefore manually verified occurrence points at the margins of HWA's eastern range using accompanying images to

account for this. Records with incorrect identifications or unverifiable images had to be removed in what was a long and relatively inefficient process. Our finding of incorrect observations at the edge of HWA's invaded range suggests the existence of other incorrect records in the dataset, although the effect of these records in the core of the invaded HWA distribution on the accuracy of our models is less significant.

Citizen science data is likely to result in unequal regional sampling. Accessible and frequently traveled areas are more intensely sampled than areas with remote or difficult terrain, resulting in the potential for selection bias within the data. The accuracy of species distribution models is negatively impacted by selection bias (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 therefore need to be implemented during data cleaning, such as the removal of aggregated points to match the scale of climate data. However, the potential for decreased model accuracy is likely to persist.

Another key consideration is the limited number of observations of HWA in western North America and Asia (Table 1). Limited datasets have been identified as an antagonistic factor in SDM performance, and limited occurrence data cause a reduction in model fit due to the statistical overfitting of limited training points (Hernandez *et al*. 2006). The regularization process incorporated into MaxEnt, however, counteracts this overfitting making it well-suited to developing SDM with small datasets (Phillips et al. 2006) with perhaps as few as five individuals (Hernandez *et al.* 2006). Despite these considerations, the potential bias resulting from the limited occurrence data must be recognized. A larger sample set of occurrence data, specifically around the margins of the HWA's expanding range in eastern North America, as well as in regions with a harsher continental climate such as the interior of western North America and continental East Asia, would therefore 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. Providing a more effective means of eliminating some of the identified potential sources of error in this study, and further increasing model confidence.

In climate-based SDMs, a discrepancy can arise between the observed and predicted population range. Species distribution models create a probability distribution based on the fundamental

climatic niche, whereas the realized niche of a species is constrained by other factors such as predation, competition, host availability, and geographic barriers (Montgomery *et al*. 2023; Wang *et al.* 2010). In environments to which the subject species is native, notably HWA in western North America and Asia, factors such as host-pest coevolution and the abundance of natural predators can also significantly influence the realized distribution (Havill *et al.* 2011). Invasive species can also exhibit disequilibrium with the invaded environment, having not yet occupied their entire available niche due to dispersal limitations (Uden *et al.* 2015). Species distribution models for invasive species should be interpreted as a hypothesis about the probability of habitat suitability, rather than as maps of the realized invasion. Instead, literature and field observations must be used to test the hypothesis of the SDM to predict the overall invasion risk.

Climate change introduces the potential for both invasive and native pests to expand their ranges beyond current climatic barriers. This allows these species to capitalize on climatically stressed host trees, and multiply more rapidly due to increased fecundity and advances in phenology (Jactel *et al.* 2019). The impacts of such significant climate-driven changes to the dynamics of forest pests are likely to have significant implications for the integrity of North America's forests (Ramsfield *et al*. 2016). For example, in western Canada this phenomenon was observed in the expansion of native mountain mine beetle (MPB), *Dendroctonus ponderosae* Hopkins, east of the Rocky Mountains (Carroll *et al*. 2003). Cold-weather-induced mortality was partly responsible for the collapse of MPB outbreaks in the mid-1980s (Sambaraju *et al*. 2012) but the increasing scarcity of winter temperatures low enough to cause significant MPB mortality is allowing for longer and more extensive outbreaks (Creeden *et al*. 2014) as are climate induced changes in phenology resulting in more rapid population growth (Logan and Powell 2001). Similar effects have been observed in other pests, and more frequent and widespread pest outbreaks will have diverse impacts on the composition and structure of forests and also influence carbon sequestration, endangered species, wildlife habitat, and timber production (Weed et al. 2013; Finch et al. 2021). Our results suggest that the application of SDMs in decision making by forest managers and policy-makers could be valuable for efficient invasive species management (Guisan *et al*. 2013). Understanding the potential geographic extent of biological invasion along with its projected timeframes enables resource managers to allocate resources effectively for preventing, mitigating, and adapting to the impacts of invasive species.

Conclusion

We found that HWA's suitable habitat 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. Further study should be carried out into the relationship between HWA survivorship and diverse 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.

Acknowledgments

We recognize the contributions of Vianney Janice Cupiche, Jian Wang, and Tomislav Sapic for their support in the preparation of the study. We also thank the GBIF, NRCan, USDA, Nathan Havill, and Purdue University, which made data publicly available for use in our study.

Competing interests statement

Competing interests: The authors declare there are no competing interests.

Author contribution statement

CC: Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Project Administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing.

CJKM: Data curation, Supervision, Writing – review & editing.

SL: Conceptualization, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Funding statement

CC was supported by University of Toronto and Lakehead University

Data availability statement

Data were obtained from publicly-available sources. Citations to these data sets are given in the Methods section.

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773

774 **Table captions**

775 **Table 1.** The number of hemlock woolly adelgid occurrences observations in each regional
776 dataset, and the total number of records used in model training, which includes simulated
777 background (absence) points.

778 **Table 2.** Summary statistics of contributions of climatic variables for present climatic condition
779 models predicting the species distribution of hemlock woolly adelgid in North America and Asia.
780 Area under the receiver operating characteristic curve (AUC) indicates the randomness of a
781 model, values closer to 1 indicate increased model performance; Permutation importance
782 measures the decrease in AUC when the values of a variable are shuffled, variables with higher
783 permutation importance contribute more to predicting habitat suitability.

784

785 Table 1.

Region	Number of Occurrences	Total Records
Eastern North America	2066	12045
Western North America	161	10149
East Asia	80	10080

786

787

788 Table 2.

Model	Variable performance metric	Variables				
		Minimum temperature of the:		Average minimum monthly temperature in:		
		coldest month (Bio6)	coldest quarter (Bio11)	January (Tm1)	February (Tm2)	March (Tm3)
Eastern North America (AUC = 0.855)						
	Permutation importance	15.7	45.3	3.5	21.2	14.3
	Percent contribution	24.0	37.1	3.7	14.3	21.0
Western North America (AUC = 0.931)						
	Permutation importance	2.4	3.2	0	94.4	0
	Percent contribution	84.4	11.5	1.5	1.4	1.2
East Asia (AUC = 0.983)						
	Permutation importance	75.8	0.6	0.8	0	22.7
	Percent contribution	32.6	17.2	19.9	0.3	30.0

789 *Terms in parentheses correspond to variable names in the WorldClim database (WorldClim
790 2022a, 2022b). See text for more details.

791

Figure 1. Predicted hemlock woolly adelgid species distribution map for eastern North America based on historic (1970-2000) climate data. Shading indicates habitat suitability with darker shading indicating higher habitat suitability. Red dots represent recorded occurrences of HWA in the region; Orange outline shows the distribution of eastern hemlock derived from Little's (1971) range maps. Figure was created using QGIS version 3.36.2 and North American map data were obtained from US Geological Survey *et al*. (2004) and the Great Lakes Commission (2022).

Figure 2. Predicted hemlock woolly adelgid species distribution map for western North America based on historic (1970-2000) climate data. Shading indicates habitat suitability with darker shading indicating higher habitat suitability. Red dots represent recorded occurrences of HWA in the region. Orange and peach outlines show the distribution of western and mountain hemlock respectively from Little's (1971) range maps. Figure was created using QGIS version 3.36.2 and North American map data were obtained from the US Geological Survey *et al*. (2004).

Figure 3. Predicted hemlock woolly adelgid species distribution map for Asia based on historic (1970-2000) climate data. Shading indicates habitat suitability with darker shading indicating higher habitat suitability. Red dots represent recorded occurrences of HWA in the region. Figure was created using QGIS version 3.36.2 and Asian map data were obtained from Opendatasoft (2023).

Figure 4. Performance of climate variables used in the generation of the present climatic condition hemlock woolly adelgid species distribution models in eastern North America (A), western North America (B), and Asia (C). Variable performance is measured with regularized training gain, a measure of model improvement as the model is trained with only the selected variable (blue), with the remaining variables (emerald), and with all variables (red). Variables included are the minimum winter temperature of the coldest month (Bio6) and coldest quarter (Bio11), and the average minimum temperature of January (Tm1), February (Tm2), and March (Tm3). Figure was created using MaxEnt version 3.4.4.

Figure 5. Predicted hemlock woolly adelgid species distribution for eastern North America based on maximum entropy modeling and future climatic conditions in 2041-2060 (left column) and 2081-2100 (right column) under low (SSP126) (A, B), mid (SSP245) (C, D), and high (SSP585) (E, F) emissions scenarios. Shading indicates habitat suitability with darker shading indicating higher habitat suitability. Eastern hemlock shapefile, outlined in red, derived from Little's (1971) range maps. Figure was created using QGIS version 3.36.2 and North American map data were obtained from the US Geological Survey *et al*. (2004) and the Great Lakes Commission (2022).

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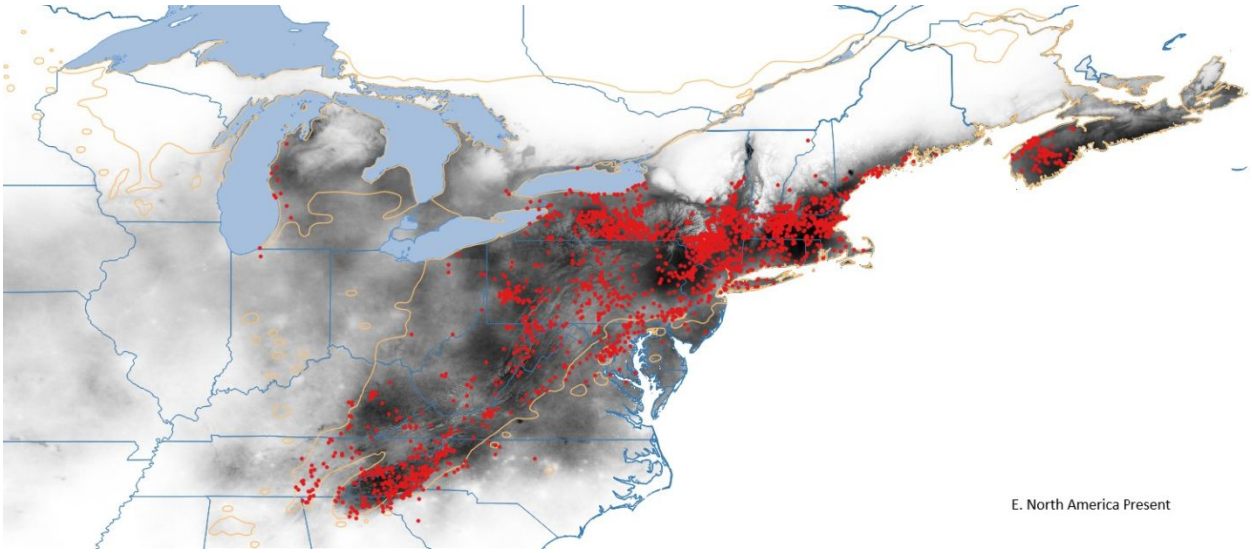

827

828 Figure 1.

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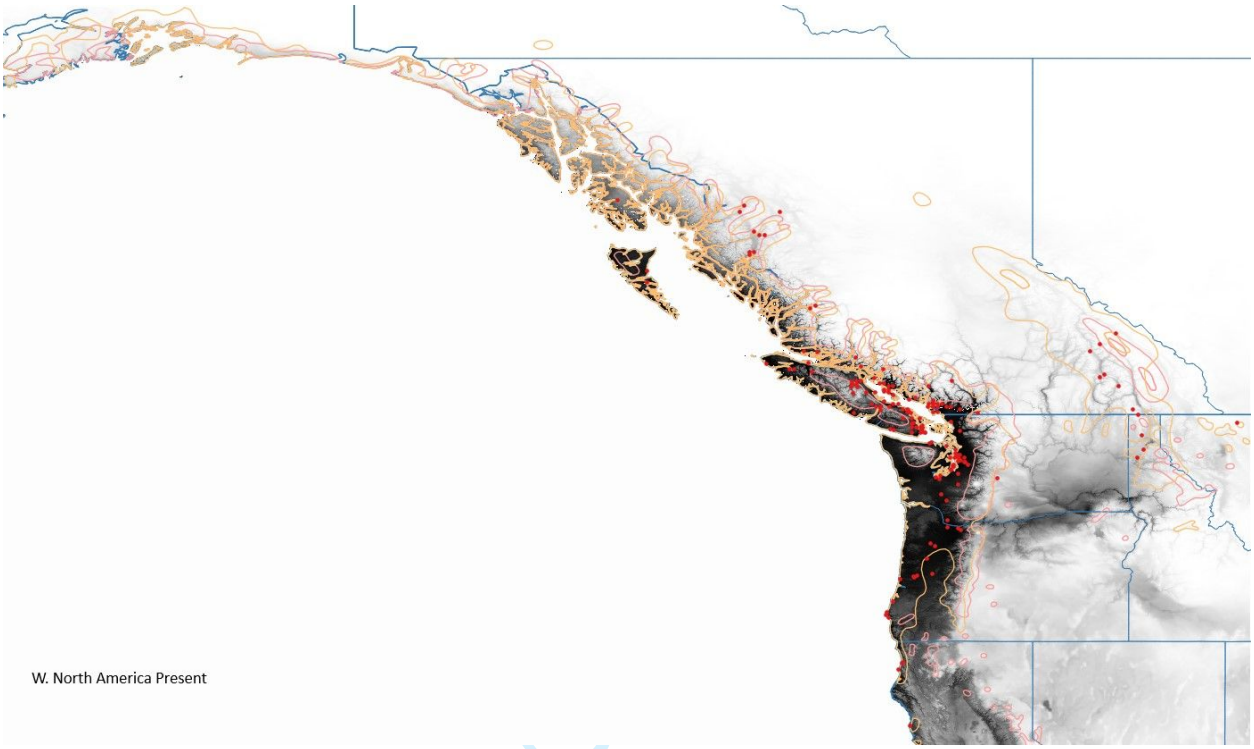

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832 Figure 2.

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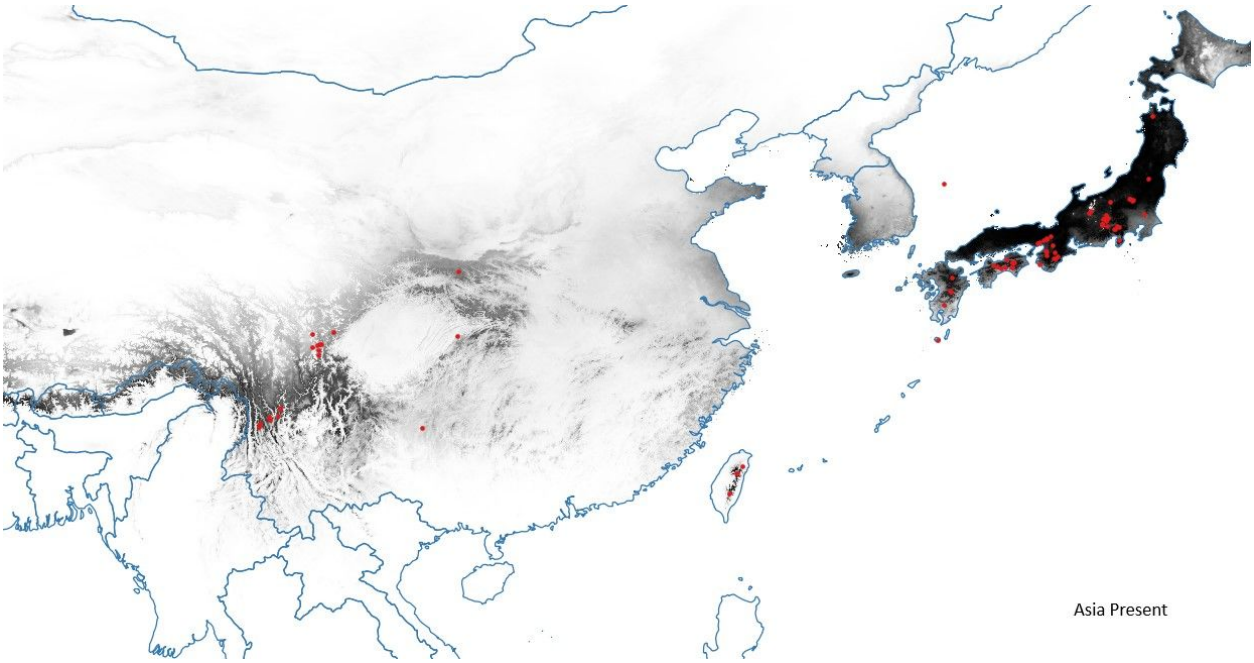

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836 Figure 3.

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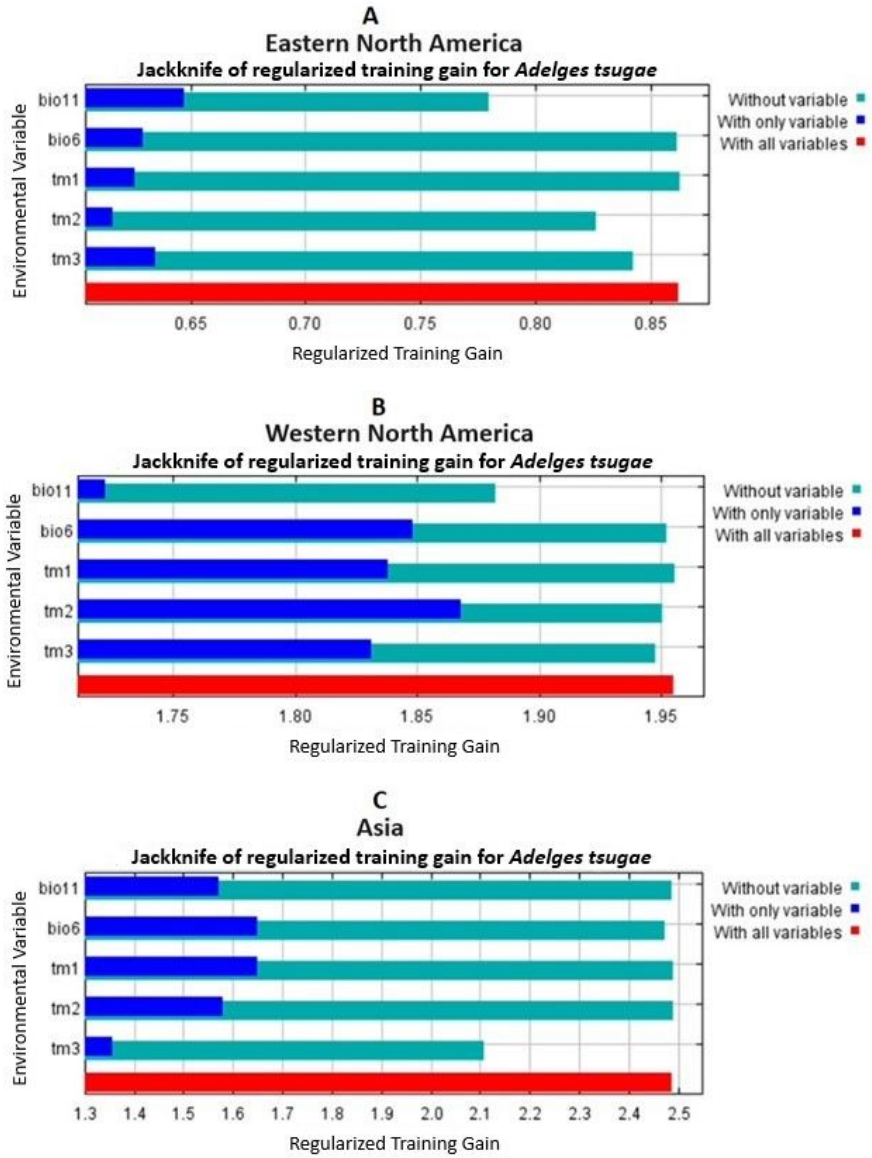

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840 Figure 4.

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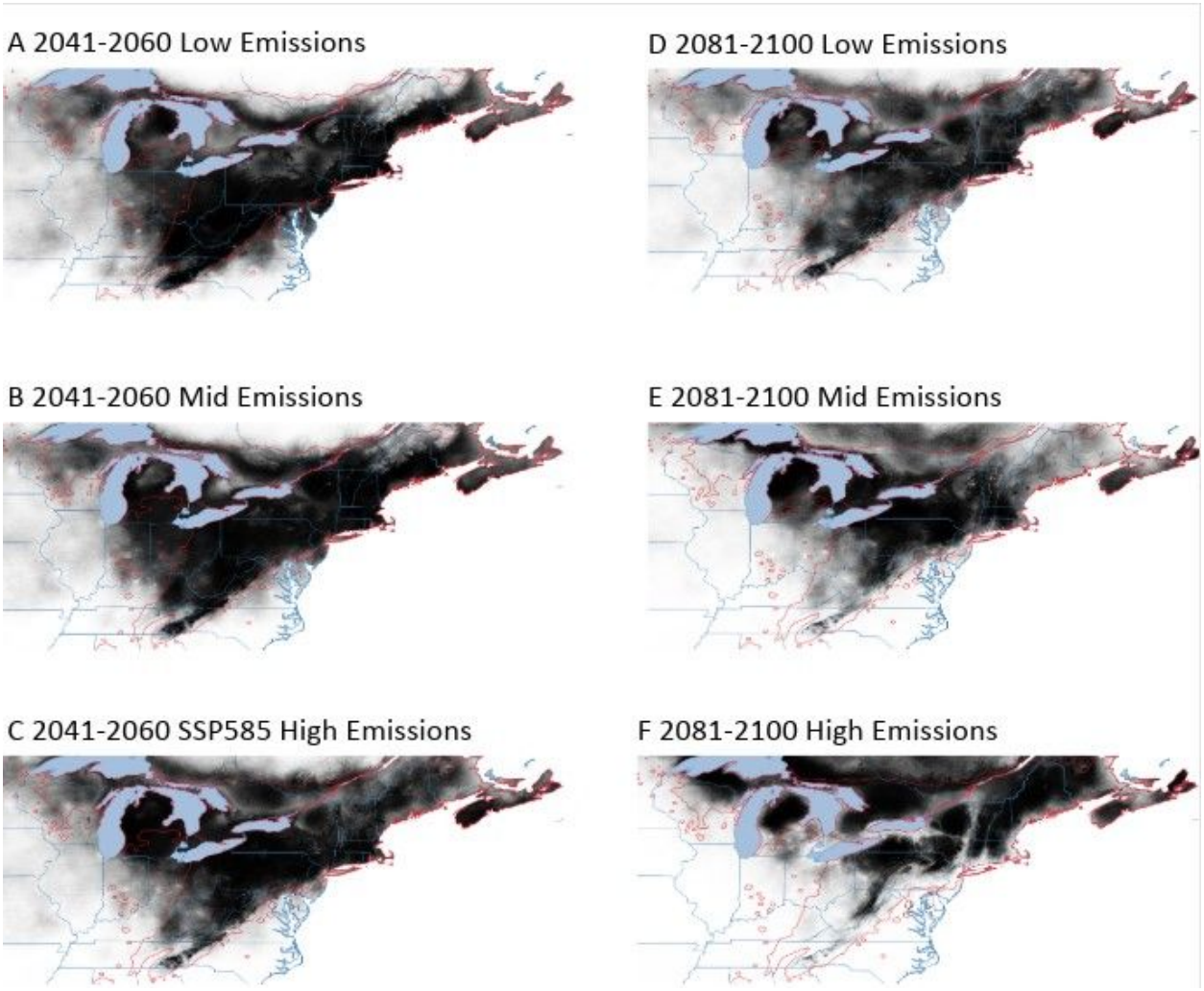

843

844 Figure 5.

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