The Impact of Climate Change on the Range of a Sample of Invasive Species in the United States

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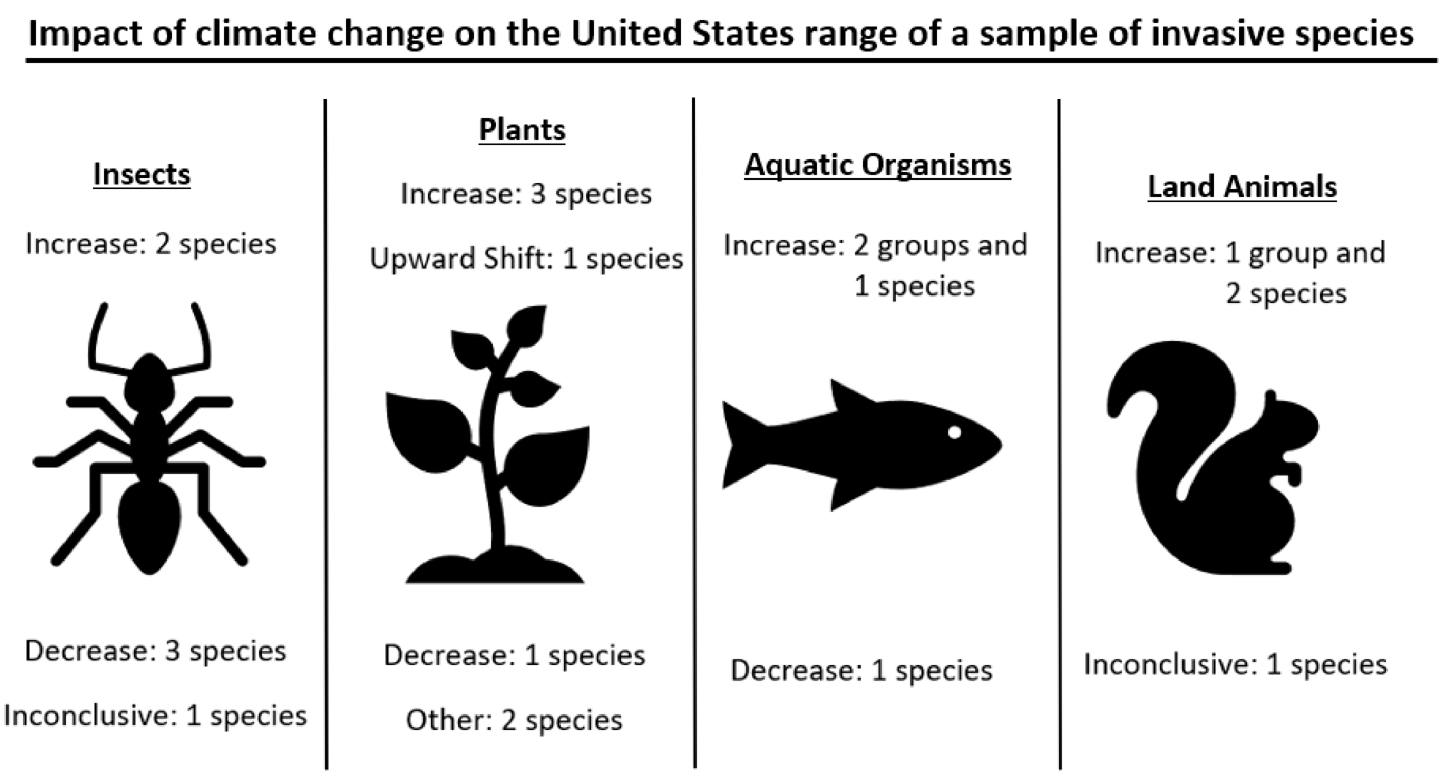
Abstract

Invasive species are non-native species that cause harm to a native ecosystem. Invasive species cause significant harm to the environment, economy, and human health. This study investigates the impact of climate change on the United States range of a sample of invasive species in the following categories: insect, plant, aquatic, and land animal. This is investigated by reviewing the primary literature related to the sampled species. In terms of insect species, the Asian tiger mosquito (*Aedes albopictus*) and tropical fire ant (*Solenopsis geminata*) will likely expand in range. The spotted wing Drosophila (*Drosophila suzukii*), Japanese beetle (*Popillia japonica*), and cycad aulacaspis scale (*Aulacaspis yasumatsui*) will likely decrease in range. The impact on pea leafminer (*Liriomyza huidobrensis*) range is inconclusive. In terms of plant species, musk thistle (*Carduus nutans*), Japanese barberry (*Berberis thunbergii*), and Japanese honeysuckle (*Lonicera japonica*) will likely expand in range. Garlic mustard (*Alliaria petiolata*) will likely decrease in range. The range of habitat suitable to the flowering rush (*Butomus umbellatus*) will likely decrease, but currently unoccupied regions will remain suitable. The change in barbed goatgrass (*Aegilops triuncialis*) range will depend on changes in precipitation. The range of Balkan toadflax (*Linaria dalmatica*) will likely increase in elevation, with decreases at lower elevations. In terms of aquatic species, freshwater fish in general, the hydroid *Cordylophora caspia*, and several marine fouling species will likely expand in range. The spiny water flea (*Bythotrephes longimanus*) will likely decrease in range. In terms of land animal species, the range of the Cuban slug (*Veronicella cubensis*) and tropical leatherleaf (*Laevicaulis alte*) will likely increase upwards in elevation. The United States is currently at risk of invasion by several squirrel species, and climate change will likely cause an increase in habitat favorability along the west coast and a decrease in the eastern half of the country. The impact on African clawed frog (*Xenopus laevis*) range is inconclusive.



Introduction

Invasive species are non-native species that cause harm to a native ecosystem. An invasion refers to the introduction of a harmful non-native species to an ecosystem. Invasions of ecosystems have occurred throughout the history of life on earth as a result of the migration of invasive species, as well as rafting to island ecosystems. However, rates of invasion have increased significantly as a result of human activities, especially as globalization has occurred, (Bellard et al., 2016). International trade is one of the most significant introduction pathways for invasive species. The popularity of exotic plants in the plant trade has led to the spread of invasive plant species. Invasive aquatic organisms have been introduced via the ballast water of ships. Invasive insects have been inadvertently introduced to ecosystems via the transportation of agriculture. The release of pets, for example from the exotic pet trade, has led to the spread and establishment of invasive animal species. It is also the case that invasive species have been released intentionally, for example in efforts to mitigate the negative effects of another species.

Invasive species are sometimes able to spread quickly in an ecosystem because of abundant food sources, as well as a lack of natural predators and competitors that would be able to keep populations in check, (FWS, 2012). The spread of, as well as damage caused by, invasive species is exacerbated by the fact that native species do not have evolved defenses against these invasive species. However, it may take a number of introductions before an invasive species is able to become established because of difficulties associated with low starting populations. In fact, the majority of non-native species introductions do not lead to the establishment of a population of that species. As is the case with other species, ongoing climate change will likely cause changes to the ranges of invasive species throughout the world, (IPCC, 2014).

This study will investigate the impact of the warming caused by ongoing climate change on the habitat range of invasive species, or non-native species that cause damage to native ecosystems, in the United States. This study will assess the impact to the ranges of a number of insect, plant, aquatic, and land animal invasive species. This will be investigated by reviewing the primary literature related to the sampled insect, plant, aquatic, and land animal invasive species. The most significant attention will be given to insect and plant invasive species, as the relationship between these species and climate change appears to have the most widely available research from the last decade. A number of research questions will be addressed, including: what are the trends in the impact of climate change on the range of the sampled species? Which species will likely increase, or decrease, in range? What environmental factors play the most significant roles in the range of suitable habitat? The results of this study will be used to inform recommendations for the mitigation and management of the sampled invasive species.

The United States is now home to thousands of invasive species, although estimates of the exact number vary, (FWS, 2012). Commonly known invasive species include the Burmese python, the emerald ash borer, kudzu, and the common tumbleweed. The Burmese python has become a growing problem in the Florida Everglades. The emerald ash borer is an insect that decimated ash tree populations in the United States, as well as Canada and Europe. Kudzu is also known as “the vine that ate the (American) south”. The common tumbleweed, although portrayed as a symbol of the American west, is damaging to the native ecosystems of the region. In terms of insects, this paper will discuss the impacts to the spotted wing Drosophila, the Asian tiger mosquito, the Japanese beetle, the pea leafminer, the tropical fire ant, and the cycad aulacaspis scale. In terms of plants, musk thistle, flowering rush, barbed goatgrass, Balkan toadflax, garlic mustard, Japanese barberry, and Japanese honeysuckle will be discussed. In terms of aquatic invasive species, there will be discussion of freshwater fish in general, a group of fouling species located in Bodega harbor, the hydroid species *Cordylophora caspia*, and the spiny water flea. In terms of land animals, there will be discussion of the African clawed frog, the Cuban slug, the tropical leatherleaf, and a group of squirrel species.

Invasive species cause significant environmental harm throughout the United States, as well as the world. Invasive species are one of the leading causes of biodiversity loss throughout the world, (Doherty et al., 2016; Dueñas et al., 2021; WWF, 2016). Invasive species cause biodiversity loss through direct predation on native species, as well as through interspecific competition with native species for resources. In the most severe cases, this direct predation or competition for resources has led to the extinction of native species. The declines, or extinctions, of native species, along with the spread of invasive species, can lead to significant alterations of the composition of ecosystems, as well as damage to ecosystem functioning. In other words, invasive species are a cause of ecosystem disturbances. In the United States, invasive species are a major contributing factor to the decline of species that are designated as either “threatened” or “endangered” under the Endangered Species Act, (Primtel, 2005). Additional environmental harm can occur as a result of efforts to manage invasive species, such as through the application of pesticides. Further, invasive species can act as vectors of disease and parasites to native species.

In addition to environmental harm, invasive species cause significant negative economic impacts in the United States, (Shwiff et al., 2018). A widely cited 2005 study by Primtel estimated that invasive species cause $120 billion of economic damage in the United States annually. However, this estimate is now more than 15 years old and newer assessments would be beneficial to assessing the current impact. Further, it can be difficult to accurately assess the economic value of ecosystem losses as these often do not have associated market prices. The economic damage caused by invasive species includes damage to economically valuable species, such as crops and tree species that are a source of lumber. Invasive species can act as vectors of disease and parasites, spreading these harms to livestock. In some instances, invasive species cause harm to infrastructure, (ISAC, 2016). For example, invasive species cause harm to housing and other buildings, roadways, water distribution systems, and electricity delivery systems. Significant expenditures occur annually in efforts by US governmental and private organizations to manage invasive species. These management efforts include attempts to mitigate the negative effects of established invasive species, reduce the population of those invasive species, and prevent the introduction of invasive species. Removing established invasive species would be ideal but is often economically infeasible because of the difficulty of removing established populations.

An additional significant harm posed by invasive species is harm to human health, (Marsh et al., 2021). In the same way that invasive species can act as vectors of disease and parasites to native species and livestock, they can also act as vectors of disease and parasites to human populations. These diseases can be spread either by direct transmission or through the contamination of food or water sources. Invasive species can cause other changes to water sources that negatively affect the quality of that water or reduce the quantity of water available for human needs. Certain invasive species contain toxins or chemical irritants that are harmful to human health, as well as the health of other animals. Damage to infrastructure caused by invasive species can decrease quality of life, as well as contribute to safety hazards. Invasive species can reduce the availability of human food sources as a result of damage to crops and livestock. These damages to human health contribute to additional economic costs caused by the effects of invasive species.

Ongoing climate change, caused by anthropogenic greenhouse gas emissions, will almost certainly cause a continuous shift in the range of suitable habitat for many species, including invasive species, (IPCC, 2014). This shift in the range of suitable habitat will occur as increasing global temperatures cause changes to environmental conditions. The environmental conditions that seem to be the most significant in terms of changes to the suitability of habitats for invasive species are temperature and precipitation, (Bellard et al., 2016). Changes in temperature, and the resulting changes in precipitation, can cause significant changes to the environmental conditions of an ecosystem. Other environmental conditions can play a significant role in habitat suitability, such as the availability of a limiting nutrient. Indirectly, changes, caused by changing environmental conditions, to the range of native species that act as a food source for invasive species can lead to a shift of the range of invasive species. The most significant concern is possible expansions in the range, as well as population size and density, of different invasive species. This could lead to an increase in the damage done by those invasive species, as well as increases in the cost of dealing with those invasive species. However, changing climatic conditions will likely cause a decrease in the range, as well as population size and density, of some invasive species.

Applications of this research include informing strategies for the management and mitigation of the sampled invasive species. Accurately predicting how the range of suitable habitat for invasive species will change in response to climate change can be used to inform which species to focus efforts on, as well as the most efficient way to use limited resources. Management efforts can be focused on invasive species that will likely experience an increased range of suitable habitat due to climate change. Management efforts could be focused away from invasive species that will likely experience a decrease in suitable habitat range as a result of climate change, although monitoring of these species would remain important. Alternatively, reductions to the range of suitable habitat could be used to speed up or increase the efficiency of efforts to reduce the population of certain invasive species.

Individuals that could benefit from this research include government employees that deal with invasive species. This includes conservation managers, park rangers, members of government committees with the aim of combating invasive species, inspectors, and other employees of federal and state agencies whose jobs involve handling invasive species. Federal agencies that do work related to invasive species include the Environmental Protection Agency and agencies within the Department of the Interior and Department of Agriculture. These agencies include the Forest Service, the National Park Service, and the Fish and Wildlife Service. A notable government committee dedicated to combating invasive species is the National Invasive Species Council. Individuals in the private sector could benefit from this research, including members of nonprofits dedicated to conservation, as well as individuals in businesses that are negatively affected by invasive species. Other individuals that could benefit from this research include landowners affected by invasive species, as well as those with a general interest in invasive species.

The research topic posed in this paper, specifically the impact of climate change on the range of invasive species in the United States, is important because of the harm invasive species cause. This harm includes environmental damage, with invasive species being a major driver of biodiversity loss. Economically, invasive species cause billions of dollars of damage in the United States annually. From a public health perspective, invasive species act as vectors of disease and cause damage to infrastructure that leads to safety and health hazards. Accurately predicting the response of the range of invasive species in the United States to climate change is vital to informing effective management strategies for those invasive species. Overall, the impact of climate change on the range of invasive species in the United States merits examination.

Invasive Insect Species

The spotted wing Drosophila, or *Drosophila suzukii*, is an invasive insect species originally native to southeast Asia. The spotted wing Drosophila threatens the soft-skinned fruit industry in the United States and Canada. Learning about possible changes in the range, size, and infestation potential of spotted wing Drosophila populations as a result of climate change is needed for effective mitigation efforts. Aaron et al. (2017) conducted a study on the impact of climate change on the future distribution of the spotted wing Drosophila. Future temperature projections were downloaded from CMIP3 and CMIP5 Climate and Hydrology Projection archives. A model of spotted wing Drosophila population dynamics was obtained and global or general circulation models, or GCMs, were used to model four different scenarios of future climate change.

These four scenarios predicting future greenhouse gas emissions were based on relative concentration predictions, or RCPs. The RCPs used were RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5. An RCP with a greater number corresponds to a future with greater greenhouse gas emissions. RCP 2.6 is representative of a future with lower greenhouse gas emissions, whereas RCP 8.5 is representative of a future with greater greenhouse gas emissions. RCP 4.5 and RCP 6.0 are representative of futures with greenhouse gas emissions intermediate between RCP 2.6 and RCP 8.5. Simulations of spotted wing Drosophila populations, as well as the readiness of their fruit food source, were run under these different climate scenarios.

Simulation results were averaged over three time periods, these being 2010 to 2039, 2040 to 2069, and 2070 to 2099. All climate scenarios predicted a decrease in overall spotted wing Drosophila distribution, as well as a continuous decrease in population densities over time. Under scenarios with greater increases in temperature, or greater RCP values, there were more significant decreases in the predicted population densities of spotted wing Drosophila populations. This decrease was because temperatures were too high for development and negatively affected soft-skinned fruit output. However, northern regions may experience an increase in spotted wing Drosophila population densities as a result of increasing temperatures causing those environments to become more favorable to the development of the spotted wing Drosophila. Those northern regions may also experience an expansion of the soft-skinned fruit industry. Based on these results, it is likely that there will be a decrease in the range of the spotted wing Drosophila as temperatures increase, and this decrease will depend on how much temperatures increase. It is notable that different changes to the ranges of invasive species may occur depending on the future course of temperature changes as a result of different greenhouse gas emission levels. Depending on the temperature increases, mitigation efforts may be able to be shifted away from spotted wing Drosophila populations. However, there may be a need for measures in the northern United States.

The Asian tiger mosquito, or *Aedes albopictus*, is an invasive insect that poses significant concern from a public health perspective because of its role as a vector of diseases to humans, such as West Nile virus. This concern is exacerbated by its presence and ability to thrive in urban environments. The Asian tiger mosquito was originally native to southeast Asia and was introduced to the United States in the late 20th century. Rochlin et al. (2013) investigated the future range of the Asian tiger mosquito under two future climate change scenarios in the northeastern United States. These climate change scenarios corresponded to a future with moderate and high greenhouse gas emissions. Adult Asian tiger mosquitos were collected to supplement other data sources on population distribution. A statistical modelling algorithm known as Maximum Entropy, or MaxEnt, was used to model distributions of the Asian tiger mosquito population.

Both climate scenarios predicted a significant increase in suitable habitat for the Asian tiger mosquito from 5%, at the time of research, to 16% of the northeastern United States by the year 2039. The most significant expansion is predicted to occur in Massachusetts, Rhode Island, and Connecticut. Further into the future, the moderate greenhouse gas emission scenario predicted an increase of suitable habitat to 43% of the northeastern United States by the end of the century, or 2099. The higher greenhouse gas emission scenario predicted a similar increase of suitable habitat to 49% of the northeastern United States by the end of the century, but with a faster rate of expansion than under the moderate scenario. This suitable habitat expansion will include most urban areas in the northeastern United States, and a population of more than 30 million individuals who will be potentially susceptible to vector borne diseases from the Asian tiger mosquito.

Limitations of this study include differences in suitable habitat outcomes, as compared to what was found, resulting from snow cover in winter, topographical features, and precipitation levels. Based on the results of this study, it is likely that there will be an expansion of Asian tiger mosquito range across the northeastern United States as a result of future climate change. This expansion will put millions of individuals at risk of contracting vector spread diseases. This is of significant concern from a public health perspective and may inform increased efforts to manage this invasive species, such as efforts to slow the spread of the Asian tiger mosquito.

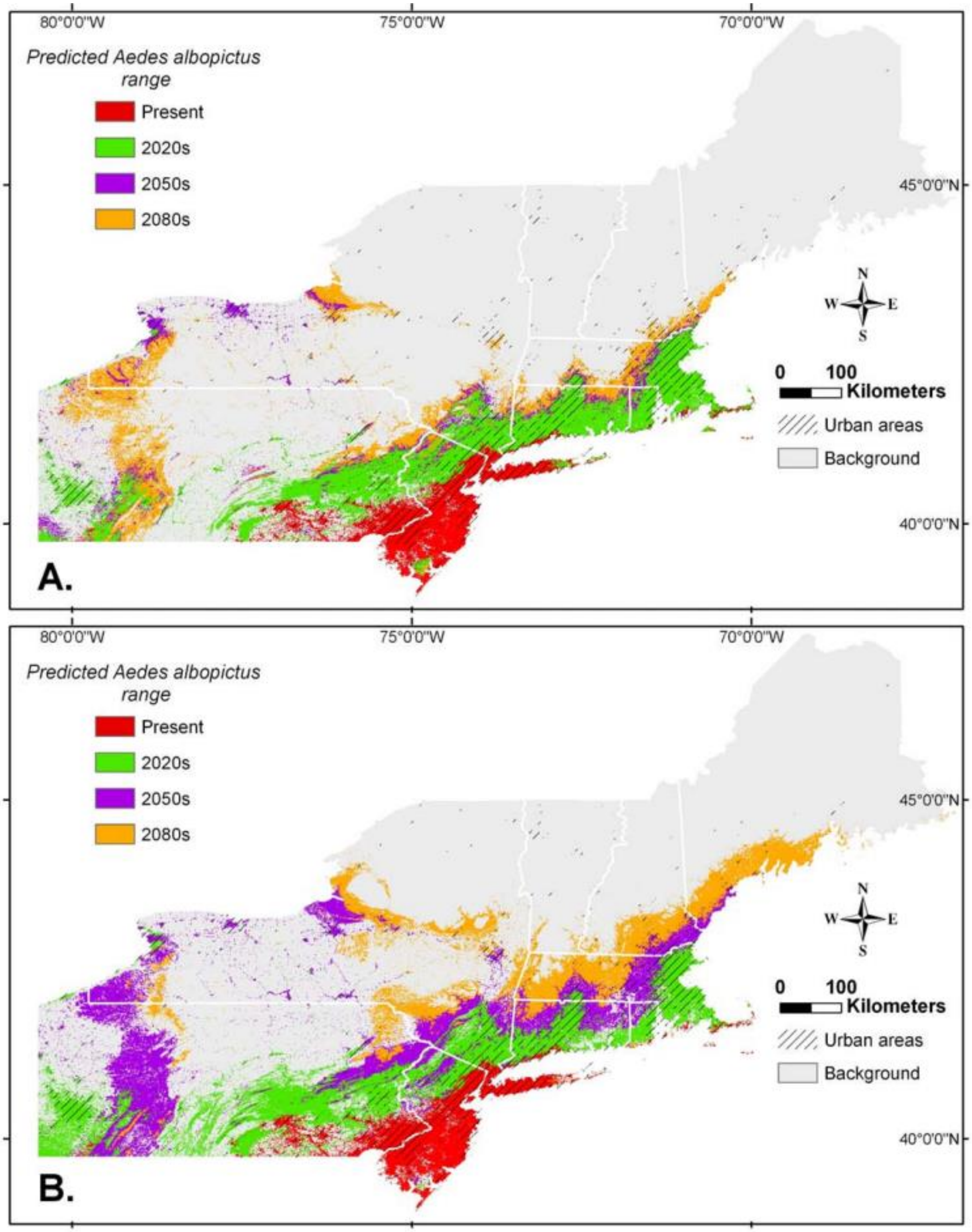


Figure 1. Predicted Asian tiger mosquito range under the A) moderate emissions scenario and B) higher emissions scenario, (Rochlin et al., 2013).

The Japanese beetle, or *Popillia japonica*, is a major agricultural pest in the United States and has also spread to Europe. The Japanese beetle causes an estimated $460 million annually in damages in the United States. The Japanese beetle is currently established across much of the eastern half of the mainland United States, with fewer populations of lower densities stretching to the west coast. Thomas and Jean (2019) modelled the worldwide range of suitable Japanese beetle habitat under both current and future climate conditions using two climate models known as CNRM-CM5 and ACCESS1-0. Both models were run with one future greenhouse gas emission scenario, that being RCP 8.5.

The United States range predicted under current climate models was consistent with observed population ranges. Under both future climate models, it was predicted that the United States range of Japanese beetle will expand northward into Canada, and that the southernmost edges of suitable habitat will shift to the north by the year 2059. This will happen because the increased temperatures and dryness of those southern boundary areas, particularly during summer months, will render them unsuitable to Japanese beetle populations. Under the ACCESS1-0 model, large areas of the southern United States will no longer be habitable to the Japanese beetle, with pockets of land that are only mildly suitable. The ACCESS1-0 model predicted a decrease of suitable habitat from 56.25%, at the time of research, to 39.89% of land area in the United States by 2059. Under the CNRM-CM5 model, this southern range boundary shift was significantly milder with a predicted shift of suitable habitat from 56.25% to 54.49% of land area in the United States, although the decreases included large portions of Florida and Texas. In the north, population growth levels may increase as a result of warmer temperatures, causing the northern border of the United States to experience increased issues from the pest.

Based on these results, there may be a northward decrease in the range of the Japanese beetle from the population's current southern boundary. However, it is notable that the two models predicted significantly different decreases in southern suitable habitat. This is further complicated by the fact that the climate models were run under a single future greenhouse gas emission scenario, and the fact that this scenario was an RCP 8.5 scenario. RCP 8.5 is representative of a future with significant greenhouse gas emissions and is sometimes referred to as a "business as usual" scenario in which little to no greenhouse gas emission mitigation occurs. As such, an RCP 8.5 scenario may not accurately reflect what future emissions will look like. If a decrease of the southern range of the Japanese beetle does occur, then management efforts can be shifted away from those regions. However, an increase in Japanese beetle population densities in the north may require additional steps to be taken in the management of the invasive beetle.

The pea leafminer, or *Liriomyza huidobrensis*, is an invasive insect that has significant negative effects on agricultural crops, such as lettuce and celery. The pea leafminer is native to South America and was introduced to the United States in the late 20th century. Currently, pea leafminer populations are established mainly in the southeast and along the western coast. Mika and Newman (2010) used both first approximation simple models and general circulation models of future climate to predict the future range of habitat suitable to the pea leafminer. The general circulation models included both CGCM2 and HADCM3, and these models were run with two different future greenhouse gas emission scenarios. These emission scenarios included a scenario where atmospheric CO_2 concentrations reach 840 ppm and a scenario where concentrations reach 620 ppm by the end of the century.

It was found that the main climatic factor limiting the distribution of the pea leafminer is cold stress. Dry stress also limits the pea leafminer to a lesser extent, but stress from heat and wetness generally do not. The results predicted by the simple models were significantly different from the results of the general circulation models. The simple models predicted a northward expansion of suitable range into Canada and a northward shift of the southern boundary of suitable habitat out of Mexico. However, habitat along the southern border of the United States remained suitable. The CGCM2 model predicted an increase in suitable habitat to cover much of the United States by the end of the century. However, the lower greenhouse gas emissions scenario predicted a lower increase in suitable habitat than the scenario with greater emissions. Under both greenhouse gas emission scenarios, the HadCM3 model predicted a shift of suitable habitat to the east and west coasts of the country by the end of the century, with an overall decrease in suitable habitat.

Both the simple models and the CGCM2 model predicted an increase in suitable habitat across the United States, although they disagreed on the overall favorability of habitats. These predictions are in contradiction to the predicted decrease of suitable habitat range made by the HadCM3 model. Overall, these results are inconclusive in predicting how climate change will affect the pea leafminer. These results show that different climate models, as well as different emission projections, will yield different results in predicting the future range of a population. This is problematic from the empirical standpoint of trying to accurately predict how the future range of invasives will change as a result of climate change. The differences in predictions of the models result from differences in how both climate parameters and feedback loops are modelled. This suggests the importance of developing climate models that accurately reflect how climatic changes will affect distributions.

The tropical fire ant, or *Solenopsis geminata*, is an invasive insect that causes significant harm to native flora and fauna, crops, equipment, and human health. The tropical fire ant is native to tropical regions of the Americas, such as the Caribbean Islands, and has spread around the world as a result of international trade. The tropical fire ant is currently invasive in the southeast and along the southern and western borders of the mainland United States. Lee et al. (2021) used a MaxEnt model to predict the worldwide current and future range of the species. This was done under two climate change scenarios, one scenario with lower greenhouse gas emissions and a scenario with a greater quantity of emissions. The lower emissions scenario represents a future in which electricity generation is done with both fossil fuels and clean energy. The greater emissions scenario represents a future in which there is high population growth and slow technological change, in terms of the world's electricity generation. The two climate scenarios were modelled to the years 2050 and 2100.

The climatic factors that had the most significant effects on the distribution of the tropical fire ant were annual precipitation, precipitation during the driest seasons, and annual mean temperature. In terms of the United States, the MaxEnt model predicted, under the lower emissions scenario, that the range of suitable habitat for the tropical fire ant will remain similar to the current range in 2050. However, slight northern expansions and an expansion along the western coast were predicted. By 2100, the model predicted a continued expansion northward and along the west coast. The model that used a greater emissions scenario predicted similar results by 2050, with a slight northern and west coast expansion of suitable range. By 2100, it predicted a continued expansion of suitable habitat to cover most of the United States, with the exception of the Rocky Mountains and other smaller pockets. This is a greater expansion of range than predicted by the lower emissions scenario. Under both scenarios, the overall habitat favorability of the southeastern United States increased.

These results suggest that there will be an expansion of the range of the tropical fire ant to the north of its current range and along the west coast of the United States as a result of climate change. The results suggest that the severity of this expansion of range will be positively correlated with the overall level of greenhouse gas emissions that occur. It is also likely that the southeast will experience increased habitat favorability, and therefore increased problems from the tropical fire ant, as global temperatures increase. These results can inform management efforts aimed at slowing the spread of the tropical fire ant, or increased mitigation efforts in the southeastern United States.

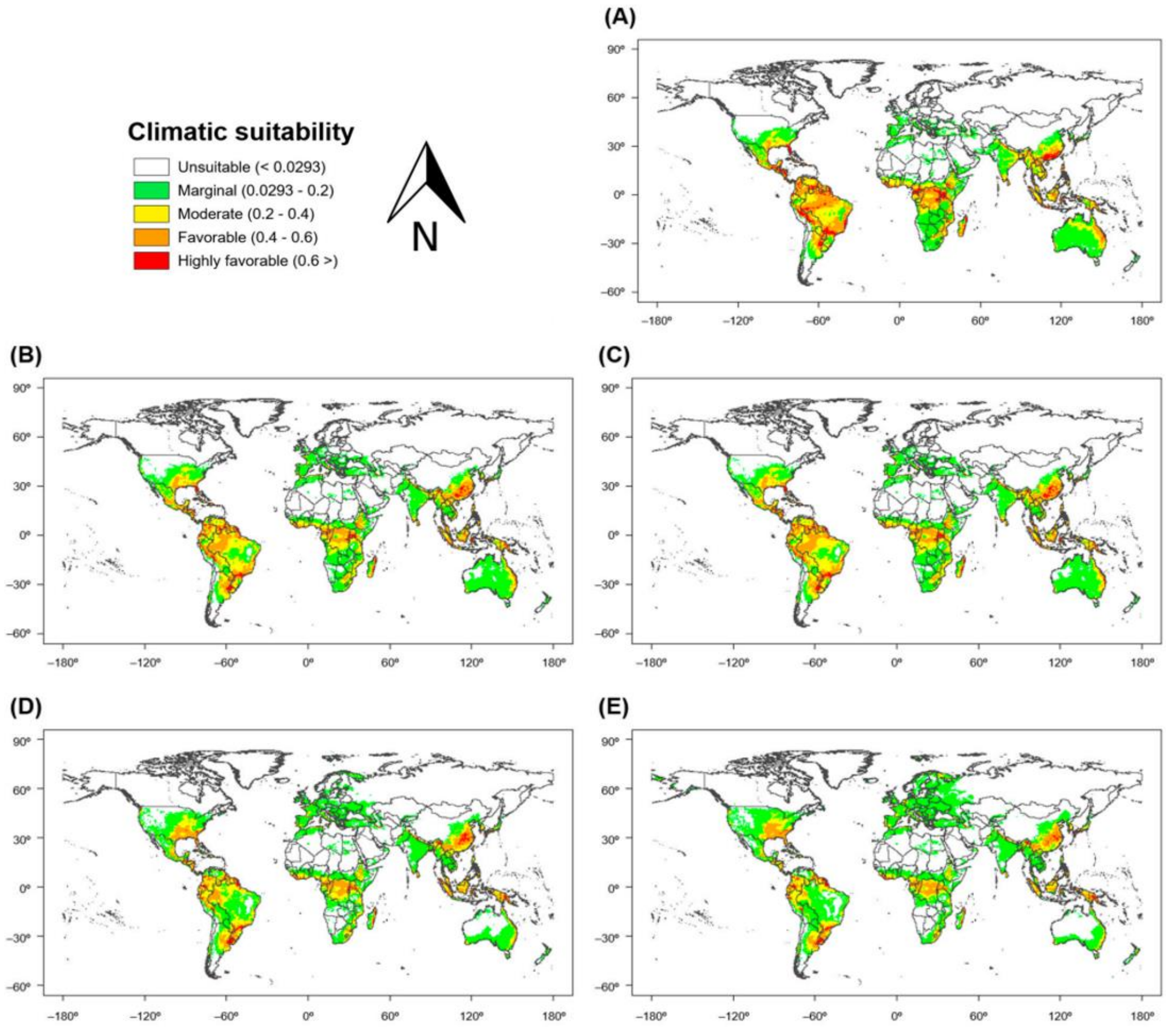


Figure 2. Predicted range of the tropical fire ant under A) current conditions, B) 2050, lower emissions scenario, C) 2050, greater emissions scenario, D) 2100, lower emissions scenario, and E) 2100, greater emissions scenario, (Lee et al., 2021).

The cycad aulacaspis scale, or *Aulacaspis yasumatsui*, is an invasive insect species that causes significant damage to the ancient lineage of plants known as cycads. Cycads are widely traded as landscaping plants and many wild cycad species are endangered. Both wild and planted populations of cycads are threatened by the cycad aulacaspis scale, as well as a number of other ornamental plant species. The cycad aulacaspis scale is native to Thailand and was introduced to the United States, via Florida, in the late 20th century. In 1996, infestations of the cycad aulacaspis scale caused significant damages to ornamental plants in Florida. The cycad aulacaspis scale is currently established in Florida, Louisiana, Alabama, Georgia, South Carolina, Texas, and the Hawaiian Islands. Wei et al. (2018) studied the worldwide range of habitat suitable to the cycad aulacaspis scale under both current and future climate conditions. This was studied using a MaxEnt climate model and future climate conditions were simulated under two greenhouse gas emissions scenarios. These scenarios were RCP 2.6 and RCP 8.5, and both were modelled to the years 2050 and 2070.

In terms of the United States, the model using current climate conditions predicted suitable habitat comprising the currently inhabited range. Under RCP 2.6 conditions, the range of suitable habitat is predicted to decrease by 48% by 2050, with an additional 1.5% decrease, or 49.5% total decrease, by 2070. Under RCP 8.5 conditions, the projected loss of suitable habitat was even greater, with a decrease of 58.2% of land area by 2050 and 69.5% by 2070. The most significant environmental factor limiting the range of the cycad aulacaspis scale was the mean temperature during the driest annual quarter. This is because temperatures greater than 15^{o}C to 20^{o}C during the driest quarter inhibit the growth and reproduction of the scale.

These results suggest that there will be a decrease in the total range of the cycad aulacaspis scale in the United States as a result of climate change, and that this decrease will be dependent on the level of warming that occurs. Greater levels of warming will likely lead to greater decreases in the range of the cycad aulacaspis scale. These results can inform a management strategy of shifting focus off the cycad aulacaspis scale as currently occupied areas of the United States become unsuitable to the scale. Alternatively, efforts could be focused at potentially speeding up the decline of the invasive cycad aulacaspis scale.

Invasive Plant Species

Musk thistle, or *Carduus nutans*, is an invasive plant species native to Europe and Asia. Musk thistle was introduced to the United States at the start of the 19th century. Musk thistle is considered to be a weed throughout the United States and crowds out the growth of native vegetation. Teller, Zhang, and Shea (2016) set out to investigate how the effects of climatic changes on wind-dispersed seed traits can affect the spread of the population of invasive plant species in general, with musk thistle as a model. Forty plots of musk thistle seeds were grown in greenhouses and open top chambers were used to artificially increase surface temperatures within. The increases in surface temperature were consistent with conservative, or low-end, projections of temperature increases or greenhouse gas emissions. Half of the forty plots were given extra water to simulate the effects of increased precipitation, which is likely to occur as a result of increasing temperatures. When mature, musk thistle capitula were subjected to wind tunnel trials at varying wind speeds to simulate natural wind dispersal. Data from these trials were used in informing variable values for a seed dispersal model that estimated the spread rate of the population.

The musk thistle grown in greenhouses released a greater proportion of seeds, as a result of increased temperature but not precipitation, than musk thistle under current climate conditions. It seems that increased temperatures increase the growth rate of musk thistle, but precipitation did not have a significant effect on growth. The median rate of population spread of musk thistle grown in the greenhouses was 38% greater than the spread rate of musk thistle under current climatic conditions. These results suggest that there will be an increase in the population growth rate, and therefore a potential increase in range, of musk thistle as a result of climate change. The results could inform increased management efforts to slow, or ideally prevent, the spread of musk thistle as warming occurs. It is notable that this experiment only studied the effects of warming consistent with lower-end estimates of temperature increases. This study could be improved by growing musk thistle at a range of levels of warming.

Flowering rush, or *Butomus umbellatus*, is an invasive wetland plant native to Europe and Asia. Flowering rush was introduced to the United States, via ballast water, at the end of the 19th century. The flowering rush is also a popular plant in the flower trade, increasing its spread. Banerjee et al. (2020) investigated the niche dynamics and distribution of flowering rush populations in North America under both the current climate and future climate projections. Data was collected and used in a number of modelling techniques, including nine algorithms, such as a MaxEnt algorithm, that were used to model niche characteristics. Three general circulation models were used to predict the distribution of the flowering rush, these being BCC_CSM1.1, CCSM4, and HAD-GEM2-AO. The distribution of the flowering rush was predicted under four different future greenhouse gas emission scenarios. These future scenarios consisted of an RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5 scenario, and were modelled to the years 2050 and 2070.

According to the general circulation models, the current range of habitat suitable to the flowering rush consists of the majority of the United States, as well as southern Canada. This is consistent with the observed northern range of flowering rush populations, and there seems to be current potential for the flowering rush to spread south. Under the RCP 2.6 and RCP 4.5

scenarios for both 2050 and 2070, as well as the RCP 6.0 scenario for 2050, there was a predicted net decrease of habitat suitable to the flowering rush. There were predicted losses along the northern border of the United States and in the western United States. Under the RCP 6.0 scenario to 2070, as well as the RCP 8.5 scenario to both 2050 and 2070, there were predicted net increases to the North American range of habitat suitable to the flowering rush. However, the majority of the predicted increases in suitable habitat were in Canada, beyond the northern boundary of the mainland United States, as well as in Alaska. The models run under these scenarios also predicted losses of habitat suitability in the western United States, including significant losses by 2070 under the RCP 8.5 scenario. The most significant environmental factors affecting flowering rush distribution were factors caused by the lowest occurring temperatures. It was found that flowering rush may have undergone a niche shift to the climate in its current range, suggesting adaptation to those climatic conditions.

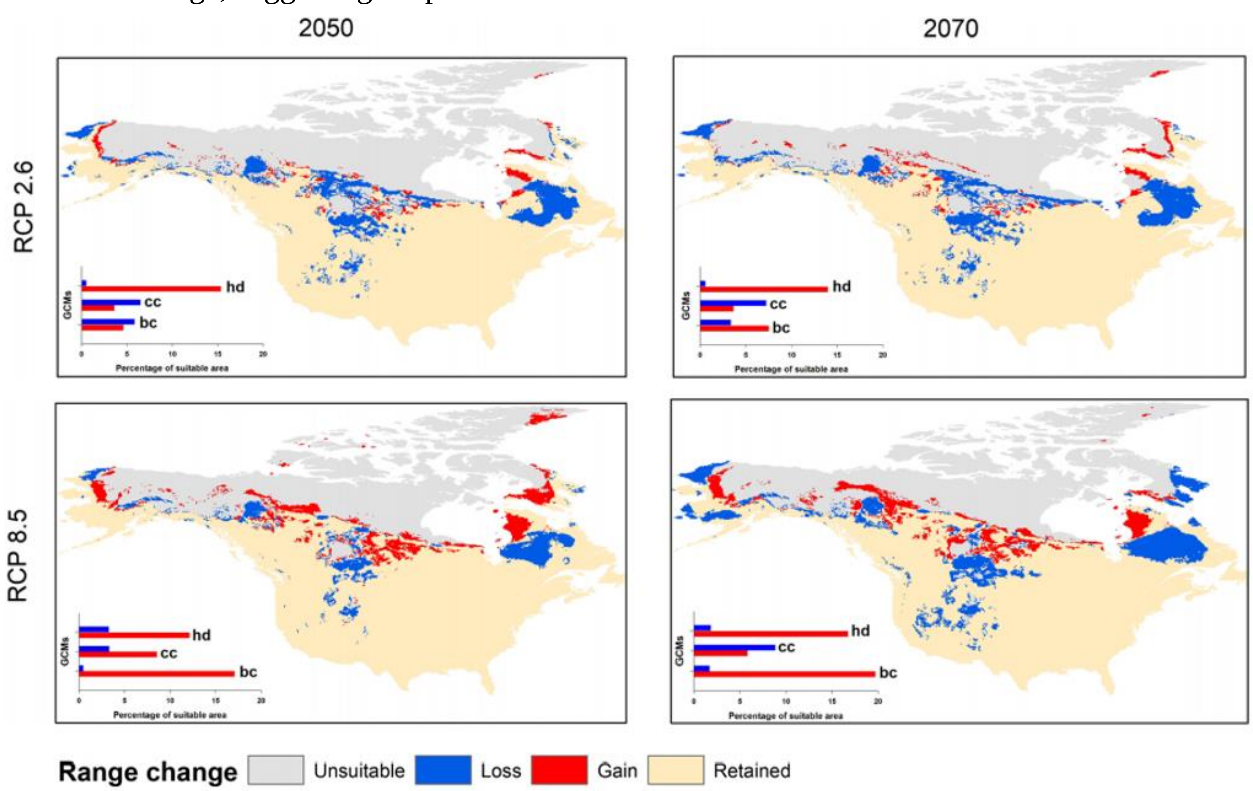


Figure 3. Predicted change in habitat suitable to the flowering rush by 2050 (left) and 2070 (right) under an RCP 2.6 emissions scenario (top) and RCP 8.5 emissions scenario (bottom), (Banerjee et al., 2020).

These results suggest that there will be a decrease in habitat suitable to the flowering rush along the northern border and in the western United States as a result of climate change, and that decrease will be dependent on the level of greenhouse gas emissions that occur. However, much of the United States will likely remain suitable to the flowering rush. This includes large regions south of currently established flowering rush populations. This could result in a net increase in the actual range of the flowering rush, while a decrease in potential suitable range occurs. There may be other factors preventing a southward expansion of the flowering rush. These results may inform a reduction of resources towards managing flowering rush populations in areas that will likely lose suitability. These results may also inform an increase in resources devoted to preventing the spread of the flowering rush southward.

Barbed goatgrass, or *Aegilops triuncialis*, is an invasive grass species that is most problematic along the western coast of the United States. Barbed goatgrass outcompetes native plant species and is native to regions in Europe and Asia. Thomason and Rice (2017) studied the interaction between the demographics of barbed goatgrass and climate change. This was done by studying the impact of precipitation and aggregation of barbed goatgrass populations on barbed goatgrass seed production. Increased exposure to precipitation reduced the seeds produced by an individual plant, and this effect was greatest on plants not in an aggregate patch. The number of seeds produced per plant were greatest in aggregated patches of barbed goatgrass.

These results suggest that the barbed goatgrass will experience contractions, or expansions, of its population, and possible range, depending on changes in the precipitation levels that occur in currently occupied areas. Further, these results suggest that aggregation of the barbed goatgrass is conducive to its survival and reproduction. This suggests that interspecific competition has a more negative effect on barbed goatgrass than intraspecific competition. It can be drawn from this that breaking apart aggregates of barbed goatgrass could be an effective part of a management strategy aimed at slowing down the spread of barbed goatgrass. Accurate predictions of future precipitation levels, as well as the response of barbed goatgrass to other environmental factors, would be beneficial to more accurately predicting the future range of barbed goatgrass. It can generally be drawn from this study that the way an invasive population is dispersed in an ecosystem can have significant effects on that population's growth and survival.

Larson et al. (2021) studied the impact of the climate between 2008 and 2015 on the invasive forb plant Balkan toadflax, or *Linaria dalmatica*, in the Greater Yellowstone Ecosystem. Balkan toadflax was introduced to the United States in the late 19th century and is native to Europe and Asia. Balkan toadflax outcompetes native plant species across the western United States. It was found that, in the time period of 2008 to 2015, Balkan toadflax expanded upwards in elevation and produced more seeds, overall and per plant, at these elevations. In lower elevations, Balkan toadflax had shown a decline in population, as well as in the number of seeds produced overall and per plant. Two main environmental drivers of this were increased summer mean temperatures and differences in winter precipitation levels. Mountain roads were identified as the route by which Balkan toadflax populations expanded upwards in elevation.

Based on these results, it is likely that Balkan toadflax populations will continue to increase in elevation along mountain roads as temperatures increase. The greater number of seeds produced, as these elevations become more suitable to the Balkan toadflax, could act as a source for a population spread deeper into interior mountain ecosystems, and away from roads. This could threaten the biodiversity of native ecosystems that have remained insulated from invasive species in the past. It is also likely that lower elevation populations of Balkan toadflax will continue to decline, and possibly eventually go extinct, facilitating a habitat range shift upwards in elevation.

Historically, an invasion of mountain ecosystems by harmful non-native species has been a rare phenomenon because of the lack of human activity in those ecosystems, as well as that those environments become more unsuitable to many invasive species as elevation increases. However, these results suggest that increasing temperatures can shift suitable habitat elevations upward for Balkan toadflax and other invasive species. In terms of management strategies, these results can inform increasing the resources devoted to slowing or preventing the spread of the Balkan toadflax. Resources could be moved away from mitigation efforts targeting the lower elevation population of the Balkan toadflax. These results also suggest that it would be beneficial to conduct research determining what other invasive plants may invade mountain ecosystems as a result of climate change.

Garlic mustard, or *Alliaria petiolata*, is an invasive plant species, originally native to Europe and Asia, that has become established throughout the eastern United States. Japanese barberry, or *Berberis thunbergii*, is an invasive shrub species, originally native to Japan, that has become established throughout the eastern United States. Japanese barberry is a popularly traded ornamental species and was introduced to the United States, and became established, as a result of this trade. Merow et al. (2017) studied the current and future range, to the year 2050, of habitat suitable for garlic mustard and Japanese barberry. This was done using a combination of experimental biogeography and demographically based population modelling techniques. This was studied in terms of the northeastern United States, specifically New England. Demographic responses of both garlic mustard and Japanese barberry were recorded in response to temperature and precipitation gradients.

The spatial pattern of observed garlic mustard and Japanese barberry populations closely resembled the predicted range of current suitable habitat. For 2050, the models predicted a decrease in the range of suitable habitat for garlic mustard and an increase in the range of suitable habitat for Japanese barberry. This will likely facilitate an expansion of the range and population of Japanese barberry northward. This is because warmer temperatures increase Japanese barberry growth and germination rates. There will likely be a decline in the New England range of habitat suitable to, as well as establishment rates of, garlic mustard. It was found that garlic mustard experiences lower fecundity in warmer environments. It is also the case that the decline of garlic mustard may contribute to an increased expansion rate of Japanese barberry due to the empty niche left by local garlic mustard loss.

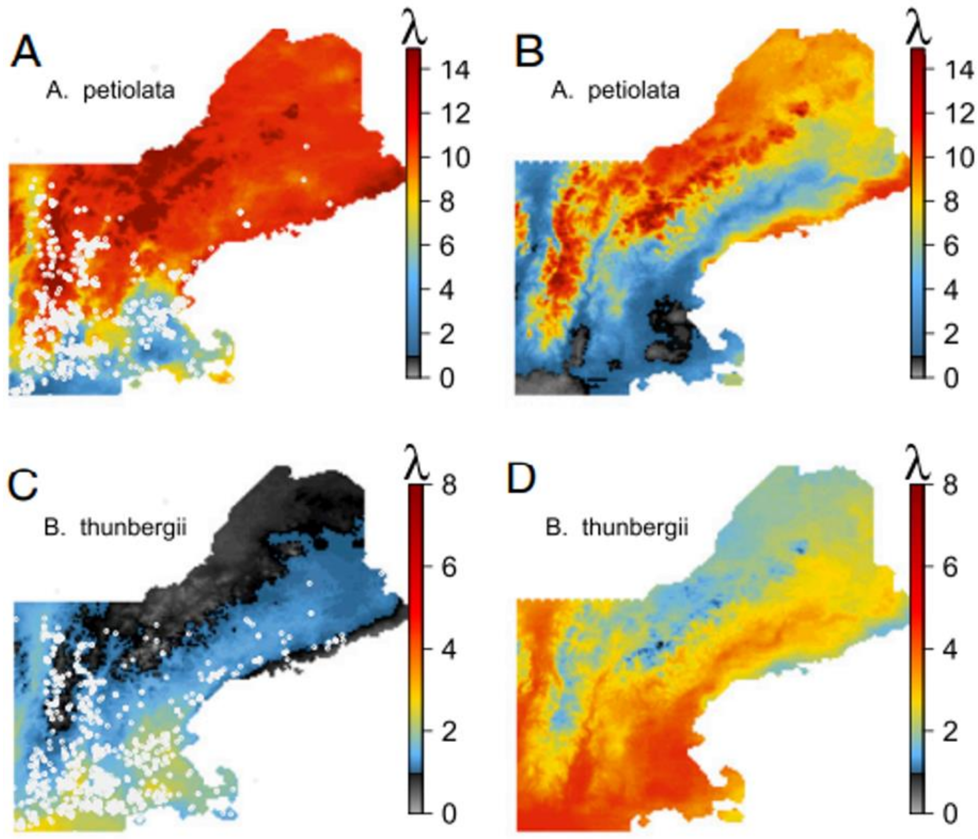


Figure 4. Predicted distribution of garlic mustard under A) current conditions and B) 2050 and Japanese barberry under C) current conditions and D) 2050. Lower numbers indicate lower predicted population, (Merow et al., 2017).

These results suggest that there will be an expansion of the range of Japanese barberry, as well as a decline of the range of garlic mustard, as a result of climate change. These results could inform increased management efforts aimed at the Japanese barberry, and decreased efforts aimed at garlic mustard. It is notable that other studies on the relationship between climate change and invasive species range often use correlative range models to predict changes in habitat suitability, but this has the issue of predicting species interaction in non-native, to the invasive species, environments. This is an issue because of the lack of data on interaction between these environments and organism response. Future studies that use demographic models, similar to the study reviewed here, may be beneficial. It is also notable that studies often focus on climate change facilitating invasions, as opposed to inhibiting invasions. This is complicated by the fact that an inhibition is difficult to observe, or there may be nothing to observe if climate change has prevented an invasion from occurring.

Japanese honeysuckle, or *Lonicera japonica*, is an invasive vine species that has become established in forests throughout the southeastern United States. Originally native to Japan, this vine species was introduced to the United States in the late 19th century. Japanese honeysuckle grows and spreads at fast rates, and damages forest ecosystems by stunting, and sometimes preventing, the growth of native vegetation. This is of particular economic concern because southeastern forests are home to tree species that are a significant source of lumber. Rogers et al. (2012) studied the relationship between various environmental variables and the likelihood of habitat invasion by Japanese honeysuckle.

It was found that there are positive correlations between the likelihood of Japanese honeysuckle invasion and habitat adjacency to bodies of water, private land ownership, species diversity, and site productivity. A negative correlation was found between the likelihood of

Japanese honeysuckle invasion and forest stand age, slope, fire disturbance, distance to nearest road, and artificial regeneration. This data was then taken and used to predict, using regression equations, the possible range expansions of Japanese honeysuckle under then-current and future climatic conditions. Under then-current conditions, it was predicted that the locations with the greatest probability of Japanese honeysuckle invasion were areas between currently occupied habitats, and in the northern region of Japanese honeysuckle range. In terms of future climate, it was predicted that a 2^{o}C increase in temperature would increase the probability of invasion of these locations by Japanese honeysuckle.

These results suggest that ongoing climate change will lead to an increase in the range, as well as the abundance of, Japanese honeysuckle along the northern border of the vine’s current extent. These results suggest a further expansion to other currently unoccupied areas adjacent to currently occupied areas. In fact, these areas are currently at risk of expansion, but climate change will likely further increase the habitat suitability. In terms of management strategies, these results suggest that it would be beneficial to put resources into preventing or slowing the expansion of Japanese honeysuckle. A limitation of this study is that the researchers did not study a possible northward expansion of Japanese honeysuckle beyond its’ current range extent. Interestingly, the researchers also found that public ownership, as well as management of land with artificial regeneration and selective burnings, would significantly reduce the likelihood of Japanese honeysuckle invasion in unoccupied habitats. The researchers argued for public ownership and managing the then publicly owned land with these strategies as a means of reducing range expansion. However, those strategies could also be employed on land that is currently privately owned.

Invasive Aquatic Species

Venezia, Samson, and Leung (2018) investigated the risk of invasive freshwater fish species in general becoming established in North American waters by the year 2050 as a result of climate change. Specifically, the hypothesis was tested that the probability of invasive freshwater fish populations, introduced via the aquarium trade, becoming established will increase as climate change occurs. This hypothesis was tested using modelling of the probability of establishment, and this modelling included multiple variables to account for both environmental changes and the behavior of the freshwater fish species. This modelling was conducted under a single scenario of future climate change, and that scenario was an RCP 8.5 scenario. Data was collected on historical imports of freshwater fish, establishments that have occurred, population estimates, and species trait information.

It was found that the risk of establishment will increase in the United States by 2050, with an average risk increase of 40% across the country. Florida, Hawaii, and Louisiana were predicted to experience the largest increases in establishment risk. On average, greater increases in establishment risk were predicted in southern states, whereas northern states either had lower overall increases or did not have significant increases in establishment risk. Canada had an increased establishment risk, but that establishment risk remained very low. The lower risks in northern states, as well as Canada, were attributed to lower temperatures than those in the more southern regions. Temperature and precipitation were the greatest environmental predictors of establishment risk, whereas maximum fish length and temperature tolerance were the greatest trait predictors.

These results suggest that climate change will increase the probability of invasion, via the aquarium trade, by non-native freshwater fish species throughout the United States, and particularly in the south. This may facilitate the expansion of the range of some invasive freshwater fish species into the United States. This may also facilitate an expansion of the range of invasive freshwater fish species currently established in the United States, such as Carp, particularly in the south. From a management perspective, these results suggest the importance of limiting the import of freshwater fish species with invasive characteristics. It may also be beneficial to devote resources towards studying what freshwater fish species have characteristics conducive to invasion. A limitation of this study is that it only considered a single scenario of future climate change. However, it could be inferred that lower increases in temperatures, than that predicted by the worst-case RCP 8.5 scenario, may also increase the suitability of the United States to invasive freshwater fish species.

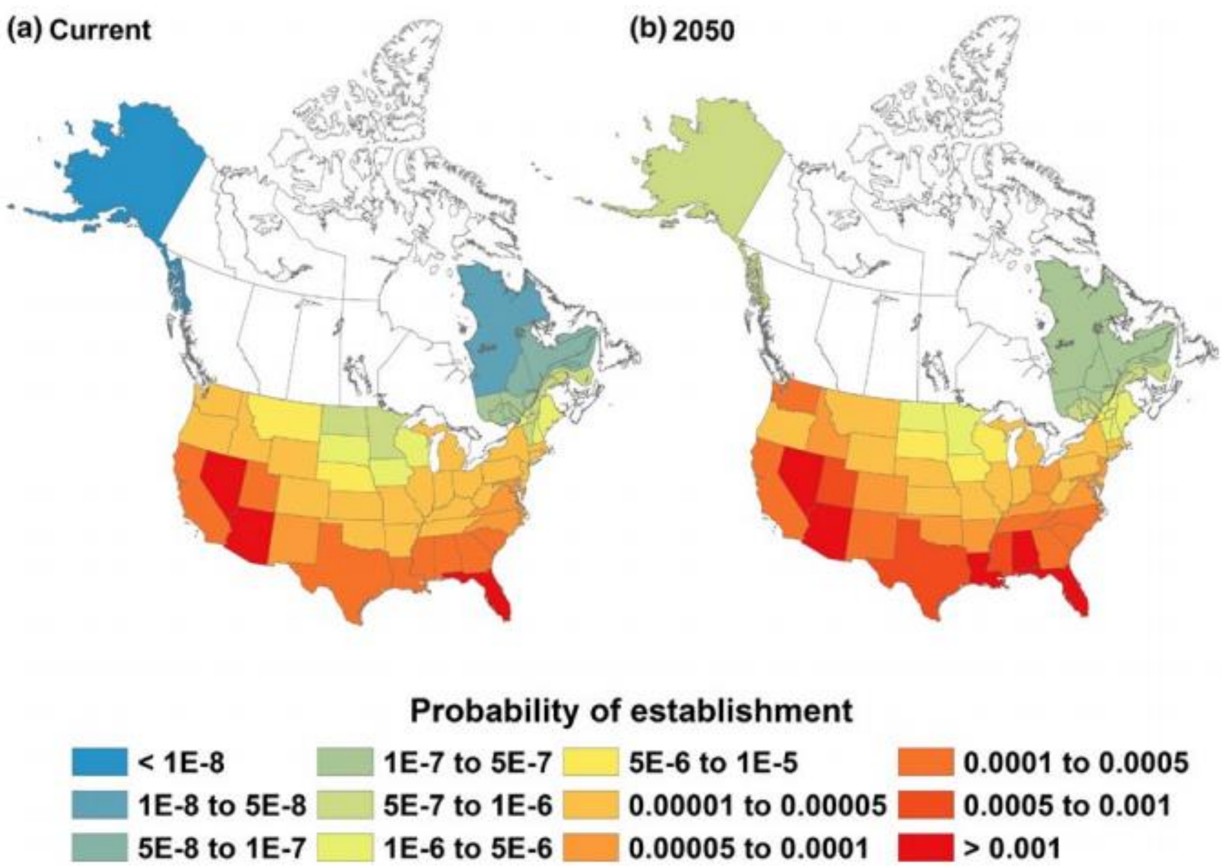


Figure 5. Probability of establishment of invasive freshwater fish under current climatic conditions (left) and in 2050 (right) under an RCP 8.5 emissions scenario, (Venezia, Samson, and Leung, 2018).

The spiny water flea, or *Bythotrephes longimanus*, is an invasive aquatic crustacean and zooplankton species native to Europe and Asia that has become established in waterways in both the northern United States and southern Canada. The spiny water flea is a predator that causes significant changes to native food chains and damages fishing equipment. The spiny water flea was introduced to the United States, via ballast water, in the late 20th century. Sorensen and Branstrator (2017) studied the relationship between spiny water flea survivability and direct oxygen (DO) concentrations. This was done because climate change is expected to exacerbate declines in the DO levels of waterways. This relationship was studied by exposing individual spiny water fleas to water with five different levels of DO. It was found that as DO levels decrease, the survival probability of the spiny water flea decreases. It can be inferred that this mechanism will likely cause a decrease in the range of the spiny water flea as continuing climatic changes cause decreases in the DO levels of currently occupied bodies of water. Further, a number of native fish eat the spiny water flea, which may exacerbate reductions of the population and range of the spiny water flea.

Walsh et al. (2020) modelled the future distribution of the invasive spiny water flea in the upper Midwestern United States. The range of habitat suitable for the spiny water flea, under current and future predicted climate conditions, was modelled using the simulation of both lake thermal regimes and air temperatures. Under current climatic conditions, air temperature models predicted that 89% of lakes within the study region were suitable. Lake thermal models predicted that 42% of those lakes were suitable. Both models predicted that there will be a decline in suitable habitat as temperatures increase. The lake thermal models predicted that, at the end of the century, 19% of lakes within the study region will be habitable. Air temperature models predicted that a single lake will remain habitable at the end of the century. Predicted future air temperatures are commonly used in predicting the future habitable range of invasive species. This can prove problematic in accurately predicting the future habitable range of aquatic organisms because of water body characteristics, such as depth and thermal gradients. The results of this study suggest that there may be a short-term expansion of spiny water flea range into currently uninhabited habitable lakes.

Overall, the results of these studies suggest that there will be a long-term decline of the range of the spiny water flea in the United States, as well as Canada, as a result of climate change. This will likely occur as a result of lowered DO levels in currently occupied bodies of water, as well as changes to the lake thermal characteristics of those bodies of water. These studies show the importance of accurately determining what environmental factors have the most significant effects on species. From a management perspective, these results suggest that efforts aimed at mitigating the spiny water flea will likely be able to be reduced as the range of this invasive aquatic species declines. However, there seems to be short-term potential for the expansion of spiny water flea populations.

Meek et al. (2012) studied the relationship between environmental variables and the population growth rates of the invasive aquatic hydroid species *Cordylophora caspia*, which has no common name. *Cordylophora caspia* is likely native to the Ponto-Caspian region, but has invaded aquatic ecosystems around the world, including along the eastern and western coasts of the United States. It is likely that *Cordylophora caspia* was introduced to the United States via ballasts and ship hulls. Hydroids, such as the invasive *Cordylophora caspia*, are known to significantly disrupt ecosystem dynamics through predation. The environmental variables that were manipulated in the conducted experiments were temperature and salinity, which are expected to change as a result of climate change. *Cordylophora caspia* polyps were collected and subjected to water in 5-gallon tanks with a range of temperature, from 15 ^{o}C to 25^{o}C, and salinity conditions, from 2 to 11 ppt. In terms of the relationship between salinity and growth rates, there was no significant relationship found. In terms of the relationship between temperature and growth rates, there was a significant positive relationship between increasing temperatures and increasing *Cordylophora caspia* growth rates. Small increases in temperature were found to greatly increase the growth rates of the invasive hydroid.

These results suggest that, as global temperatures increase, there will be an increase in *Cordylophora caspia* population sizes and a possible expansion of range in coastal waters along the United States. *Cordylophora caspia* shows a tolerance to a range of salinity levels and will likely be unaffected by changes to salinity levels. In terms of management strategies, these results suggest that it would be beneficial to devote resources towards slowing or preventing the spread of *Cordylophora caspia* populations. It is notable that *Cordylophora caspia* may have to compete with other non-native species in ecosystems it invades, adding a possible limiting factor to their population growth that was not studied in this experiment.

Sorte et al. (2010) studied the impact of temperature on the growth rates and survival of a group of invasive aquatic species that had become established in marine fouling communities located in Bodega Harbor off California. These invasive species occupied 71% of cover within the studied fouling ecosystem, showing that these invasive fouling species have significantly displaced native fouling species. The studied invasive species were *Schizoporella sp*., *Watersipora subtorquata*, *Botrylloides violaceus*, *Botryllus sp*., *Didemnum sp*., and *Diplosoma listerianum*. The relationship between temperature and the growth rates, as well as survival, of four native species was also studied. Water conditions with temperatures ranging from the natural ambient temperature of the environment to 4.5^{o}C greater than this temperature were used.

It was found that the studied invasive species had a greater survivability in warmer temperatures than the native species. Increases in temperature were positively correlated with growth rates for the majority of the invasive species, with the exception of *Watersipora subtorquata. Watersipora subtorquata* individuals were unaffected, in terms of both survival and growth rate, by increases in temperature.

The results of this study suggest that the abundance of invasive marine fouling species, with the exception of *Watersipora subtorquata*, will increase in Bodega Harbor as temperatures increase. It is likely that native species will continue to decline as environmental conditions favor invasives in this habitat. The results also suggest that there may be an increase in the range of the studied species along the west coast, as well as invasive marine fouling species in general, as a result of climate change. In terms of management strategies, these results suggest that it would be beneficial to devote resources towards mitigating the spread of invasive marine fouling species, as well as towards efforts aimed at reducing current populations. Further, it is noteworthy from these results that climate change can cause environmental conditions to become such that they are more favorable to invasive, or other non-native, species than native species.

Invasive Land Animal Species

The African clawed frog, or *Xenopus laevis,* is an invasive amphibian native to South Africa that has spread across the world to the Americas, Europe, and Asia. Ihlow et al. (2016) used two climate models with four future greenhouse gas emission scenarios to predict the current and future worldwide range of the African clawed frog. The climate models used were a MaxEnt model and an ensemble Species Distribution Model, or SDM. The four greenhouse gas emission scenarios were an RCP 2.6, RCP 4.5, RCP 6.0, and an RCP 8.5 scenario. Precipitation during the driest quarter of the year and mean temperatures were the most significant predictors of African clawed frog suitable habitat range.

In terms of the United States, the MaxEnt model predicted a current distribution of African clawed frog suitable habitat in Florida, parts of the west coast, and an area comprising Texas and areas north of Texas. The ensemble SDM predicted a current distribution of suitable habitat covering the west coast, Texas, and a stretch of land in the southeastern United States, with the exception of Florida. The MaxEnt model predicted a decrease in the United States range of habitat suitable to the African clawed frog under all four future greenhouse gas emission scenarios. However, the ensemble SDM predicted an increase in the overall United States range of suitable habitat under all four greenhouse gas emission scenarios. Overall, the results of this study are inconclusive in determining the impact of climate change on the range of the African clawed frog in the United States. The results do suggest that temperature and precipitation will likely be the most significant determining factor of the United States range. It is notable that both the MaxEnt and ensemble SDM models consistently predicted a global decline in the net total range of habitat suitable to the African clawed frog. Further research would be beneficial in accurately determining the response of the African clawed frog to climate change, as well as determining the best management strategies for dealing with the African clawed frog.

Di Febbraro et al. (2016) studied the worldwide invasion risk posed by eight squirrel species, including one species native to the United States. These squirrel species were *Atlantoxerus getulus*, *Funambulus pennantii*, *Callosciurus erythraeus*, *Callosciurus finlaysonii*, *Sciurus aureogaster*, *Sciurus carolinensis*, *Sciurus vulgaris*, and *Tamias sibiricus*. *Sciurus carolinensis*, or the grey squirrel, is the species that is native to the United States. No populations of the other squirrel species are currently established on the mainland of the United States. The studied squirrels are known to have been transferred between countries in the past as a result of trade, and particularly the pet trade. Squirrels generally have characteristics that give them significant invasive potential. Invasive squirrel species displace native species and act as vectors of disease. The invasion risk was studied by modelling current and future, to 2070, habitat suitability using an SDM with 19 bioclimatic variables and two climate models, HadGEM2 and CCSM4, under an RCP 6.0 and RCP 8.5 future greenhouse gas emission scenario.

In terms of the United States, it was found that the majority of the country, including Alaska and Hawaii, are at risk for the establishment of the seven squirrel species not native to the country. The non-native squirrel species posing the greatest risk of establishment were *Atlantoxerus getulus*, *Funambulus pennantii*, *Sciurus vulgaris*, and *Tamias sibiricus*. It was predicted, under both future greenhouse gas emission scenarios and both climate models, that by 2070 the range of suitable habitat for the squirrel species will remain relatively similar, with important differences. It was predicted that there will be an increase in overall habitat favorability along coastal regions, including the west coast, the west coast of Hawaii, and the southern coast of Alaska. There was a predicted decrease in the overall habitat favorability along the eastern coast of the United States and in sections of the middle of the country. Interestingly, the RCP 8.5 scenario predicted greater increases and decreases of favorability than the RCP 6.0 scenario. These greater increases or decreases were caused by the RCP 8.5 scenario causing more significant environmental changes than the RCP 6.0 scenario.

These results suggest that much of the United States, including Alaska and Hawaii, is currently at risk of establishment by potentially invasive squirrel species. These results suggest that climate change will likely increase the habitat suitability along the western coast of the United States while decreasing the habitat suitability along the eastern coast and in the middle of the country. It is important to note that these regions will remain suitable habitat, but there will be changes in their overall suitability. This suggests that there will be declines in the risk of invasion by non-native squirrels along the east coast and in the middle of the country, but an increase in that risk along the western coast. Current and future conditions may facilitate the range expansion of one or more non-native squirrel species into the United States, especially along the western coast as temperatures increase. In terms of management strategies, these results suggest that it would be beneficial to devote resources towards preventing the introduction of non-native squirrel species into the United States. This will especially be the case for the western coast of the country as climatic changes occur.

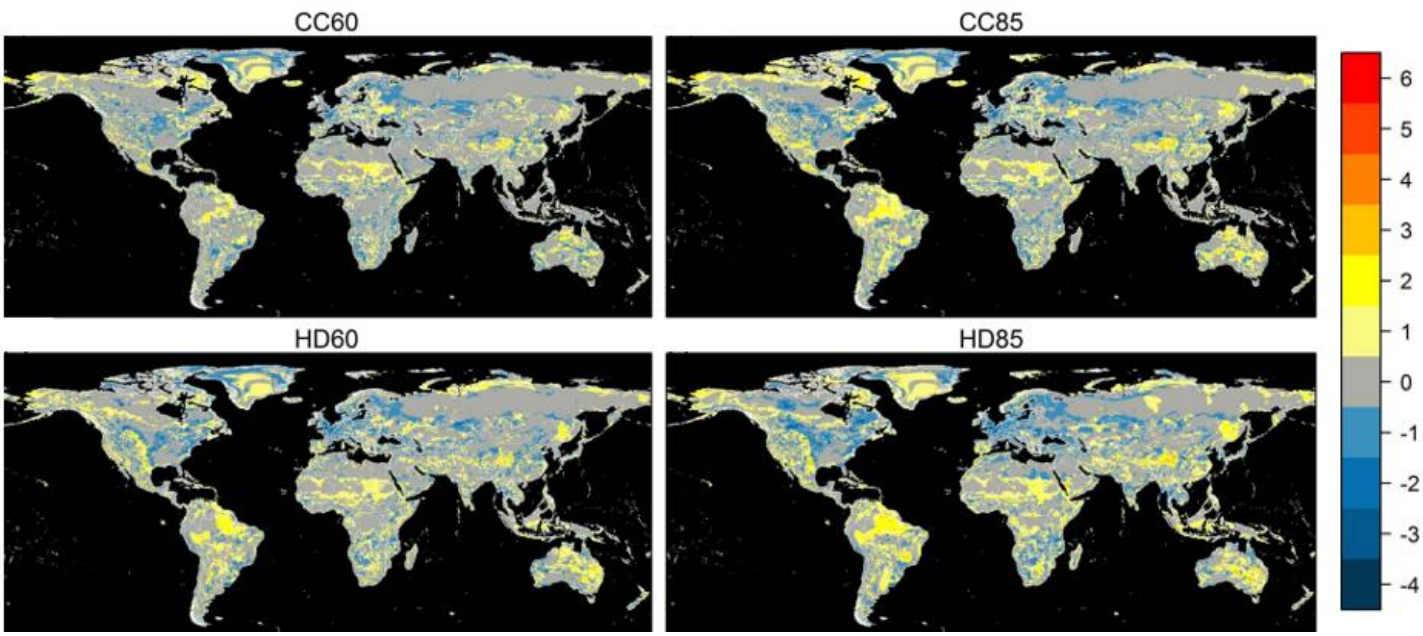


Figure 6. Predicted 2070 change in invasion risk by non-native squirrel species under an RCP 6.0 (left) and RCP 8.5 scenario (right) and the CCSM4 model (top) and HadGEM2 model (bottom). Positive numbers indicate an increased risk, negative numbers a decreased risk, (Di Febbraro et al., 2016).

Two invasive slug species, the Cuban slug, or *Veronicella cubensis*, and the tropical leatherleaf, or *Laevicaulis alte*, are currently established across the Hawaiian Islands. The Cuban slug is native to the Bahamas, Cuba, Puerto Rico, and the southeast of the United States mainland. It is likely that the tropical leatherleaf is native to the African continent. Sommer and

Cowie (2020) studied the relationship between temperature and the two invasive slug species. Nine Cuban slugs and nine tropical leatherleaf slugs were collected and allowed to reproduce, producing 15 single and 15 pairs of Cuban slugs and two single and four pairs of tropical leatherleaf slugs. The researchers ran into issues when attempting to reproduce tropical leatherleaf slugs. 10 additional Cuban slugs and 20 additional tropical leatherleaf slugs were collected from the University of Hawaii. The slugs were divided in half, with one half being put in 22^{o}C and the other in 27^{o}C conditions to simulate the effects of different temperature conditions.

The slugs were then observed to study the effects of these temperature differences on growth, reproduction, egg characteristics, and hatching. In terms of the Cuban slug, it was found that eggs hatched significantly sooner, 4 days sooner, in 27^{o}C conditions than in 22^{o}C conditions. Growth rates were also greater in 27^{o}C conditions than in 22^{o}C conditions. Eggs per egg-laying and percent hatchability of those eggs were not significantly affected by temperature differences. In terms of the tropical leatherleaf, growth was slightly slower in the 27^{o}C conditions, but egg hatching occurred significantly sooner, by 6 days. Similarly, eggs per egg-laying and percent hatchability were unaffected by temperature differences.

These results suggest that Cuban slugs and tropical leatherleaf populations will increase as temperatures increase over time. Currently, Cuban slugs and tropical leatherleaf slugs are not present on higher elevations in Hawaii, likely because of cooler temperatures. The results suggest that these elevations will likely become suitable to the invasive slug species as temperatures increase. This will likely facilitate a range expansion of the Cuban slug and tropical leatherleaf to increased elevations as a result of climate change. In terms of management practices, these results suggest that it would be beneficial to devote more resources towards dealing with these slug species as temperatures increase. The study has the limitations that it had small sample sizes and that it only looked at the effects of temperature, and not the effects of other environmental factors.

Recommendations

In terms of the sampled species, it would be beneficial to devote resources towards slowing, or preventing, the spread of the species that will likely experience an increase in suitable range as a result of climate change. Resources could be prepared to mitigate the negative effects of the invasive species in areas that are likely to be invaded. Further resources could be devoted towards mitigating the impacts of invasive species in areas where currently existing populations will likely increase in abundance. Resources could be moved away from the mitigation of the invasive species that will likely decrease in range as this decrease occurs. Alternatively, the reduction in the suitable habitat of certain invasive species could be used in tandem with strategies to reduce their populations more quickly. It would be beneficial to conduct further research on the sampled invasive species with inconclusive results. In general, research on the impact of climate change on the range of other invasive species could be used to inform management decisions for those species. Where this research is lacking, it would be beneficial to conduct such research on the impact, especially for invasive species that cause significant damage. Further, there seems to be a lack of research on the impact of climate change on the range of larger invasive species.

Management strategies that could be employed in dealing with these invasive species include, ideally, preventing their introduction to new areas through inspections and decontamination, as well as the quarantine of transported goods that contain invasive species. Once established, or in areas where populations are currently established, strategies can be employed to contain the invasive species to that area and to reduce the population of that invasive species, (USDOI, 2019). Methods of reducing the population size of an invasive species include mechanistic removal by hand or with tools, the use of chemical controls such as pesticides, and the introduction of predators of the invasive species to keep populations in check, (NISIC, 2020). However, the introduction of predators is not recommended because those predators could become invasive, adding more damage to already disturbed ecosystems. Ideally, mitigation strategies that could cause environmental harm, such as the use of certain pesticides, should be used sparingly or after other, more environmentally friendly, methods have failed. Other mitigation efforts include educating the public about invasive species that are vectors of disease or about the invasiveness of commonly traded species, such as popular invasive plant species. Monitoring of the population of invasive species is essential to accurately understand how climate change is impacting those populations, as well as for informing management strategies for those populations.

From a legal perspective, there is currently no comprehensive legal framework for dealing with invasive species in the United States. Instead, a combination of different laws and policies related to invasive species constitutes the current legal framework related to invasive species, (CRS, 2017; Adams et al., 2018). These policies include the Lacey Act, which bans the import of species listed under its injurious species provision. Notably, under the Lacey Act, only those species that have been listed, after going through a review process, are banned. This means that unlisted harmful non-native species are legal to import, and getting those species listed would require a potentially long review process. Executive Order 13112 on Invasive Species, signed in 1999, prohibits the federal government from committing any actions that would likely cause the introduction or spread of invasive species in the United States. The Endangered

Species Act is relevant when invasive species are a cause of the decline of the population of an "endangered" or "threatened" species. In light of the significant harms caused by invasive species in the United States, as well as that these harms will likely be exacerbated by ongoing climate change, it would be beneficial for a more comprehensive legal framework to be developed. Further, it would be beneficial to review, and possibly overhaul, currently existing laws related to dealing with invasive species.

Limitations

Due to the number of invasive species in the United States, as well as a lack of research on how climate change will affect all of them, it was outside the scope of this paper to review the impacts of climate change on the range of every invasive species in the United States. Studies predicting the future habitat range of invasive species, as well as species in general, are sometimes conducted using climate models, and sometimes under different future greenhouse gas emission scenarios with those models. Different models and greenhouse gas scenarios sometimes yield different results, making it difficult to accurately predict how climate change will impact future range. This is particularly problematic when there are contradictions between the results of different climate models. This shows the importance of accurately determining how environmental factors will affect different invasive species, as well as the importance of confirming the accuracy of different climate models. Luckily, it seems that methods of modelling habitat ranges have significantly improved in the last 20 years in terms of accuracy, (Lantschner, 2019). Different greenhouse gas emission levels in the next 100 years would cause different changes to the range of environmentally suitable habitat for invasive species. The actual change in the range of habitat suitable to, as well as the actual range of, invasive species will depend on what future greenhouse gas emission levels take place.

Conclusion

In terms of the sampled invasive insect species, the Asian tiger mosquito and tropical fire ant will likely experience an expansion of range in the United States as a result of climate change. The spotted wing Drosophila, Japanese beetle, and cycad aulacaspis scale will likely experience a decrease in United States range as a result of climate change. Results were inconclusive in terms of determining the impact of climate change on the range of the pea leafminer. In terms of the sampled invasive plant species, musk thistle, Japanese barberry, and Japanese honeysuckle will likely expand in range in the United States as a result of climate change. Garlic mustard will likely experience a contraction in United States range as a result of climate change. The range of habitat suitable to the flowering rush will likely decrease as a result of climate change, but there may be an overall increase in the range of the flowering rush due to currently unoccupied regions of the United States remaining climatically suitable. The overall population size, as well as future range, of barbed goatgrass will depend on how precipitation levels change in currently occupied areas, as well as areas adjacent to them. The United States range of Balkan toadflax will likely increase in elevation, with a decline in lower elevation populations, as a result of climate change.

In terms of invasive aquatic species, freshwater fish in general, the hydroid *Cordylophora caspia*, and several marine fouling species will likely experience an increase in range, as well as overall habitat favorability, in the United States as a result of climate change. The spiny water flea will likely decrease in range in the United States as direct oxygen, or DO, levels decrease in currently occupied waterways. In terms of invasive land animal species, much of the United States is currently at risk of invasion by several non-native squirrel species due to favorable environmental conditions. It is likely that the United States will remain suitable to invasion by these squirrel species, with an increase in habitat favorability along the west coast and a decrease along the east coast and in the middle of the country, as climatic conditions change. The Cuban slug and tropical leatherleaf will likely experience an expansion of range upwards in elevation in Hawaii as a result of climate change. Results were inconclusive in terms of determining how climate change will impact the United States range of the African clawed frog.

Overall, climate change will very likely cause changes to the range of invasive species in the United States. Some invasive species will likely increase, while others will likely decrease, in range as a result of changing climatic conditions. The extent of these range changes will depend on the course of future greenhouse gas emissions. Future scenarios with greater levels of greenhouse gas emissions tend to predict more significant changes in range than scenarios with lower levels. The environmental factors that seem to be most significant in terms of changes to habitat suitability are temperature and precipitation, although other environmental factors can be significant. Further research on the impact of climate change on invasive species range, as well as other population dynamics, would be beneficial to developing an accurate understanding. Further research would also be beneficial for informing management strategies with the aim of dealing with invasive species.

References

Aaron, L. B., Ellen, A. M., & Newman, J. A. (2017). The impacts of climate change on the abundance and distribution of the Spotted Wing Drosophila (*Drosophila suzukii*) in the United States and Canada. *PeerJ, 5*, e3192. https://doi.org/10.7717/peerj.3192

Adams, D. C., Olexa, M. T., & Reynolds, T. (2018). Federal Invasive Alien Species Policy: Incremental Approaches and the Promise of Comprehensive Reform. *Drake Journal of Agricultural Law*, *23*, 291–351.

Banerjee, A. K., Harms, N. E., Mukherjee, A., & Gaskin, J. F. (2020). Niche dynamics and potential distribution of Butomus umbellatus under current and future climate scenarios in North America. *Hydrobiologia*, *847*(6), 1505–1520. https://doi.org/10.1007/s10750-020-04205-1

Bellard C., Leroy, B., Thuiller, W., Rysman, J., & Courchamp, F. (2016). Major drivers of invasion risks throughout the world. *Ecosphere*, *7*(3). https://doi.org/10.1002/ecs2.1241

CRS. (2017). *Invasive Species: Major Law and the Role of Selected Federal Agencies*. Congressional Research Service.

Di Febbraro, M., Martinoli, A., Russo, D., Preatoni, D., & Bertolino, S. (2016). Modelling the effects of climate change on the risk of invasion by alien squirrels. *Hystrix*, *27*(1), 1–8.

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(40), 11261–11265.

Dueñas, M., Hemming, D. J., Roberts, A., Diaz-Soltero, H. (2021). The threat of invasive species to IUCN-listed critically endangered species: A systematic review. *Global Ecology and Conservation*, *26*(e01476). https://doi.org/10.1016/j.gecco.2021.e01476

FWS. (2012). *Frequently Asked Question About Invasive Species*. U.S. Fish and Wildlife Service. https://www.fws.gov/invasives/faq.html.

Ihlow, F., Courant, J., Secondi, J., Herrel, A., Rebelo, R., Measey, G. J., Lillo, F., De Villiers, F. A., Vogt, S., De Busschere, C., Backeljau, T., & Rödder, D. (2016). Impacts of Climate Change on the Global Invasion Potential of the African Clawed Frog Xenopus laevis. *PLoS ONE*, *11*(6), 1–19. https://doi.org/10.1371/journal.pone.0154869

IPCC. (2014). *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects*. Intergovernmental Panel on Climate Change. https://www.ipcc.ch/report/ar5/wg2/.

ISAC. (2016). *Invasive Species Impacts on Infrastructure*. Invasive Species Advisory Committee. https://www.doi.gov/sites/doi.gov/files/uploads/isac_infrastructure_white_paper.pdf

Lantschner, M. V., De la Vega, G., & Corley, J. (2019). Modelling the establishment, spread and distribution shifts of pests. *International Journal of Pest Management*, *65*(3), 187–189. https://doi.org/10.1080/09670874.2019.1575490

Larson, C. D., Pollnac, F. W., Schmitz, K., & Rew, L. J. (2021). Climate change and micro-topography are facilitating the mountain invasion by a non-native perennial plant species. *NeoBiota*, *65*, 23–45. https://doi.org/10.3897/neobiota.65.61673

Lee, C. M., Lee, D. S., Kwon, T. S., Athar, M., & Park, Y. S. (2021). Predicting the Global Distribution of Solenopsis geminata (Hymenoptera: Formicidae) under Climate Change Using the MaxEnt Model. *Insects (2075-4450)*, *12*(3), 229. https://doi.org/10.3390/insects12030229

Marsh, A., Hayes, D., Klein, P., Zimmerman, N., Dalsimer, A., Burkett, D., Huebner, C., Rabaglia, R., Meyerson, L., Harper-Lore, B., Davidson, J., Emery, M., Warziniack, T., Flitcroft, R., Kerns, B., & Lopez, V. (2021). 9. Sectoral Impacts of Invasive Species in the United States and Approaches to Management. In *Invasive Species in Forests and Rangelands of the United States: A Comprehensive Science Synthesis for the United States Forest Sector* (pp. 203–230). essay, Springer International Publishing / USDA / USFS. https://www.fs.fed.us/research/publications/book/invasiveSpecies/invasiveSpeciesChap9.pdf.

Meek, M. H., Wintzer, A. P., Wetzel, W. C., & May, B. (2012). Climate Change Likely to Facilitate the Invasion of the Non-Native Hydroid, Cordylophora caspia, in the San Francisco Estuary. *PLoS ONE*, *7*(10), 1–6. https://doi.org/10.1371/journal.pone.0046373

Merow, C., Bois, S. T., Allen, J. M., Yingying Xie, & Silander Jr., J. A. (2017). Climate change both facilitates and inhibits invasive plant ranges in New England. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(16), E3276–E3284.

Mika, A. M., & Newman, J. A. (2010). Climate change scenarios and models yield conflicting predictions about the future risk of an invasive species in North America. *Agricultural & Forest Entomology*, *12*(3), 213–221. https://doi.org/10.1111/j.1461-9563.2009.00464.x

NISIC. (2020). *Control Mechanisms*. National Invasive Species Information Center. https://www.invasivespeciesinfo.gov/subject/control-mechanisms.

Primtel, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*. *52*(3): 273-288. doi:10.1016/j.ecolecon.2004.10.002

Rochlin, I., Ninivaggi, D. V., Hutchinson, M. L., Farajollahi, A. (2013). Climate Change and Range Expansion of the Asian Tiger Mosquito (Aedes albopictus) in Northeastern USA: Implications for Public Health Practitioners. *PloS ONE*, 8(4), 1–9.

Rogers, W. E., Wang, H., Grant, W. E., & Wonkka, C. L. (2012). Potential Range Expansion of Japanese Honeysuckle (Lonicera japonica Thunb.) in Southern U.S. Forestlands. *Forests*, *3*(3), 573–590. https://doi.org/10.3390/f3030573

Shwiff, S., Shwiff, S., Holderieath, J., Haden-Chomphosy, W., & Anderson, A. (2018). 3. Economics of Invasive Species Damage and Damage Management. In *Ecology and Management of Terrestrial Vertebrate Invasive Species in the United States* (pp. 35–59). USDA. https://nwrc.contentdm.oclc.org/digital/collection/NWRCPubs1/id/60562/rec/7.

Sommer, R. M., & Cowie, R. H. (2020). Invasive traits of veronicellid slugs in the Hawaiian Islands and temperature response suggesting possible range shifts under a changing climate. *Journal of Molluscan Studies*, *86*(2), 147–155. https://doi.org/10.1093/mollus/eyz042

Sorensen, M. L., & Branstrator, D. K. (2017). The North American invasive zooplanktivore Bythotrephes longimanus is less hypoxia-tolerant than the native Leptodora kindtii. *Canadian Journal of Fisheries and Aquatic Sciences*, *6*, 824.

Sorte, C. J. B., Williams, S. L., & Zerebecki, R. A. (2010). Ocean warming increases threat of invasive species in a marine fouling community. *Ecology*, *91*(8), 2198.

Teller, B. J., Zhang, R., & Shea, K. (2016). Seed release in a changing climate: initiation of movement increases spread of an invasive species under simulated climate warming. *Diversity & Distributions*, *22*(6), 708–716. https://doi.org/10.1111/ddi.12436

Thomas, K., Jean, E. (2019). The Potential Global Distribution and Voltinism of the Japanese Beetle (Coleoptera: Scarabaeidae) Under Current and Future Climates. *Journal of Insect Science*, *19*(2). https://doi.org/10.1093/jisesa/iez023

Thomason, M. J. S., Rice, K. J., (2017). Spatial Pattern and Scale Influence Invader Demographic Response to Simulated Precipitation Change in an Annual Grassland Community. *PloS ONE*, 12(1), 1–18. https://doi.org/10.1371/journal.pone.0169328

USDOI. (2019). *Invasive species: Finding solutions to stop their spread*. U.S. Department of the Interior. https://www.doi.gov/blog/invasive-species-finding-solutions-stop-their-spread.

Venezia, L. D., Samson, J., & Leung, B. (2018). The rich get richer: Invasion risk across North America from the aquarium pathway under climate change. *Diversity and Distributions*, *24*(3), 285-296. https://doi.org/10.1111/ddi.12681

Walsh, J. R., Hansen, G. J., Read, J. S., Zanden, J. V. (2020). Comparing models using air and water temperature to forecast an aquatic invasive species response to climate change. *Ecosphere*, *11*(7). https://doi.org/10.1002/ecs2.3137

Wei, J., Zhao, Q., Zhao W., & Zhang, H., (2018). Predicting the potential distributions of the invasive cycad scale Aulacaspis yasumatsui (Hemiptera: Diaspididae) under different climate change scenarios and the implications for management. *PeerJ*, *6*, e4832. https://doi.org/10.7717/peerj.4832

WWF. (2016). *Living Planet Report 2016: Risk and resilience in a new era.* WWF International, Gland, Switzerland.

Appendix

Contact: Joshua Ash, Adjunct Professor at Point Park University

Joshua helped me learn, and get access to information, about how the United States legal system deals with invasive species. Joshua also reviewed my thesis and gave me general feedback.

Contact: Mary Spiro, Science Writer at the American Society for Cell Biology

Mary reviewed my thesis and gave me feedback on my writing, as well as the formatting of the paper.

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