Designing biology informed anthropogenically driven invasive forest pests risk models

by

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Abstract

Forest invasive species (FIS) pose significant threats to the economic and ecological stability of our forests. Given the potential impact of invasive species, tools are needed that will help prevent invasions, or enable effective early responses through robust interception and surveillance frameworks. Spatial models aim at identifying meaningful spatial relationships between different geographical features. Climate based spatial models have the ability to provide information on current and future potential for invasion and spread. Species distribution modelling (SDM) is a valuable tool for predicting the potential distribution of invasive species across space and time. While recent developments in modeling approaches and wider availability of environmental datasets have create advanced and more accurate SDM, in many cases the developed models ignore the associated underlying ecological processes. Moreover, bioclimatic variables usually included in the SDMs do not account for anthropogenic impacts on the response variable and the methods to integrate species traits as predicted by genetics into projections of species distributions are not generally used. In this PhD dissertation I address these key issues in particular reference to two pests and two pathogens that represent urgent threats. I explored the sensitivity of SDM modelling in two of the major ports in Canada and produced dispersal restricted projections of individual FIS distributions in various climate change scenarios. I also analyzed the methodology of determining climatic niches and compared the native and post-invasion niches of chosen FIS.

I found that if I ignored the underlying FIS biology such as use of biologically relevant predictors, appropriate feature selection and inclusion of dispersal and biotic interactions when I developed SDMs, I obtained complex SDMs that provided an incomplete picture of the potential FIS invasion. Most of the representative invasives were far away from reaching niche equilibrium.

In this thesis throughout I discuss the potential of spatial models in risk analysis of FIS. I provide an improved framework for invasive species risk mapping using spatial models. The methodology presented in this dissertation to develop pest risk maps is robust and easy and the presented results can guide monitoring and help inform management of these and other invasive species.

Lay summary

Biological invasions are becoming one of the main causes of global loss of biodiversity and the extinction of species. Early detection and rapid action to prevent introduction or establishment of incoming invasives are required for a successful response. Therefore, it is extremely important to determine potential areas at risk and identify other relevant factors well in advance for species from different geographic sources if effective invasive mitigation strategies are to be formulated. This study aims at enhancing understanding of species distribution modelling of invasive species with a goal to develop a framework to produce robust risk maps for early assessment of pest risks. The mapping framework presented is robust and easy to follow by the risk assessors and the results can guide monitoring and help inform management of invasive species.

Preface

This PhD dissertation is an original research, proposed and designed by me, Vivek Srivastava, with support and guidance of my PhD Supervisory committee and project collaborators Dr. Melody A. Keena and Dr. Amanda D. Roe. The research, data collection, data analyses and interpretation of results were done by me under guidance of my supervisors. My co-authors in the below mentioned list of publications advised me on improving the methods and data for the analyses. Along with the supervisory committee, Dr Melody A. Keena and Dr. Amanda D. Roe have helped me in improving the manuscripts and presentation of the results. Dr A. Townsend Peterson, Dr R. Talbot Trotter, III (US Forest Service), Dr Robert A. Haack and colleagues at Canadian Food Inspection Agency have helped in reviewing the manuscripts.

Chapter 1

- a) Srivastava, V*., Lafond, V., & Griess, V. C. (2019). Species distribution models (SDM): applications, benefits and challenges in invasive species management. CAB Reviews, 14(020), 1-13.
- b) Lafond, V., Lingua, F., Lumnitz, S., Paradis, G., Srivastava, V., & Griess, V. C. (2019). Challenges and opportunities in developing decision support systems for risk assessment and management of forest invasive alien species. Environmental Reviews, (ja).

Chapter 2

- a) Srivastava, V*., Griess, V. C., & Keena, M. A. (2020). Assessing the potential Distribution of Asian Gypsy Moth in Canada: A comparison of two Methodological Approaches. Scientific Reports, 10(1), 1-10.
- b) Srivastava, V*., Roe, A., Keena, M., Hamelin, R., Griess, V. C. (2020). Oh the places they'll go: improving species distribution modelling for invasive forest pests in an uncertain world. Under revision with Biological Invasions. Manuscript number is BINV-D-20-00065.

Chapter 3

 a) Srivastava, V*., Liang, W., Keena, M., Roe, A., Hamelin, R., Griess, V. C. (2020). Assessing niche shifts and conservatism by comparing major forest invasive species between native and invasive ranges. Under review with Global Ecology and Biogeography. Manuscript number is GEB-2020-0201.

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List of abbreviations

AGM	Asian gypsy moth
AICc	Akaike information criterion corrected
ALB	Asian longhorned bettle
ANN	Artificial neural networks
AUC	Area under curve
CCSM4	Community Climate System Model
CFIA	Canadian food inspection agency
DED	Dutch elm disease
ENFA	Ecological niche factor analysis
FIS	Forest invasive species
FN	Fundamnetal niche
GARP	Genetic rule set for prediction
GBIF	Global Biodiversity Information Facility database
GCMs	General circulation models
GLM	Generalized linear models
HadGEM2-ES	Hadley Global Environment Model 2 - Earth System
HEMI-2	Hyper-envelope modeling interface-V2
HII	Human Influence Index
MaxEnt	Maximum entropy
MIROC5	Model for Interdisciplinary Research on Climate
PAs	Pseudo absences
PN	Potential niche
RCP	Representative Concentration pathways
RD	Risk distribution
RDM	Reciprocal distribution modelling
RDMaps	Risk distribution maps
RF	Random forests
RN	Realized niche

SDMs	Species distribution models
SOD	Sudden oak death
TSS	True skill statistic
WW	Sirex woodwasp

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Dedication

Dedicated to Mahadeva and Parents!

Introduction

Background

Biological invasions are becoming one of the main causes of global loss of biodiversity and the extinction of species (Groombridge, 1992; Mooney, 2005; Woiwod et al., 1991). They are also responsible for substantial monetary losses (e.g. direct economic losses from sectors like agriculture, forestry, environment, human health, etc. were reported to be around US\$14.45 billion in China during 2001-2003 and US\$128 billion annually in US) (Pejchar & Mooney, 2009; Xu et al., 2006). Biological invasions are usually caused by invasive species [but see (Valéry et al., 2008)], which the International Union for Conservation of Nature (IUCN) defines as: (i) "a species, sub-species or lower taxon occurring outside of its natural range (past or present) and dispersal potential (...)" - i.e. *alien* - that (ii) "becomes established in natural or semi-natural ecosystems or habitat, is an agent of change, and threatens native biological diversity" - i.e. *invasive* (Shine et al., 2000). Invasive species can be plants, animals, or microorganisms, and their introduction to the invaded ecosystem can be either natural or induced by human activities (e.g. as international trade, travel and tourism). For this dissertation, forest invasive species (FIS), are referred to as invasive species that continue to spread to new areas and pose significant threats to forest health.

There has been a constant rise in the number of invasive species successfully establishing in new habitats (Allen & Humble, 2002; Chornesky & Randall, 2003) and their impacts are anticipated to be significant throughout all ecosystems (Levine & D'Antonio, 2003; Musselman, 1994). Moreover, the global, national and regional spatial patterns of future species invasion might worsen due to rise in international trade (Seebens et al., 2015), increases in human population (Seebens et al., 2018) and changes in climate (Peterson et al., 2008). Invasive species are of high relevance to both natural and managed ecosystems (Dodds & Orwig, 2011; Kenis et al., 2008; Liebhold et al., 1992). The risks for our current ecosystems are so substantial that the Convention on Biological Diversity asks for measures "*to prevent the introduction, control or even eradication of those alien species which threaten ecosystems, habitats or species*" ("Convention on biological diversity," 1992).

In Canada forests are a major source of capital, providing US\$19.8 billion in annual revenue, in addition to other social and environmental benefits (NRCan, 2016b). These valued forests have historically felt the economic effects of FIS introductions. Significant tree losses in these forests were caused by the spruce budworm, European gypsy moth and Dutch elm disease. Additionally, several major Canadian cities suffered from widespread tree mortality caused by the Dutch elm disease (DED). In Quebec alone, nearly 600,000 elm trees were removed as a result of DED infestation between 1945 and 1965 (NRCan, 2016a). In the early 1900s, an alien disease, known as the white pine blister rust, accounted for significant annual loss of two white pine species within Canada. The white pine blister rust is currently one of several FIS endangering white bark pine, a high-elevation species that grows within British Columbia and Alberta (NRCan, 2017a).

A report prepared by the Canadian government in 2014 stated that 20.3 million ha of forest were damaged by non-native forest insects (NRCan, 2016c). The European gypsy moth is considered to be one of the most destructive FIS in Canada (Brockerhoff et al., 2010). This species has defoliated hardwoods throughout the regions of eastern Canada at different times throughout the last century (Journal et al., 2016). The emerald ash borer, another non-native FIS, is known to have killed urban ash trees in Ontario in 2002. Furthermore, it is estimated that up to 15 million ash trees in urban and forested areas have been killed by the borer so far (Poland & McCullough, 2006). A report prepared for the Canadian Council of Forest Ministers in the year 2009 stated that Canada could have avoided an annual cost of \$165 million by preventing the introduction and establishment of four damaging FIS: Asian longhorn beetle, emerald ash borer, sirex woodwasp, and sudden oak death disease (NRCan, 2017a).

It is estimated that there are thousands of invasive species with the potential to harm Canadian forests (Allen et al., 2002). The World Conservation Union's list of the 100 worst invasive species globally includes many species that have already established in Canada. It was assessed that these previous introductions account for an annual loss of \$7.5 billion in damages to agricultural crops and forests (Government of Canada, 2004). Moreover, Colautti et al., (2006), projected a cost of \$187 million CDN per year that would be required to combat the 16 established non-native FIS in Canada. In addition, international trade could be severely threatened by FIS further affecting the economy. The detection of ALB in 1998 almost derailed trade between Canada, China, and Hong Kong valued at of \$30 billion (Government of Canada, 2004). These costs could have been reduced

or perhaps, entirely saved if preventive measures were taken well in advance. This includes documenting more information about potential FIS, as well as adding comprehensive surveys and inspections at locations with the highest potential risk. Having FIS risk distribution maps and additional information on FIS ecology and behavior in advance of introductions and outbreaks would greatly help resource managers to plan site specific preventative measures.

Introductions of FIS to new ecosystems are both inevitable, and predictable (Walther et al., 2009). Thus, early detection and rapid response to incoming invasives are required for a successful response (Kaiser & Burnett, 2010). Early FIS detections are preferred so the species will not have time to occupy its entire potential range (Kaiser & Burnett, 2010; Meyerson & Mooney, 2007). Early response strategies involve surveying and monitoring of risk areas under threat of invasion to find infestations in their earliest stages of invasion. To identify such areas at risk, that are suitable for the establishment of invasive species, climate matching methods show promise as they are based on the classical assumption that species will be able to establish populations in areas outside of their native range that closely match the environmental conditions of their native distribution (Wiens, 2011). Thus, by matching climatic conditions, researchers can discern meaningful information about invasive species potential establishment range in new habitats.

Given the potential impact of invasive species, tools are needed that will help prevent invasions, or enable effective early responses through robust interception and surveillance frameworks (Barbosa et al., 2012; Jiménez-Valverde et al., 2011; Lafond et al., 2019). Unfortunately, these programs are costly and require regional prioritization. Species distribution models (SDMs) are one approach used to identify areas at risk of invasion. SDMs are a combination of tools that translate environmental conditions from a species' known distribution to predict its potential distribution in a new habitat. These can be combined with climatic models that forecast future climate scenarios, providing further information on the future potential for invasion and spread. The information provided by SDMs is critical for conservation and management planning and for understanding invasive species ecology and behavior under changing climatic conditions (Padalia et al., 2014).

FIS distribution maps generated from species distribution models are effective risk depiction tools that inform managers about probable outbreaks of invasive species. Here, risk is defined as the

probability that a FIS will establish in a specific area and cause damage. In addition to this, the maps can also describe the spread patterns and potential establishment ranges of FIS and support strategic pest management decisions and efforts. This becomes especially important when considering global trade restrictions, planning field surveys, and setting up domestic quarantines (Venette et al., 2010a).

SDMs can be broadly classified into two groups: correlative models and process-based /mechanistic models (Peterson et al., 2015). Correlative SDMs are trained with species occurrence data and associated environmental layers from a known distribution, which is then used to identify suitable habitats in a new range for a given invasive species (Elith et al., 2010a). The entire process is complex and must manage uncertainties within the modelling process (Gould et al., 2014). Recent advances in iterative model development, model fitting, evaluation and improvement have led to an increase in accuracy, however questions remain around the practice of model building. Without biologically informed baseline data, complex default SDM models could be selected, even though alternative settings may be more appropriate (Merow et al., 2013). Additional scrutiny has come to other aspects of SDM modelling, such as estimating FIS distributions accurately within a new geography (transferability), the choice of bioclimatic variables, and the effect of varying model-fitting parameters on the resulting distribution predictions (Jiménez-Valverde et al., 2008; Srivastava et al., 2019).

Currently, modelling FIS distributions using SDMs present three major challenges: first, use of default model settings even though the alternative settings may offer better and more accurate outputs. Secondly, bioclimatic variables usually included in the SDMs do not account for anthropogenic impacts on the response variable (Lippitt et al., 2008). And finally the methods to integrate FIS heritable traits into projections of species distributions are not generally used (Engler et al., 2012). This is despite the fact that FIS invasions can be hypothesized as a result of an increase in dispersal capabilities (Groves & Di Castri, 1991). Given the prevalence of SDMs within the invasion literature, addressing these issues in a SDM framework is critical.

In this dissertation I present a modelling framework for assessing the invasion risk of FIS. I chose four FIS that represent urgent threats to serve as case studies i: two insects (Asian longhorned beetle [ALB], *Anoplophora glabripennis* (Motschulsky); Asian gypsy moth [AGM], *Lymantria*

dispar asiatica Vnukovskij and L. d. japonica Motschulsky) and two pathogens (sudden oak death [SOD], Phytophthora ramorum Werres; Dutch elm disease [DED], Ophiostoma ulmi (Buisman) Melin & Nannf. and O. novo-ulmi Brasier). In chapter 3, I have replaced AGM with another invasive insect i.e. sirex woodwasp [WW], Sirex noctilio (Fabricus) due to different objectives and also due to the fact that AGM has not been yet established outside its native range. The selected FIS pose significant threats to Canadian forests (Hamelin & Roe, 2019). The two insects are considered high risk invasives and subject to regulatory action (e.g., removal of tree hosts for ALB eradication, denying vessel entry if AGM is detected) by the Canadian Food Inspection Agency, the national regulatory body responsible for protecting Canada's plant resources from invasive species. SOD has been found associated with nursery plants in the southern coastal area of BC, but not yet in urban or forest environments in Canada. The CFIA conducts annual surveys for SOD in nurseries, and if detected, the nursery is placed under quarantine and infected plant material is destroyed resulting in economic losses to the owner. DED has devastated elms across most of Canada since its arrival in the 1940's but does not yet occur in Alberta or BC. There are various provincial and municipal groups across the country supporting programs to protect remaining elms from the deadly disease. Despite these efforts from various plant protection groups, these species continue to pose a risk to Canada. For example, a new ALB population was detected in Toronto in 2013 after the first population, detected in 2003, was successfully eliminated. (Turgeon et al., 2015). Similarly, the CFIA continues to detect AGM on vessels coming from Asian ports (recent find in 2019) after being eradicated around the Vancouver port in 1992 (Nealis, 2009).

Gypsy moth (*Lymantria dispar* L.) is an invasive insect which is listed as one of the 100 worst invasive species in the world, selected from global invasive species database by the International Union for Conservation of Nature (IUCN). Gypsy moth can cause serious defoliation and weakening of trees and shrubs, that either leads to tree death directly or indirectly by subsequent infestation by a secondary pest. Currently, gypsy moth is spreading in North America (primarily in the United States) damaging both commercial and native forest ecosystems over much of the introduced range. The pest also poses a significant economic threat to several other countries that are taking actions to prevent its introduction (Limbu et al., 2017). Two subspecies, Asian gypsy moth (*L. dispar asiatica* Vinkovskij), distributed throughout temperate Asia, and the Japanese gypsy moth (*L. dispar japonica* Motschulsky), distributed throughout Japan, are of serious concern

although they have not yet permanently established (though several incursions have been eradicated) outside their native range (Paini et al., 2018). The two subspecies, *L. d. asiatica* and *L. d. japonica* collectively referred to as Asian gypsy moth (AGM) have a broad host range (over 600 plant species, including conifers) and the females are flight capable (Keena et al., 2008). They have an affinity to fly towards light sources and strong dispersal traits, which makes them a greater threat than their European counterpart. The AGM females have been found to fly to lights in port areas and lay their egg masses on cargo and the superstructure of ships. A study by Paini et al., (2018) found that more than 7,500 ships that have the potential to carry AGM egg masses from Asia arrived in 2005 at Canadian ports that fall into the climatically suitable range of AGM. Several detections of AGM egg masses on vessels coming from Asian ports have occurred in Canada (the first eradication effort occurred around the Vancouver port in 1992) which have led to the implementation of international phytosanitary measures to prevent AGM establishment that are significantly reducing the risk of invasion (Nealis, 2009).

Asian longhorned beetle is a large cerambycid woodboring beetle that attacks >100 species of hardwood trees. ALB is native to Asia (21 to 45 ° N latitude), though predominantly found within central and northern China, as well as the Korean peninsula. ALB infested large monocultures of hybrid poplars and windbreaks of willows that were planted as part of an afforestation effort in northern China in the 1970s and 1980s, and subsequently became recognized as an important forest pest (Meng et al., 2015, 2014). The first invasive population of ALB in North America was detected in New York in 1996 (Haack et al., 1997; Blackburn et al. 2020) and the first detection in Europe was in 2001 (Hérard et al., 2006). Subsequently more invasive populations have been discovered in North America between 38 and 44° N latitude (five states and one Canadian province) and Europe between 33 and 60 ° N latitude (11 countries, (Javal et al., 2019a; Moussa & Cocquempot, 2017; Blackburn et al. 2020). To date the most northern invasive population of ALB was in Finland and the most southern is in Lebanon, indicating that the species can tolerate a wide thermal range. The source of the invasive populations remains unclear due to complex genetic structure in the native range and potentially reticulated invasion pathways due to secondary spread from invasive populations (Javal et al., 2019a, 2019b).

Sudden oak death is an invasive disease caused by *Phytophthora ramorum*, a pathogen that was discovered simultaneously on oaks in California and rhododendron in Europe in the mid-1990s (Grünwald et al., 2019; Rizzo et al., 2005). The pathogen is native to Indochina and the source of the two introductions was recently discovered to be in Vietnam (Jung et al., 2020). It has an extremely broad host range, which facilitates its spread through the horticulture industry. But the pathogen can also spread from nurseries into natural forests where it can cause severe outbreaks. The epidemic spread is quite different in nurseries, where it is driven by the movement of infected material via trade, and in forests where the presence of sporulating hosts, such as bay laurel and tanoak in California, is responsible for the production of spores and the intensification of outbreaks. The pathogen sporulation and host infection appear to be restricted to the rainy season in the Pacific Northwest and the annual variation in precipitation is likely an important factor influencing the epidemic (Rizzo et al. 2005). The disease has so far been reported in western North America, throughout Europe and recently in Japan and Vietnam (Grünwald et al., 2019; Jung et al., 2020).

Dutch elm disease is caused by a pathogen complex that comprises *Ophiostoma novo-ulmi*, *O. ulmi* and *O. himal-ulmi*. The origin of the pathogen is still unclear, but is assumed to have originated from the Himalayas (Brasier & Mehrotra, 1995). The first disease pandemic was caused by *O. ulmi* in the 1940s in North America and Europe, followed by a second pandemic by the more virulent *O. novo-ulmi*. The pathogen is vectored by elm bark beetles that carry the fungus spores into the vascular system of the host. The pathogen can be spread both by long-term transport of elm wood and by the spread of the beetle. The pathogens appear to thrive under various environmental conditions. In North America it is found from the West Coast to the East Coast and from Saskatchewan to Texas. All North American and European elms are susceptible to various degrees, but several Asian elm species are resistant.

Woodwasp *Sirex noctilio* is native to Europe, northern Asia and northern Africa where it has few negative impacts on *Pinus* plantations and rarely outbreaks (Spradbery & Kirk, 1978; Wermelinger & Thomsen, 2012). The first invasive population of *Sirex noctilio* was found in New Zealand in the early 1900's and it has since invaded many pine producing countries in the southern hemisphere (Australia, Uruguay, Argentina, Brazil, Chile, Western Cape, Eastern Cape, Kwazulu-

Natal, Mpumalanga and Limpopo). In 2004, it was first discovered in North America (Hoebeke et al., 2005) and it is now found in seven U.S. states and 2 Canadian provinces. Genetic analyses have revealed a complicated invasion history, with invasive populations showing at least some level of admixture, meaning derived from more than one source population (Boissin et al., 2012). The Oceania populations came from Europe, then insects from there spread to South Africa and South America. South African populations also received insects from South America and an unknown location. South American populations received insects from Europe directly and Chile also received insects from the same unknown population as is found in South Africa. North American populations are a mixture of insects from South America, Europe and possibly Australia. Interestingly, the population of sirex sampled in Switzerland shows invasion by a mixture of the unknown source and South American genotypes, even though it is part of the native range. It uses many Pinus species, but P. radiata, P. taeda and P. patula are very susceptible to attack. In the invaded areas in the southern hemisphere damaging outbreaks occur. Tree death occurs after female wasps oviposit eggs along with a phytotoxic mucus and a symbiotic wood decay fungus (Amylostereum areolatum) into stressed trees. Since the larvae require the decaying wood to develop, conditions must be right for fungal growth to occur. The temperature range over which sirex can complete development is 12.5-33.5°C but 60% die at 33.5°C (Madden, 1981). In warmer climates it can have two generations per year and in colder climates it may take multiple years to complete a generation (Yousuf et al., 2014).

Rationale

Canada's relatively cool climate has acted as a barrier to many invasive species in the past but increases in temperature and lack of natural enemies could eventually lead to much higher probabilities of new species invasions (NRCan, 2017b). Several FIS that have already established in the US, are gradually advancing north to Canada (NRCan, 2016d). In recognition of FIS ability to threaten the country's environment and economy (Roy et al., 2014), a set of proactive measures must be introduced to prevent their introduction and establishment in Canada (NRCan, 2016a). Therefore, it is extremely important to design a robust SDM framework in order to identify potential areas at risk well in advance if effective FIS mitigation strategies are to be formulated. Recent increased accessibility to high resolution environmental and FIS data can provide the data needed for precise modelling of species distributions (Kumar & Stohlgren, 2009).

Currently, for the focal FIS, there is information on preferred hosts, responses to temperature, and other biological information, but their specific niche characteristics in their respective introduced and invasive ranges have not been defined or compared. Moreover, there are limited studies that examine the potential risk distribution regions and spread patterns of the focal FIS across Canada. Also, studies addressing impacts of FIS dispersal on projections of their distributions are very rare (Srivastava et al., 2019). Providing such information is important in understanding their ecology leading to better early detection rates. The outcomes of this study are highly important, as advanced modelling approaches presented here allow the evaluation of risk for non-native FIS, even before they invade new regions. The present work will assist decision makers with related FIS control decisions.

Research objectives

The overall aim of my doctoral thesis is to enhance the understanding of species distribution modelling for invasive species with a goal to develop a framework to produce robust risk maps for early assessment of pest risks. The specific research objectives are listed below.

- Research objective 1 (Chapter 1): Identify current applications of SDMs and review the benefits and challenges of using SDMs to estimate, and spatially project, invasion risk.
- Research objective 2 (Chapter 2): Map FIS potential distribution, dispersal and prediction uncertainty and propose a framework to produce robust pest risk maps.
- Research objective 3 (Chapter 3): Compare post invasion realized niche shifts across diverse populations of FIS.

Chapter 1 is a review chapter on applications, benefits and challenges of species distribution models in invasive species management. Here, I have reviewed basic concepts and the recent developments in the fields of SDMs, and related spatial modelling tools and techniques. **Chapter 2** is a research chapter wherein I have developed SDMs to map the potential distributions of the focal FIS across Canada and their respective native regions. Here, I have presented a framework to produce a dispersal restricted potential distribution of invasives in changing climate scenarios. The chapter is important for establishing a risk mapping framework and further identifying the risk areas that are more likely to be invaded, given introduction of the FIS, either accidentally or by other means. The chapter brings a novel approach to bring the elements of species genetic traits

into projections of species distributions. In *Chapter 3*, I have investigated niche conservatism for major FIS. Exploring niche characteristics between native and introduced ranges offered additional insights that will be useful in understanding range expansion and invasion potential of non-native species. Figure 1 provides a conceptual diagram outlining the structure of the dissertation.

Designing biology informed anthropogenically driven invasive forest pests risk models



Figure 1 Conceptual diagram outlining the structure of this dissertation. SDMs- Species distribution models; FIS- Forest invasive species; FN- Fundamental niche; RN- Realized niche

Chapter I: Species distribution models (SDMs): applications, benefits and challenges in invasive species management- A review¹

1.1. Introduction

SDMs are predictive tools that identify relationships between observed occurrences and environmental predictors by using statistical models or theoretically derived response curves (Elith & Leathwick, 2009; Guisan & Thuiller, 2005; Stohlgren et al., 2010). SDMs are also referred to as correlative or statistical models, habitat models, or ecological niche models and are broadly divided into two groups: correlative, and process-based or mechanistic models (Coops et al., 2009). These correlative and process based models are derived from various statistical approaches which include generalized linear models (GLM), ordination and classification methods, Bayesian models, locally weighted approaches, environmental envelopes, or combinations of these models (Elith & Leathwick, 2009). Correlative SDMs approaches utilize species occurrence data and associated environmental layers of the study area, to produce maps of probability of occurrence or relative environmental suitability for a species, whereas process-based, or mechanistic niche models, use species functional characteristics and physiological thresholds for model fitting (Kearney & Porter, 2009). The correlative SDMs make use of existing species occurrence data collected from surveys, online databases or museums/herbaria records for fitting (Elith & Leathwick, 2009). In practice, most mechanistic models require exhaustive experimental data on species functional traits which becomes a challenge for the target species under study (Shabani et al., 2016). The correlative approach also differs from the mechanistic from the way it represents species' niche. A common understanding is that correlative approaches only measure the realized niche, which is a subset of a fundamental niche where the species is not absent due to biotic competition. Whereas, the mechanistic approach approximates species fundamental niche (Dormann et al., 2012). This can be a challenge for correlative approaches as for them the

¹The content of this chapter has been adapted from:

⁻Srivastava, V*., Lafond, V., & Griess, V. C. (2019). Species distribution models (SDM): applications, benefits and challenges in invasive species management. CAB Reviews, 14(020), 1-13.

⁻Lafond, V., Lingua, F., Lumnitz, S., Paradis, G., **Srivastava, V.**, & Griess, V. C. (2019). Challenges and opportunities in developing decision support systems for risk assessment and management of forest invasive alien species. Environmental Reviews, (ja).

fundamental niche of the species remains unknown. However, both of the approaches have their own strengths and weaknesses.

Amongst correlative SDMs, several algorithms are available for predicting species potential distributions (Elith & Graham, 2009). MaxEnt is one of the most popular choices for correlative models (Merow et al., 2013). MaxEnt is a presence-only based method which has been successfully applied to model the distributions of invasive species in different parts of the world [e.g., (Fernández & Hamilton, 2015; Ficetola et al., 2007; Kumar et al., 2016; Meyer et al., 2010; Padalia et al., 2014; Poulos et al., 2012; Stohlgren et al., 2010; Ward, 2007)]. MaxEnt generates a probability estimate of presence (or relative environmental suitability) of a species that varies from 0 (lowest) to 1 (highest). Whereas, CLIMEX is a process-based species distribution modeling tool (Merow et al., 2013; Sutherst, 1985) which generates a climatic suitability index for the species, known as the Eco climatic Index (EI). EI ranges from 0 to 100; values close to 100 represent landscape suitability for the species. Both of them have been found to be very effective in each of the categories that aim to predict invasive species establishment risk (Gallien et al., 2010; Jones, 2012; Kumar et al., 2014b, 2015, 2016; Webber et al., 2011).

The popularity and rise in the availability of SDMs has facilitated their use in invasive species management (Elith & Leathwick, 2009). However, the robustness of risk maps created using SDMs has been questioned due to the way the models are developed and the manner in which output maps are interpreted (Venette et al., 2010). Guisan & Thuiller, (2005) attribute this to the practice of constructing weak ecological baseline assumptions when building an SDM. This might lead to inaccurate assessments of invasion risk, which in turn has the potential to support the selection of sub- optimal response measures, as well as an over-, or under investment in mitigation activities (Venette et al., 2010).

This research chapter provides an overview of various approaches used to build a robust correlative SDM that incorporate strong ecological baseline assumptions for accurate assessments of the invasion risk, while also reviewing various applications, benefits and challenges of SDMs, particularly in the areas of biological invasions. I have consciously excluded process based models [see (Kearney & Porter, 2009)], as they require thorough understanding of species physiological

responses to environmental factors and are often unavailable for new arriving alien species. I address the following questions:

- 1) What are the current applications of SDM in ecology and biological invasions in particular?
- 2) What are the benefits and challenges of using SDM to estimate, and spatially project, invasion risk?
- 3) What are the important aspects to consider when building a SDM for mapping invasion risk?

1.2 Methods and materials

1.2.1 Review methodology

I conducted a literature search using Clarivate Analytic's web of science search platform using the search phrases "Species Distribution Modelling", "Niche Modelling", "Habitat Predictive Modelling", "Habitat Mapping", Invasive Species Niche Modelling", and "Invasive Species Risk Mapping". I used these search phrases as published articles in this field often contains these phrases in the title of the article. Hence, I sought papers that contained these search phrases in the title. The search phrases were entered separately with an "OR" separator on the basic search function, which yielded a total of 3,457 articles published between 2000 and 2019. I first restricted this selection to papers published between 2000 and 2019, to focus the review on recent SDM applications and methodological advancements along with modelling challenges. Later, I refined the search based on the research areas in which they were published: environmental sciences ecology, biodiversity conservation, zoology, plant sciences, forestry, and entomology. I did this to analyze the trend of using SDM in different areas of ecology and biogeography. I then selected 100 scientific papers centered on invasive species distribution modelling. Papers were chosen based on the relevancy to the topic. I also analyzed the temporal trend of using SDMs in the fields of ecology, biodiversity conservation, environmental sciences, plant sciences, evolutionary biology, entomology and multidisciplinary sciences (Figure 3 and 4). This was accomplished by using Web of Science research categories. Considering these resources, I provide a brief review of the various aspects

related to creating an effective distribution model for invasive species, along with the benefits, challenges and good practices associated with correlative species distribution models (SDMs).

1.3 Review text

1.3.1 Current trends in applications of SDMs in ecology and invasion biology

SDMs are currently in use for a wide range of applications (Table 1). From characterizing niche and ecological requirements of a particular species (Peters & Peters, 1991; Thum & Lennon, 2010; York et al., 2011), to mapping the potential distribution of plants and animals (Kumar et al., 2016; Peterson et al., 2001, 2004, 2007, 2008; Ward, 2007), or using output maps in policy making, and to prioritize conservation efforts (Barrio et al., 2006; Beaumont et al., 2007; Burgess et al., 2017; Cayuela et al., 2009; Jeschke & Strayer, 2008; Porfirio et al., 2014; Thomson et al., 2006). Williams et al., (2009) successfully used a suite of SDMs as a tool to discover populations of rare plant species with highly specialized habitat needs. Their models included generalized linear models (GLM), artificial neural networks (ANN), random forests (RF) and MaxEnt. Engler et al., (2004) provided an enhanced method for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data by simulating pseudo-absences based on ecological niche factor analysis (ENFA) and concluded that ENFA weighted pseudo-absences could be a possible way to enhance a SDMs explanatory power. Raes et al., (2009) assessed botanical richness and endemicity patterns of all species in Flora Malesiana in Borneo using SDM and concluded that SDM can effectively guide conservation efforts. Esselman & Allan, (2011) explored SDM applications in a data-limited freshwater setting (inadequate human capacity and technology, lack of investment in research and monitoring) in developing countries of northeastern Mesoamerica to enhance conservation planning and Brotons et al., (2004) used data from long-term monitoring programs data to map habitat suitability for 99 bird species. Furthermore, Svenning et al., (2011) concluded that SDMs can also be used in paleobotany, where it can provide a quantitative ecological perspective, while offering potential for an enhanced contribution of paleobiology to ecology and conservation biology. This compliments the ability of the SDMs to provide predictions of past organism's distributions and assessment of their range determinants. Overall, the applications of SDMs have evolved continually over the past decade (Figures 2 and 3).

Type of applications	Example reference(s)
Projecting potential impacts of climate	Dullinger et al., 2004; Elith et al., 2010; Medley, 2010; Padalia et al.,
change on species distributions	2015; Vanhanen et al., 2007
Predicting species invasion	Febbraro et al., 2019; Jiménez-Valverde et al., 2011; Régnière et al.,2008; Williamson, 2006
Characterizing the niche and exploring the ecological requirements	Brotons et al., 2004; Kumar et al., 2014a; Leibold, 1995; Lippitt et al., 2008; Meentemeyer et al., 2008
Conservation and policy making	Abolmaali et al., 2018; Breiner et al., 2015; Cayuela et al., 2009; Daehler et al., 2004; Lawler et al., 2011; Meller et al., 2014.
Assessing the impacts of land cover	Ancillotto et al., 2016; Fuller et al., 2012; Gallardo et al., 2015; Smolik
change and human footprint on species	et al., 2010; Thuiller et al., 2004; Westphal et al., 2008
distributions	
Predicting the distribution of rare and	Abrha et al., 2018; Breiner et al., 2015; Cayuela et al., 2009; Daehler
endangered species	et al., 2004; Guisan et al., 2006; Meller et al., 2014; Thapa et al., 2018;
	Tran, 2018; Yi et al., 2016
Testing an ecological theory	Austin, 2007; Elith & Leathwick, 2009; Guisan & Thuiller, 2005;
	Hoffman et al., 2010; Peterson, Townsend Peterson, & Vieglais, 2001;
	Soberon & Townsend Peterson, 2005
Risk assessment	Jiménez-Valverde et al., 2011; Matsuki et al., 2001; Mckenney et al.,
	2003; Venette et al., 2010; Yemshanov et al., 2010; Zimmermann et
	al., 2000
Assessing disease risk	Kluza et al., 2007; Meentemeyer et al., 2008; Peterson & Samy, 2016; Václavík et al., 2010

Table 1 Examples of species distribution models applications in the fields of ecology and biogeography



Figure 2 Publications on primary applications of species distribution models in various fields of ecology and biogeography.



Figure 3 Publications on species distribution models and their various areas of application.

Most SDMs applications fall in the fields of ecology and biodiversity conservation (Figure 3). Within these broad fields SDMs are used for diverse applications, primarily related to climate change studies, exploring range shifts of species and studying species invasion (Figure 2). It should however be noted that this often involves extrapolating the predictions to novel climates, which often requires extreme cautions (see 1.3.3.2).

SDMs applications related to invasive species and risk mapping are relatively recent but the field is evolving (Febbraro et al., 2019; Meentemeyer et al., 2008; Padalia et al., 2014; Poulos et al., 2012; Smolik et al., 2010; Srivastava et al., 2018). In the recent years a gradual increase in the number of studies using SDM to answer questions related to biological invasions has been observed (Figure 2). I reviewed current applications of the SDMs concerning biological invasions and found that the major applications were around investigating species invasion ecology (Ficetola et al., 2007; Meyer et al., 2010; Muirhead et al., 2006; Stiels et al., 2011, 2012; Václavík & Meentemeyer, 2009), estimate disease risk (Kluza et al., 2007; Meentemeyer et al., 2008; Peterson & Samy, 2016; Václavík et al., 2010), determine possible invasive species range shifts under climate change (Dullinger et al., 2004; Elith et al., 2010; Medley, 2010; Padalia et al., 2015; Vanhanen et al., 2007) and assess the impacts of land cover change (Ancillotto et al., 2016; Fuller et al., 2012; Gallardo et al., 2015; Smolik et al., 2010; Thuiller et al., 2004; Westphal et al., 2008) and human footprint (Ancillotto et al., 2016; Fuller et al., 2012; Gallardo et al., 2015; Smolik et al., 2010; Thuiller et al., 2004; Westphal et al., 2008) on invasive species distribution. Although SDMs can be applied in a variety of ways to solve the complex issues related to invasive species, numerous challenges are linked to the process involved in developing SDMs and predicting the distributions. In the following sections I review the benefits and challenges associated with the SDMs in brief.

1.3.2 Benefits and challenges of using SDM in invasion biology

In regions where invasive species are a significant contributor to the global change in biodiversity and considered one of the key reasons for species extinctions (Holmes et al., 2009), preventive measures assisted by SDMs can be of great value. For example, a report prepared for the Canadian Council of Forest Ministers in the year 2009 stated that Canada could have avoided spending \$165 million annually by preventing the introduction and establishment of four damaging a forest invasive species (FIS): Asian longhorn beetle, emerald ash borer, sirex woodwasp, and sudden oak death disease. Using risk maps to guide surveying and monitoring programs aimed at finding infestations in their earliest stages of invasion appears to be a promising and cost-effective approach (Brockerhoff et al., 2012; Kumar et al., 2014b). These distribution maps generated from SDMs are becoming the favored guide for resource managers who repeatedly survey for non-native species (Jiménez-Valverde et al., 2011; Venette et al., 2010). Risk maps derived from SDMs support decision making for pest management and depict risk probability based on the likelihood of an alien species arrival or establishment (Jiménez-Valverde et al., 2011). These maps can play a pivotal role in the study of alien species and have potential to describe where invasive species might arrive, establish, spread, or cause harmful impacts. They might also aid in pest management decisions such as international trade regulations, design of surveys and local quarantines (Venette et al., 2010).

Though SDMs have multiple benefits as discussed above in estimating and projecting invasion risk and can be used in variety of ways to assist decision makers, building SDMs and projecting the distributions of an invasive species is not an easy task. Many uncertainties are associated with these projections, particularly when it comes to building a robust SDM for an invasive species. Invasive species often encounter novel environment settings in their nonnative range and it becomes hard for a SDM to capture the new settings from the native range of the species (Kumar et al., 2015). The key challenges with respect to using SDMs to estimate and spatially project invasive risk have been discussed and highlighted in various reviews. For example, Venette et al. (2010) addressed the challenges around unavailability or inadequate information for model construction, choice of model, selection of predictors, calibration and validation of models and lastly interpretation of the outputs. Whereas, Araújo & Guisan, (2006) identified: clarification of the niche notion, sampling design, parameterization, model selection and predictor contribution and model evaluation as major challenges. I found major challenges of using SDMs to estimate and spatially project invasion risks were related to projection (transferability), niche characterization, biotic interactions, species dispersal and uncertainty.
1.3.3 Building SDM for mapping invasion risk

Building a SDM for mapping invasion risk is a multifaceted exercise. Below are outlined the required focal steps to build a correlative SDM (Elith & Leathwick, 2009):

- 1. Collection of species occurrence data.
- 2. Assessment of the accuracy and completeness of the occurrence data.
- 3. Inspecting the relevance of the environmental variables to be included in the model.
- 4. Minimalizing the correlation effect among the predictor variables.
- 5. Selecting a suitable algorithm and later fitting the model to train the datasets.
- 6. Evaluating the predictive performance on the test data.
- 7. Projecting predictions onto geographic space.
- 8. Iterating the process to improve the model performance

Each of these steps is associated with a set of challenges related to data and method choice, which can be even more pronounced in the case of invasive species (Venette et al., 2010). Several factors that are involved at each step of SDM development may affect the model predictions, for e.g. biased sampling (step 1), inaccurate data (step 2), autocorrelation among the predictor variables (step 3) etc.

Species observation data, their quality and treatment, appear as a critical aspect to achieve more robust models for accurate predictions of invasion risk. SDMs indeed heavily rely on good occurrence data and relevant environmental dataset. Although current availability of high-resolution bio-climatic data on various aspects of environments aids for better SDM, occurrence information for invasive species often comes as a challenge due to lack of resources or knowledge. The knowledge on absence information of invasive species is also often lacking. Therefore, different SDMs method have been developed to use either presence-absence (PA) or presence-only (PO) data (Brotons et al., 2004). In addition, some modelling techniques also use 'pseudo-absence' data for model fitting (e.g., GARP), but these are counted as presence-only methods as absence of species is not guaranteed regarding these pseudo-absence locations. Yet, selection of pseudo-absence or background sampling is often neglected by modelers, who should try to constrain the pseudo-absence or background sampling to the same spatial extent as presences

(Liang et al., 2018). The lack of observation data for invasive species demands for more sampling and exchange of data between countries.

SDMs are based on the notion of niche conservatism to which invasive species seldom complies. Therefore, issues like transferability, biotic interactions in native and invaded ranges, niche characteristics, species dispersal and uncertainty associated with modelled predictions should get addressed to appropriately represent invasion risk. In the following sections I discuss these aspects and best practices to incorporate them in the SDMs.

a) Invasive species niche characterization

SDMs are strongly dependent on the concept of niches in ecology (Jiménez-Valverde et al., 2011) as niche requirements are a key factor in determining suitable areas where an alien species can establish. Distribution models of invasive species are generally trained on native distributional areas (Padalia et al., 2015; Rodda et al., 2011), which often have higher probability to meet the distributional equilibrium (Anderson et al., 2003). However, the presence/absence of information from invaded regions may offer additional insights into novel environments and biotic contexts (Thuiller et al., 2005). Some invasive species might have different niche requirements in non-native areas than from their native ranges and can also evolve at rapid rates to modify their environmental requirements with change in the climate i.e. evolutionary niche shift (Sinclair et al., 2010), thus it becomes important to check niche conservatism. For example, Fernández & Hamilton, (2015) studied the ecological niche transferability of an invasive species and concluded that the ecological niche a species holds in their native range is generally a poor predictor of invaded range, despite the fact that niche conservatism has often been assumed when predicting the spread of invasive species (Medley, 2010).

In these cases, SDMs won't be able to precisely predict the spread of invasive species, nor the characteristics of the niche for non-native ranges. To limit this risk, Medley (2010) used a reciprocal distribution modelling (RDM) approach to investigate niche conservatism for the Asian tiger mosquito (*Aedes albopictus*) and highlighted the importance of the reciprocal models in controlling bi-directional dispersal between native and non-native distributions. Reciprocal model is a combination of two models i.e., one created using native occurrences and projected onto invaded regions, and the other using invasive occurrences which is projected back onto the native

distribution (Fernández & Hamilton, 2015). If the native model accurately predicts the introduced distribution, and vice versa, the niche has been conserved. It is vital to characterize the niche prior to creating a pest risk map, as it can provide additional novel insights on invasive species ecology and will yield better informed forecasts of invasive species distributions.

b) Projecting invasive species distributions

Novel correlative methods (e.g. MaxEnt; Elith et al., 2006) outperforms more established methods, particularly due to ability to fit complex functions, include interactions amongst predictors and use of penalty functions to avoid overfitting. Concern is that these correlative models do not perform well when projected to novel environments (transferability; Kumar et al., 2014b). Reason being their underlying assumption of conservation of niches, which cannot be always true in case of alien species (see 1.3.3.1). Since correlative SDMs only measures realized niche, the concept of niche conservation has been increasingly doubted because of species environmental variability (Dormann et al., 2012). Also, the performances of correlative SDMs might suffer if not fitted properly while projecting into novel environments.

Another study by Sobek-Swant et al., (2012) raises similar concern over SDMs transferability abilities. It is widely known that correlative models work best in well sampled regions but much of the efforts are needed when predicting species distributions in unsampled regions (nonnative ranges in case of alien species). Peterson et al. (2007) chose MaxEnt and GARP to compare model transferability success. They chose three bird species Caprimulgus vociferus, Coccyzus americanus, and Zenaida macroura that had broad geographical distributions along with a set of 19 bioclimatic variables in addition to topographical variables. Best subset method was applied in the case of GARP while MaxEnt software was used with default settings except tuning the regularization multiplier value. Authors found that MaxEnt predictions showed overfitting to the input data and was only transferable at low thresholds. Whereas, GARP had a higher success rate at the prediction with increased commission errors. GARP models constantly showed similarity with species known distributions while MaxEnt models produced an odd pattern in coherence with the input data, interestingly, there were no significant differences between their validation scores. Contrary to it, Sobek-Swant et al., (2012) found higher AUC scores for GARP for their comparative study with MaxEnt. Authors modelled potential distribution of invasive emerald ash borer (Agrilus planipennis) in its invaded and native ranges using four ecologically relevant

bioclimatic variables. They found that the MaxEnt model did not provide a reliable estimate whereas, GARP when trained in the native range performed well. This better performance of GARP leads to the notion that this model might deal with spatial bias better than MaxEnt . GARP has been found successful for predicting invasive species distributions. However, it has been criticized for over prediction (Padalia et al., 2014) as it fails to model less important relationships in the data (Elith & Graham, 2009).

In an attempt to minimize the prediction errors (false presences and absences) due to poor transferability of SDMs and non-equilibrium distribution of alien species, both correlative and mechanistic approaches should be used in cohesion. The predictive performance of MaxEnt has been found to be significantly improved when fitted with outputs from process based mechanistic models (Kumar et al., 2014b). Authors used MaxEnt and CLIMEX to assess the risk of establishment of western cherry fruit fly in California. They included climatic, topographic, and species-specific phenology variables along with human footprint as variables and found that the MaxEnt model was improved by including the Eco climatic index generated from the CLIMEX models. In recent years, following the same line of development of combining the two approaches, hybrid models have been developed (Gallien et al., 2010). These models combine correlative SDMs with expert knowledge driven mechanistic models. The hybrid models overcome limitations of traditional models as they take advantage of both the approaches and yield more reliable predictions. Golding & Purse, (2016) developed a Bayesian SDM using Gaussian process (GP). This GP model enables the user to incorporate prior ecological knowledge via a prior estimate of a model function (Golding & Purse, 2016), for example, effect of moisture limits on a pathogen (sudden oak death: *Phytophthora ramorum*) distributions. This approach can effectively bridge mechanistic and correlative models, such that it retains the information from a mechanistic process while extrapolating the model to novel environments. I recommend critical evaluation of the available modelling options and further refine the model with a hybrid approach to allow more robust estimates of future distribution of invasive species in novel environments.

Additionally, extreme caution should be taken when projecting alien species distributions, specifically under changing climatic conditions as extrapolation beyond climatic limits in the training data is an unreliable practice (Anderson et al., 2003), since alien species are seldom at equilibrium within their environments. Studies in the past have addressed issues related to

extrapolation when projecting SDM into novel environments and suggested linking SDM with landscape, population, and physiological models representing processes of change to improve the model extrapolations (Aitken et al., 2008; Fernández & Hamilton, 2015; Uribe-Rivera et al., 2017).

c) Biotic interactions and dispersal constraints

Invasive species are dynamic in nature and can compete with native biological communities such that the complete invasive mechanism is hard to determine or forecast. In the past, scientists have debated the utility of incorporating biotic interactions into SDM (Araújo & Luoto, 2007; Wisz et al., 2013). These could include: the presence of competitors/predators, or the absence of mutualists in the SDM. A limited number of studies are available which explicitly include predictors describing biological interactions (Venette et al., 2010), despite the fact that habitat projections into future climate conditions where biotic interactions may have transformed are likely to result in inaccurate assessments (Araújo & Luoto, 2007).

In a study, Araújo & Luoto, (2007) used generalized additive modelling (GAM) to investigate relationships between species and climate; species and host plants; and species and climate + host plants and found that inclusion of biotic interactions significantly increases the explanatory power of the SDM at macro scales. Another similar study carried out by Meier et al., (2010) using variance partitioning to estimate the proportion of the variance explained by biotic and abiotic predictors, found that non-inclusion of community composition and other local biotic factors will strongly influence prediction of species distributions. Distribution models of invasive species generally improve after inclusion of information on biotic interactions and the availability of related information on these interactions can advance the SDM projections.

Additionally, development of SDM for alien species is commonly based on climatic and land use predictor variables. However, the distribution of non-native species is heavily governed by the influence of humans on the landscape (Vitousek, 1997). Studies considering the impacts of human footprint on alien species distributions shows that human footprint can significantly affect the distribution of alien species (Ancillotto et al., 2016; Gallardo et al., 2015; Masin et al., 2014; Smolik et al., 2010; Strubbe et al., 2015; Westphal et al., 2008). Thus, inclusion of related variables explaining human pressure on landscapes becomes imperative when building a SDM for alien species. Datasets like "human footprint" (Sanderson et al., 2002), "Global Human Influence Index

(HII)" (http://sedac.ciesin.columbia.edu), "population density", "road density", "urbanization" and "tourism" available from World resources institute (https://www.wri.org) can be of immense significance (Ancillotto et al., 2016). The availability of various datasets explaining human footprint on landscapes provides new opportunities for researchers to model the impact of human influence on the distribution of alien species.

Alien species are mobile in nature and often have traits that facilitate dispersal. However, for most alien species, it is still unknown how much of their complete potential distribution range is represented by observed individuals. This leads to an unknown fundamental niche, although Guisan & Thuiller, (2005) relate this issue to species competitive and dispersal abilities. So far, most studies have ignored the dispersal limitations of alien species (Engler et al., 2012; López-Darias et al., 2008), assuming their distribution to be either unlimited, or null (Engler et al., 2009). This strategy can work for species with a wide host range and strong dispersal abilities. Despite this, these assumptions can often provide inaccurate information regarding potential distributions and further lead to under- or over- estimation of potential suitable areas. This can also yield greater uncertainties with respect to conservation decisions. Despite these risks, very few studies acknowledge the importance of a species dispersal ability while projecting the distribution across space and time (Bancroft & Smith, 2005; Smith et al., 2004).

Also some major invasive species have been known to be introduced by human mediation (Bartell & Nair, 2004; Lippitt et al., 2008) and international trade and movement of people are attributed to increased numbers of alien species introductions to novel environments (Meurisse et al., 2019; Roe et al., 2019). In their nonnative range their movement is either through stratified local diffusion (Tobin et al., 2016) or long distance dispersal associated with human movement (Muirhead et al., 2006). The human footprint variables (for e.g. port and road proximity, roads, navigable rivers, etc.) discussed previously can be directly linked to the vectors and pathways of alien species distributions (Gallardo et al., 2015). However, models are needed to predict distribution based on patterns and density of propagule dispersal addressing both local diffusion and long-distance movement. There are several studies that have tried to include information on species dispersal traits to model their distributions (Bancroft & Smith, 2005; Smith et al., 2004). These dispersal traits can then be used to inform spread models such as a modular dispersal framework (MDIG)

(Lustig et al., 2017), individual-based spread model (Adams et al., 2015) and MigClim (Engler et al., 2012). Dispersal is a key factor when predicting invasive species distribution, since, generally, all potentially suitable areas cannot be colonizable. Thus, I strongly recommend addressing dispersal and biotic interactions when building SDM for mapping invasion risk.

d) Mapping impacts of uncertainty

SDMs are complex tools which inevitably include some degree of uncertainty (Heikkinen et al., 2006).The uncertainty in SDM predictions and performances results both from incomplete knowledge of the species, and from errors in specification of the model (Beale & Lennon, 2012; Refsgaard et al., 2007). Furthermore, many correlative SDMs are projected at high resolutions and under climate change scenarios without explicitly addressing uncertainty, making many invasive species risk maps of questionable accuracy (Yemshanov et al., 2010). This further affects the decision making and resource allocation measures in conservation planning (Barry & Elith, 2006).

In order to lessen the risk of adverse uncertainties in species distribution, SDMs should explicitly address levels of uncertainties in their modelled predictions (Beaumont et al., 2007). Various authors have also advocated to depict levels of uncertainties in the modelled predictions (Beale & Lennon, 2012; Refsgaard et al., 2007) but received less consideration. Gould et al., (2014) created a tool to provide spatially explicit illustrations of the impact of uncertainty on their modelled projections. Their uncertainty tool uses a Monte Carlo process to produce probabilistic and spatially explicit output. Another approach yet faster are GP models (Golding & Purse, 2016) which automatically produces levels of uncertainty in modelled predictions without bootstrapping procedures. The produced prediction uncertainty map measures uncertainty as the variance of the estimated function for the group of predictors (Golding & Purse, 2016). The most recent method to tackle uncertainty in SDM projections is hyper-envelope modeling interface-V2 (HEMI-2) tool. HEMI-2 uses Monte Carlo methods to perform uncertainty, validation, and sensitivity analyses (Graham & Kimble, 2019). Another R based "mopa" package also exist (Iturbide et al., 2018). The package can handle multi-factor SDM ensemble experiments and can explore various uncertainty factors (e.g. occurrence datasets, pseudo-absence/background data, future climate projections, SDM algorithms, etc.), in addition to assessing contribution of independent factors to the overall uncertainty. It is obvious that conservation and management actions regarding invasive species distributions are linked with huge investments and substantial impacts on ecosystems globally

(Marbuah et al., 2014). Therefore, with so much at stake it has become vital to assess the impacts of uncertainty on modelled predictions.

1.4 Conclusion

SDMs with strong underlying biological assumptions will have better predictive powers and produce invasive species risk maps that will be more likely to forecast precise estimates of invasion risk. Here in this review chapter I have discussed the major aspects to consider when building SDMs for mapping invasion risk. I limited myself to issues related to model transferability, biotic interactions along with dispersal limitations (local and regional) and uncertainty, which appeared especially relevant in the case of invasive species. However, I do acknowledge other important aspects to consider such as autocorrelation amongst predictors (Segurado et al., 2006), extent and resolution of the study area (Anderson & Raza, 2010), variable selection, pseudo-absence generation procedures (Boyce, 2010; Pearce & Boyce, 2006; Vanderwal et al., 2009) and model evaluation (Anderson et al., 2003). These discussed challenges need to be addressed to ensure that the predictions match the foreseeable distributional scenario, especially under influence of climate change.

Furthermore, the critical issues and related best practices discussed in this chapter will aid species distribution modelers in creating more scientifically sound models and ecologically relevant predictions. Future work should be around developing more easy to use hybrid models (Anderson et al., 2003) that are capable of addressing both local diffusion and long distance movement of alien species. These findings form a foundation for the analysis presented in the following chapter that shows how best practices suggested above in designing SDMs for invasive species produce more accurate models.

Chapter II: Species distribution modelling for FIS- Implementing species specific genetic traits into SDMs projections under climate change²

2.1 Introduction

In the previous chapter, I have outlined various challenges and best practices in constructing species distribution models. I have also argued that most SDMs lack strong underlying biological assumptions and often fail to address model complexity and biotic interactions. I claimed that to build a robust SDM, critical issues outlined must be addressed in a modelling framework. Hence, in this chapter I took the opportunity to design and evaluate SDMs while incorporating the suggested best practices and later recommend SDM framework for assessing the invasion risk.

The use of MaxEnt has grown regularly every year since 2008, in part due to increasing focus on invasive species. Accessibility to software platforms that implement MaxEnt, as well as forest invasive species (FIS) distribution data have further accelerated its use within the literature. With this accessibility there is increased need for methodological studies that ideally analyze effects of various SDM design strategies implementing MaxEnt. Evaluations of SDMs are not rare (Guisan, Thuiller, & Zimmermann, 2017; Liu, White, & Newell, 2011; Potts & Elith, 2006; Senay & Worner, 2019), but studies evaluating the effects of SDM design strategies on model performance with FIS are limited. Furthermore, a recent review (Srivastava et al., 2019), suggested that SDM outputs should address prediction uncertainty, biotic interactions, and link species dispersal traits with projections of species distributions, details which are often missing in many SDM studies (Araújo & Guisan, 2006; Engler, Hordijk, & Guisan, 2012). Also, SDM studies should account for the effects of sampling bias in the occurrence data, critical yet rarely reported details for models based on presence-only datasets (Phillips et al., 2009). Failing to correct for sampling bias may lead to distribution projects reflecting the sampling bias rather than the true potential distribution of a species (Støa, Halvorsen, Mazzoni, & Gusarov, 2018; Syfert, Smith, & Coomes, 2013). These different aspects of SDMs need to be addressed in an accurate modelling framework to ensure that

-Srivastava, V*., Griess, V. C., & Keena, M. A. (2020). Assessing the potential Distribution of Asian Gypsy Moth in Canada: A comparison of two Methodological Approaches. Scientific Reports, 10(1), 1-10.

² The content of this chapter has been adapted from:

⁻Srivastava, V*., Roe, A., Keena, M., Hamelin, R., Griess, V. C. (2020). Oh the places they'll go: improving species distribution modelling for invasive forest pests in an uncertain world. Under review with Biological Invasions.

the FIS distribution predictions match future invasion scenarios, especially under the inherently unpredictable changing global climate (Venette et al., 2010).

In the past, studies have shown that model complexity also plays a major role in transferability of SDMs in novel environments (Moreno-Amat et al., 2015; Warren & Seifert, 2011); when an SDM is overfit it underestimates the species potential habitat whereas when it is under fitted SDM it tends to overestimate it. Studies recommend to optimally balance the model complexity and accuracy by fine tuning model parameters (Moreno-Amat et al., 2015; Warren, Wright, Seifert, & Bradley Shaffer, 2014). The practice of fine tuning SDM parameters includes calibrating several initial models with a wide array of model parameters, selecting the optimal set of parameters that results in the "best model", and then further calibrating the model with the chosen parameters (Cobos, Townsend Peterson, Barve, & Osorio-Olvera, 2019; Warren & Seifert, 2011). MaxEnt, one of the most popular correlative SDMs (Morales, Fernández, & Baca-González, 2017; Potts & Elith, 2006) enables users to map potential distributions while making a number of modelling assumptions and choosing a number of model settings (Barry & Elith, 2006). This includes choice of background samples or pseudo absences (PAs), selection of appropriate features and regularization (β) multiplier (Elith et al., 2011). The choice of background impacts the transferability of SDMs, thus it becomes important to modify the background sample so that there is a clear ecological justification for the selection (Chapman, Pescott, Roy, & Tanner, 2019; Liang et al., 2018). It is recommended to constrain the PA locations to the same geographic range as presences for accurate predictions (Liang et al., 2018). MaxEnt is a powerful SDM capable of incorporating complex and highly non-linear response curves using various feature classes and it is also equally vital to select appropriate feature shape prior to model development along with optimal regularization value to reduce over fitting (Anderson & Gonzalez, 2011; Merow et al., 2013). Regularization penalizes the model in proportion to the magnitude of the coefficients and consequently shrinks many coefficients toward zero while setting others to zero, thereby putting off many features from the model (Merow et al., 2013; Tibshirani, 1996).

Here I focused on four focal FIS to evaluate the effects of various SDM design strategies on FIS distribution predictions in Canada, as well as their overall global distributions (Figure 4). Readers are referred to the background section of the thesis for details on focal FIS. In addition to focusing

on these four species, I also chose to explore the sensitivity of SDM modelling in two of the major ports in Canada: Vancouver, British Columbia and Toronto, Ontario. The ports of Vancouver and Toronto are one of the major ports in Canada wherein cargo volume reached a record high of 147 million tons and 2.2 million metric tons in 2018 respectively. In addition to high trade volumes, CFIA continue to detect FIS around these two ports. Continued detections suggest that these ports are high risk entry points (Paini, Mwebaze, Kuhnert, & Kriticos, 2018). Thus, I hypothesize that the ports of Vancouver and Toronto are likely to serve as points of entry for the FIS, so I produced dispersal restricted projections of individual FIS distributions in various climate change scenarios that also accounted for anthropogenic factors governing the species spread.



Asian gypsy moth



Dutch elm disease



Asian longhorned beetle



Sudden oak death

Credits: AGM & SOD- Canadian Food Inspection Agency (CFIA), ALB- Amanda Roe (Natural Resources Canada), DED- CFANS, University of Minnesota

Figure 4 Selected FIS to serve as case studies

2.2 Research objectives

The key objectives of this research chapter are:

- 1) To evaluate the effects of various SDM design strategies on FIS distribution predictions in Canada, as well as their overall global distributions
- To explore the sensitivity of SDM modelling in two major ports in Canada: Vancouver, British Columbia and Toronto, Ontario via implementing species-specific dispersal traits into projections of species distribution.

- 3) To evaluate impacts of uncertainty in modelled predictions with respect to input data.
- 4) Develop method to create FIS proxy presence data.

2.3 Methods and materials

In general, I took the following steps below to develop SDMs for focal FIS and evaluate the effects of model design on distribution predictions. I summarize the technical workflow in Figure 5 and break down each step in further detail below:

(1) Obtain occurrence records for each target species (see 2.1 Occurrence Data).

(2) Develop spatial datasets representing current environmental conditions and future climate scenarios, alongside spatial information on the human footprint in the area of interest (see 2.2 Environmental Variables).

(3) Build MaxEnt models to predict the potential distribution of focal FIS in Canada. (See 2.3 Species distribution model)

(4) Quantify uncertainty with respect to input data and map using hyper-envelope modeling interface-V2. (See 2.3 Uncertainty mapping)

(5) Create dispersal limited projections of future FIS distributions under selected climate change scenarios using MigClim. (See 2.3 Dispersal mapping)

(6) Develop FIS proxy presence data based on presence of hosts.



Figure 5 Flowchart representing the modelling flow used to model FIS distribution, dispersal and uncertainty in this study.

2.3.1 Occurrence data

Presence records of AGM, ALB, DED and SOD were collected from various sources to map the known distributions of the selected FIS. The sources included (1) Records provided by the Canadian Food Inspection Agency (CFIA); (2) Global Biodiversity Information Facility database, an online database for species occurrences; (3) CABI invasive species compendium and (4) Scientific articles and maps. I deleted duplicate records such that each observation falls inside a separate 10 km grid cell, leading to a total of 186, 198, 193 and 95 distinct occurrence records for AGM, ALB, DED and SOD respectively (Figure 6).



Figure 6 Selected forest invasive species occurrences in their respective native and introduced ranges. The Köppen-Geiger climate classification (vegetation-based) system (Kriticos et al., 2012) was used as a background. This is done to allow assessing preliminary risk based on whether a species is found in the same climate zone as the pest risk assessment area. Refer Kottek et al., (2006) for a detailed description of the parameters.

2.3.2 Environmental variables

I downloaded 19 bioclimatic variables from the WorldClim database version 1.4 (http://www.worldclim.org/) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), averaged for the 1950–2000 period, at a spatial resolution of 5 arc minutes (approximately 9 km resolution at the equator). For future 2050 climate projections, I used three representative concentration pathways (RCPs) of the IPCC—RCP 2.6 (greenhouse gas emissions peak in 2010-2020 and declining after), 4.5 (emissions peak around 2040 and then decline), and 8.5. (rise temperature throughout the 21st century). I chose three general circulation models (GCMs) of physical climate processes for which the predicted values of each of the bioclimatic variables were available: Community Climate System Model (CCSM4), Hadley Global Environment Model 2 - Earth System (HadGEM2-ES)

and Model for Interdisciplinary Research on Climate (MIROC5). The selected GCMs are being used in Climate BC/WNA/NA model for producing future grid projections of climate and species range in Canada and North America (Wang et al., 2012). In order to incorporate responses of dispersal and human footprint on FIS distributions I incorporated additional data on human footprint "Human Influence Index-HII" at 1 km from SEDAC and resampled to match the native climate grid resolution. The Human Influence Index (HII) is a measure of direct human influence on terrestrial ecosystems, derived from nine global variables including land cover, population density, built-up areas, roads, navigable rivers and nighttime lights ("Socioeconomic Data and Applications Center | SEDAC," n.d.)).

2.3.3 Species distribution model

2.3.3.1 MaxEnt

MaxEnt version 3.3.3k (Phillips, Anderson, & Schapire, 2006) was used to map the potential distribution of the focal FIS due to unavailability of FIS absence data. MaxEnt being presence-background model has been successfully used in mapping the potential distribution of FIS in past (Elith et al., 2006; Kumar, Neven, & Yee, 2014; Kumar, Yee, & Neven, 2016; Lira-Noriega, Soberón, & Equihua, 2018). MaxEnt is a machine learning algorithm used for describing probability distributions following the principle of maximum entropy, subject to restraints imposed by the presence of species and their surrounding environment (Phillips & Dudík, 2008). The entropy is defined by the following equation:

$$H(\hat{\pi}) = \sum_{x \in X} \hat{\pi}(x) In \hat{\pi}(x)$$

Where π is the unknown probability distribution; $\hat{\pi}$ is the approximation of π ; X is a finite set; x is an individual element in set X; and ln is the natural logarithm. The entropy is nonnegative and is at most the natural log of the number of elements in X.

MaxEnt model for each FIS was built separately using available training data from native as well as introduced ranges and was later projected onto Canada to map potential suitable areas for FIS establishment.

2.3.3.2 Model design and evaluation

The occurrence data was partitioned randomly into training and evaluation sets (30% for the AGM and DED models and 20% for ALB and SOD). The best set of relevant uncorrelated environmental variables along with the optimal regularization multiplier for selected FIS was selected using R package "MaxentVariableSelection" (Jueterbock et al., 2016). 10,000 background locations were generated within an area defined by a minimum sized convex polygon encompassing FIS occurrences using SDM toolbox (Brown et al., 2017). FIS accessible areas were included in background generation as suggested by Chapman et al. (2019). The environmental variables were reduced in a stepwise manner in order to avoid overfitting the occurrence records for regularization multipliers ranging from two to four as over fitted models are poorly transferable in novel environments (Elith et al., 2010b). The Pearson's correlation coefficient threshold was set to 0.8 and when variables were found to be correlated only the variable with the highest contribution was kept. The variable contribution threshold was set to 1, below which the environmental variables were excluded from the model. The best performing model was chosen based on the lowest Akaike's Information Criterion for small sample size scores (AICc) (Warren & Seifert, 2011).

Once the best performing predictor set of variables and a regularization parameter value was chosen for all focal FIS the model was evaluated using the training data set. The training data was portioned into ten random subsets using k-fold cross validation function in MaxEnt. This was done to evaluate the average behavior of the model. In order to produce simple models with smooth fitted functions I used only hinge features (Elith et al., 2010b). Jackknife resampling was used to identify those variables that contributed most to the model. The method provides systematic resampling and leads to improved estimates of the sample parameter and a lower sampling bias (Tukey, 1958). To account for sampling bias in the FIS occurrence data I generated a bias grid that up-weights occurrence data points with fewer neighbors in the geographic landscape using the Gaussian kernel density of sampling localities tool in SDMToolbox (Brown, 2014). Additionally, the fade by clamping function was used to limit extrapolations beyond the environmental range of the training data.

2.3.3.3 Model comparisons with different SDM approaches

In order to evaluate the effects of various SDM design strategies and to find the best SDM design strategy for the case-based FIS I individually designed and evaluated seven different MaxEnt models (Table 2). The seven MaxEnt models were (i) MaxEnt model with default parameters and all environmental variables (climatic predictors + HII) (ii) MaxEnt model with default parameters and all climatic variables (here only climatic predictors) (iii) MaxEnt model with default parameters and selected variables (ref. above section on variable selection, only selected environmental variables were kept) (iv) MaxEnt model with default parameters and selected climatic variables (ref. above section on variable selection, here only climatic predictors were used) (v) MaxEnt model with tuned parameters (selected environmental variables along with tuned regularization value) (vi) MaxEnt model with sampling correction (selected environmental variables along with tuned regularization value plus restricted background. Here there was no sampling correction implemented).

		Madal dataila				
Model	AGM	ALB	DED	SOD	woder details	
Type i	20 (BIO1- BIO19+HII)	20 (BIO1- BIO19+HII)	20 (BIO1-BIO19+HII)	20 (BIO1- BIO19+HII)	MaxEnt default + all environmental variables (climatic predictors + HII)	
Type ii	19 (BIO1- BIO19)	19 (BIO1-BIO19)	19 (BIO1-BIO19)	19 (BIO1-BIO19)	MaxEnt default + all climatic variables (here only climatic predictors)	
Type iii	4 (BIO1,2,14, HII)	6 (BIO1,4,6,11,13 ,HII)	8 (BIO1,3,7,11, 14,15,19,HII)	5 BIO4,14,15,19,HI I)	MaxEnt default + selected variables (ref. above section on variable selection, only selected environmental variables were kept)	
Type iv	4 (BIO1,13,14)	3 (BIO1,4,13)	4 (BIO1,3,14,15)	3 (BIO4,15,19)	MaxEnt default + selected climatic variables (ref. above section on variable selection, here only climatic predictors were used)	
Type v	4 (BIO1,2,14, HII)	6 (BIO1,4,6,11,13, HII)	8 (BIO1,3,7,11, 14,15,19,HII)	5 BIO4,14,15,19,HI I)	MaxEnt tuned (selected environmental variables along with tuned regularization value)	
vi	4 (BIO1,2,14, HII)	6 (BIO1,4,6,11,13, HII)	8 (BIO1,3,7,11, 14,15,19,HII)	5 BIO4,14,15,19,HI I)	MaxEnt tuned + sampling correction (selected environmental variables along with tuned regularization value plus restricted background with sampling bias grid)	
Type vii	4 (BIO1,2,14, HII)	6 (BIO1,4,6,11,13, HII)	8 (BIO1,3,7,11, 14,15,19,HII)	5 BIO4,14,15,19,HI I)	MaxEnt tuned - sampling correction (selected environmental variables along with tuned regularization value plus restricted background. Here there was no sampling correction implemented)	

Table 2 Summary of individually designed default and tuned MaxEnt models along with their predictors. MaxEnt model types from i to iv are with default parameters whereas model types from v to vii are with tuned settings.

2.3.4 Model evaluation

Model evaluation was performed using the withheld presence data for the selected FIS. True skill statistic (TSS) (difference between the rate of successes and errors), sensitivity (fraction of correctly predicted presences), correct classification rate and omission error scores at maximizing test sensitivity and specificity threshold were used to evaluate the models. I extracted the same number of pseudo absences (PAs) as testing presences in order to calculate the evaluation scores. PAs were extracted in the same spatial range as the presences. The TSS ranges from -1 to +1, where values of 0 or less indicate a model performance no better than random, and a value of +1 indicates perfect performance (Allouche et al., 2006). The evaluation scores were calculated using NicheToolBox.

I also performed a transferability test with DED and AGM. I created two models: default with only climatic data and a tuned with selected predictors. For DED, I fitted both models with occurrences that excluded Canadian localities. On a similar basis, transferability of AGM was also analyzed. It should be noted that I had only few interceptions of AGM in Canada, so I decided to visualize the transferability success with overlaying interception location records of EGM (European gypsy moth), since EGM and AGM are assumed to have similar ecological characteristics and hosts (Keena et al. 2019).

2.3.5 Uncertainty mapping

Prediction uncertainty in the modelled outputs before projecting (i.e. modelled predictions in areas of recorded presence) was analyzed using hyper-envelope modeling interface-V2 (HEMI-2) through injecting random noise in the input data (occurrence records and environmental variables). HEMI-2 uses Monte Carlo methods to perform uncertainty, validation, and sensitivity analyses. It generates mean and standard deviation habitat suitability maps (Graham & Kimble, 2019). Since most of my records came from online databases, it might contain a location error that might be off by several kilometers, increasing the overall uncertainty of the model outputs. Also, the environmental data contains various levels of uncertainty and might not correlate well with the time of species establishment (Gould et al., 2014; Graham & Kimble, 2019). Thus, for each FIS I injected a normally distributed noise in the occurrence (10 km) and environmental data with 10

cross-validation runs to combine uncertainty based on occurrence, predictors and cross-validation. I iterated the individual FIS model 100 times to achieve a stable output.

2.3.6 Dispersal mapping

In order to include selected FIS specific dispersal constraints into projections of their potential distributions under climate change, I used MigClim (Engler et al., 2012). MigClim is a function library built in R software that allows implementation of species dispersal limitations in SDM predictions under climate change conditions. MigClim is a cellular automaton model so cells are the measured units and here each cell corresponds to 10 km pixel. Here a target cell becomes colonized with the combined probability P col:

$$P col = (1 - \prod_{i=1}^{n} (1 - P Disp i \times P Prop i)) \times P inv$$

Here *P Disp i* is a probability function of the distance between the target cell and the source cell *i*. *P prop i* is a probability that is function of time since the source cell *i* became occupied and represents the propagule production potential of the source cell *i* over the time. *P inv* denotes the habitat invisibility of the target cell.

Since MigClim does not generate habitat suitability maps itself, I used MaxEnt to generate the required inputs. Future FIS distribution maps for the year 2050 were produced for climate change scenarios using MaxEnt for three RCPs (2.6, 4.5, and 8.5) and three GCMs (CCSM4, HadGEM2-ES and MIROC5). These maps were used as an input along with an initial distribution map of the FIS. I assumed two initial infestation points i.e. Vancouver port and Toronto port, since the chosen FIS have been intercepted at these introduction points in the past (Hamelin & Roe, 2019; Nealis, 2009). A reclassification threshold was selected based upon maximum test sensitivity and specificity for each FIS along with their respective dispersal kernel. A dispersal kernel with dispersal probabilities of 1, 0.8, 0.6 and 0.4 was set for AGM, since females can fly from less than 1km up to 20-40km (Keena, et al., 2001; Srivastava et al., 2020). For the other FIS a dispersal kernel was set to 1 with maximum probability since the short distance dispersal was found to be

limited (<10 km) (Dunn, 2012; Grünwald et al., 2012; Grünwald et al., 2019; Smith et al., 2001). Additional, random long-distance dispersal events were generated at a frequency of 0.1 at minmax distance range of 100 (10 cells) and 200km (20 cells) since the selected FIS are capable of dispersal through various means of transport, such as human-assisted transportation (Koch et al., 2013). Since, DED dispersal is limited to the presence of Elm trees, a strong barrier was implemented in the model to simulate dispersal events only in the pixels having Elm presence. Additional information on considered FIS biology and ecology is provided in appendix vii. I had one environment change step (2050) where in total 40 dispersal steps were simulated [envChgSteps] \times [dispSteps], here 40, which corresponds to 40 years from 2010 to 2050. The simulations were repeated for 10 times producing dispersal limited future distribution maps of FIS from 2010 to 2050 under selected climate change scenarios.

2.3.7 FIS proxy data

I prepared a database on known localities of *Ulmus americana* (main host for DED, n= 234) and developed a MaxEnt model based on the methods described in the section 2.3.3. A comparison was then made with the modeled output of DED in order to access the similarities/dissimilarities between the predictions.

2.4 Results

2.4.1 Model selection and fitting

The best model for AGM included four variables (bio1- Annual Mean Temperature, bio 2- Mean Diurnal Range, bio 14- Precipitation of Driest Month and HII- Human influence index) and for ALB included six variables (bio1- Annual Mean Temperature, bio4- Temperature Seasonality, bio6- Min Temperature of Coldest Month, bio11- Mean Temperature of Coldest Quarter, bio13- Precipitation of Wettest Month and HII). Similarly, for DED it had eight variables (bio 1, bio3- Isothermality, bio 7, bio 11, bio 14, bio 15-Precipitation Seasonality, bio 19- Precipitation of Coldest Quarter and HII) and for SOD five variables (bio4, bio14, bio15, bio19 and HII) (Figure 4). The best fitting model parameters for the top FIS model are shown in table 3 and figure 7.

Table 3 Summary of best performing FIS	model and	evaluation scores
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Species	Betamultiplier	Variables	AIC	AICc	BIC
AGM	4.00	4.00	4738.31	4743.21	4798.44
ALB	3.00	6.00	3946.04	3952.88	4010.22
DED	3.50	8.00	4725.63	4731.03	4794.14
SOD	2.00	5.00	1913.74	1945.24	1976.67



Figure 7 Variable selection and regularization fitting for FIS distribution models. The optimal set of variables along with the best beta multiplier is identified as the model of lowest AICc value. The number of environmental variables included in each model is coded by dot color and size and the model with highest minimum AICc value is marked in red.

2.4.2 Effects of SDM design on predictive performance

The performance of the seven SDM designs for individual FIS varied. When the models were evaluated using the withheld presence data, I found the best SDM design strategy to be model type vi with "sampling correction" for each FIS. The worst model was model type iv "default with select climate variables". However, the performance of models created with default parameters was found to improve by tuning of the model parameters and correcting the sampling bias and further improved when both were implemented together for each FIS. For example, TSS score increased from 0.481 (average TSS for all four SDMs created from default settings) to 0.64 when model parameters were tuned and sampling corrections were applied in AGM model. Likewise, for ALB, DED and SOD it increased from 0.586 to 0.655, 0.606 to 0.75 and 0.733 to 0.900 respectively. The detailed model evaluations for comparison between different SDM designs for DED is shown in figure 8 and for other three FIS in appendix i.



Dutch elm disease

Figure 8 Evaluation summary of Dutch elm disease models using true skill statistic, correct classification rates, omission error and sensitivity metrics. The worst performing model (type iv) is highlighted with a horizontal across for comparison purposes. Summary of other FIS models are shown in Appendix I.

2.4.3 Potential distribution of FIS

Modelled predictions selected from best SDM design practice for each FIS matched closely with the observed FIS observations in their respective environment (cabi.org/ISC & Appendix iii-a). Associated uncertainty with the modelled FIS predictions in their individual ranges is depicted in appendix iii-b. Prediction uncertainties about input data for AGM and ALB was more confined in the north west direction (cold and humid) when compared to DED and SOD which were in the southern (hot and humid) and eastern (hot and dry) locations respectively.

Predictions obtained from transferring these FIS models to a nonnative range (Canada) highlighted areas at risk (available for their potential establishment). Similar provinces were modelled to be suitable for AGM, ALB and DED potential establishment, however different suitability scores were recorded in these provinces for these three FIS. The identified suitable areas were in the provinces of British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec, New Brunswick, Nova Scotia and Newfoundland. Whereas, SOD suitability was modelled only in the province of British Columbia, near the western coast (Appendix ii). With climate change FIS distributions in Canada expanded to the north and west (Figure 9 and Appendix ii).



Figure 9 Potential distribution of Dutch elm disease in current and future climate change scenario.

Upon comparing the current Canadian potential distributional ranges of FIS with their future suitability ranges in various climate change scenarios, I found that AGM, ALB and DED expanded their ranges in all considered GCMs and RCPs. The greatest range expansion was recorded in RCP 8.5 and the least in RCP 2.6 for all selected GCMs (Figure 10).



Figure 10 FIS range expansion in km² in different climate change scenarios.

2.4.4 Environmental responses and variable contribution

Suitable conditions (probability of presence >0.45, based on maximum test sensitivity and specificity threshold) for AGM were modelled in areas with annual temperatures between 5 and 25°C which agrees with the temperature responses of AGM and that its populations may struggle in areas that experience longer periods of temperatures $\geq 30^{\circ}$ C (Limbu et al., 2017). AGM distributions were found to expand into areas where temperatures warmed to acceptable levels and to decline in areas where temperatures began to exceed the 30°C level for longer periods of time. The occurrence data and modelled distributions also indicate that areas receiving precipitation between 10 and 160 mm in the driest month are suitable for AGM establishment (Figure 11a). ALB suitable areas (probability of presence >0.44, based on maximum test sensitivity and specificity threshold) were modelled in areas receiving annual mean temperature of 7 to 25°C and minimum temperature of the coldest month between -15 to 15°C with 50-500 mm precipitation in the wettest month. This agrees with ALB's ability to develop at temperatures between 10 and 35°C

and the fact that larvae are freeze tolerant (Keena & Moore, 2010, Torson et al. in prep, Roe. unpublished data). The DED suitability (probability of presence >0.48) was modelled in areas having annual mean temperature between 3 to 10°C and temperature annual range between 15 to 44°C. This supports the findings of Brasier & Mehrotra, (1995) where DED was found to be adapted to a subtropical environment due to its high optimum growth temperature. Sporulation of DED fungus are inhibited by prolonged exposure to high summer temperatures and low moisture content (Webber, 1990). SOD potential distributions were modelled in areas with moderate temperature variability and high variability in precipitation (Appendix v). I showed that the SOD populations can be strongly influenced by variability in precipitation sites in California and Oregon are located within 30 km of the Pacific coastline or San Francisco bay (David M. Rizzo & Garbelotto, 2003). Also, moisture is critical for the germination of spores and fungal growth (see Appendix vii)





Figure 11(a) Relationships between environmental predictors and the probability of the presence of Asian gypsy moth: Red curves show the mean response and blue margins are ± 1 SD calculated over 10 replicates. (b) Jackknife test for AUC of individual environmental variable importance (blue bars) relative to all environmental variables (red bar) for the MaxEnt model. Values shown are averages over 10 model runs. Refer to table 4 for description on the coded climatic variables used in the analysis.

The jackknife test identified Human Influence Index (HII) and Mean Diurnal Range (Bio 2) as the most important predictors of AGM distribution, while identifying HII and Min Temperature of Coldest Month (Bio 6) for ALB distribution (Figure 11b and appendix v). Jackknife test found Annual Mean Temperature (Bio 1) and Isothermality (Bio 3) for DED and Temperature Seasonality (Bio 4) and Precipitation of Driest Month (Bio 14) for SOD. HII made the largest contribution to the MaxEnt model of AGM and ALB distribution when used in isolation and reduced the model's predictive ability the most when omitted. Similarly, Annual Mean Temperature (Bio 1) was identified for DED and Temperature Seasonality Bio 4 for SOD (Appendix v).

2.4.5 FIS dispersal

Inclusion of FIS specific dispersal limitations into projections of FIS distributions under climate change conditions limited the distribution range when compared with scenarios of unlimited dispersal for all selected FIS (Appendix v). Figure 12 shows the total area found to be colonized at the end of a simulation for each FIS under multiple climate change conditions starting from two infestation points. The increase in the area colonized by AGM and ALB was found to be highest in RCP 8.5 and when the infestation started from port of Toronto. No cells were colonized for DED when infestation started from port of Vancouver and similarly, for SOD when infestation started from port of Toronto. The area colonized by DED was higher in RCP 8.5 than RCP 2.6 and 4.5 but for SOD the colonization was lowest in RCP 8.5 and highest in RCP 2.6. Detailed dispersal limited output maps for each FIS under each considered scenario are shown in appendix vi.









Figure 12 Colonization in dispersal restricted future distribution of FIS under different climate change scenarios. I assumed Vancouver port and Toronto port as two initial infestation points.

2.4.6 FIS proxy data

The results generated with the host locations of DED matched very closely to the modelled distributions of the DED pathogen. Suitability predictions matched in all the provinces however small changes in the suitability scores were observed in the regions of Eastern Canada (Appendix ix).

2.5 Discussion & conclusions

The results I generated are in agreement with the recent findings that have shown the effects of model complexity and varying parameters on SDM performance (Halvorsen et al., 2016; Morales et al., 2017; Rodda et al., 2011; Stolar & Nielsen, 2015; Syfert et al., 2013). My analysis clearly found that the use of default settings for the distribution modelling of FIS were not adequate in each of the considered cases, instead high accuracy was achieved when model parameters were finely tuned and model complexity was optimally balanced. The method proposed by Brown et al. (2017) to correct sample selection bias greatly improved the predictive performance of SDMs when the collected data resulted from an unclear survey design or was derived from online databases. The importance of the background data selection strategy in SDMs have been highlighted for a long time (Barbet-Massin et al., 2012; Syfert et al., 2013) and here I validated its importance in working with FIS by improving the accuracy of the SDMs by following the recommendation of Chapman et al. (2019) to include all areas for which data is available. I achieved both significant improvements in the predictive performances of SDMs with less complex models and found them to be more accurate in providing predictions upon transferring to Canadian (i.e. novel) environments. I validated transferability success using DED records in Canada since the other three FIS are not yet established in Canada (Appendix viii). However, for AGM predictions I assessed transferability success by overlaying interception location records of EGM (European gypsy moth) provided by the CFIA, since EGM and AGM are assumed to have similar ecological characteristics and hosts (Keena & Shi, 2019). This is consistent with earlier findings that showed that complex models have poor transferability due to overfitting (Moreno-Amat et al., 2015; Petitpierre, et al., 2017).

HII is a measure of direct human influence on terrestrial ecosystems which includes access routes, navigable rivers, nighttime lights along with other important variables, it effectively contributed in correctly identifying the suitable areas for each FIS. Inclusion of human influence index "HII", in addition to climatic predictors to account for FIS dispersal and human footprint, increased the overall accuracy of the FIS model. HII also significantly contributed to each FIS model (Figure 11b). The effectiveness of HII in the models can be directly linked to the biology of each FIS. For example, AGM can hitchhike on man-made objects and disperse along the transportation corridors, particularly as egg masses or pupae. Dispersal of adult moths along transportation corridors is

further promoted by their attraction to light sources. The SOD pathogen shows similar association with human influence. Spores can move with infected plants, which helps explain why more infected trees were detected on public lands open to general recreation than on adjacent lands lacking public access (Cushman et al., 2008). Furthermore, the chances of an SOD infection increased when sites were within 50km of human habitation (Cushman et al., 2008). DED and ALB, the remaining focal taxa, also showed higher dispersal in areas with an increased human footprint. In fact, most of the ALB invasions are located in or near urban areas (Appendix vi).

Climate has been considered a critical barrier for the establishment and spread of invasive species into temperate regions. However, climatic models predict that eastern Canada's average temperature will increase by 3-5°C by 2100 (Dukes et al., 2009). This increase in temperature, particularly winter temperatures, could eventually lead to much higher probabilities of successful FIS establishments (Dukes et al., 2009; Huang et al., 2011). I chose to examine how FIS distributions changed as I accounted for temperature increases associated with climate change. Three of the four species (AGM, ALB, and DED) showed greater distributions under future climate projections (Figure 11). FIS range is expected to expand with highest range expansion in rcp 8.5, thus leading to much higher probabilities of FIS establishments. Given the combined threat of invasion and climate change, it is critical to model future distributions to ensure resources are adequately allocated to at risk areas based on current or future climate regimes rather than historical estimations (Huang et al., 2011).

Correlative SDMs (MaxEnt) are focused primarily on the realized niche (actual distribution) so may underestimate the fundamental niche (potential distribution). This is because the model is representing only a portion of niche that is represented by the observed records and it is highly unlikely that a new FIS is at equilibrium with its current environmental conditions. This might provide an inaccurate assessment of overall species niche. Additionally, the habitat that is colonizable may differ from the potential habitat so including dispersal into habitat projections can greatly improve projections. This was shown for SOD when several types of models were evaluated (Václavík & Meentemeyer, 2009). Uncertainty when deciding on resource allocation for FIS control measures can lead to poor targeting and unnecessary economic expenditures. My approach of addressing dispersal limitations using MigClim integrates species-specific genetic
traits (flight capacity, long dispersal distance, etc.) and allows for better simulating FIS spread under potential future climate conditions. I have found suitable areas where FIS likely to spread if it gets introduced and establishes in Vancouver and Toronto. Such information can be used by managers to more finely focus eradication efforts.

I find that ignoring underlying FIS ecology and biology in SDMs and using complex (i.e. default) SDMs provide an incomplete picture of FIS invasion both in space and time. In these focal cases I recommend simplifying model complexity and including dispersal and biotic factors to achieve more accurate outputs for each species when projecting models across time. I strongly encourage SDM users to perform species-specific tuning when modeling FIS distributions with MaxEnt to determine the best SDM design, as suggested by other authors (Halvorsen et al., 2015; Moreno-Amat et al., 2015; Muscarella et al., 2014; Shcheglovitova & Anderson, 2013). However, often the biological and ecological knowledge of new incoming FIS is unavailable. In such cases, climate suitability seems to be the most widely-accepted approach to delineate the probable target regions for the FIS (Srivastava et al., 2019). Yet, climate suitability alone cannot explain the niche requirements of the species, though occasionally it is the most important factor (Stohlgren & Schnase, 2006). In such cases I suggest performing species specific model parameterization using recently developed tools like kuenm (Cobos et al., 2019) that offers more rigorous processes of model evaluation and selection and further linking the SDM with simplified dispersal models like KISSMig (Nobis & Normand, 2014) which seems to be a sound alternative since it does not require information on species demography and dispersal processes.

Two of the major limitations of SDMs when it comes to input data are the spatial biases linked with the occurrence dataset (Elith, 2017; Phillips et al., 2006b) and limited/no presence information for the FIS in question (Venette et al., 2010). This becomes a serious concern when there is a fresh arrival of an invading species but limited or no information regarding potential habitat distributions consequences. In this regard, FIS known host tree distributions can significantly assist in estimating potential spatial distribution of suitable habitats. There is an increasing trend of integrating remotely sensed datasets to model species distributions (Web & Troll, 2013). This has proven to assist SDMs and improve the model performances (He et al., 2015). Remotely derived information on host tree distributions has been used to mask the spatial extent of suitable landscapes for the FIS establishment (Kluza et al., 2007). However, host

distributions can also be assumed to be a suitable landscape in which a species can establish, and the same notion can be hypothesized for a presence locality of the FIS. Here, I have shown that by using presence locations of the FIS host an information on potential areas of FIS establishments can be obtained. This immediate assessment of the potential areas at risk due to the new incoming invasive can be of high significance when there's no or limited data on the FIS presence. This novel approach provides risk assessors with the ability to develop SDMs for less surveyed FIS and for FIS that have recently arrived.

Preventing FIS introductions completely is by far the best method to protect the forest resources of a country (Myers et al., 2000) and a key component of the strategy involves detection of infestation areas in the early stages of invasion by means of surveys and constant monitoring. Maps produced from this study provide information about the potential suitable distribution ranges of focal FIS. This type of information is useful in designing early pest surveys and setting of domestic quarantines. Additionally, these maps can be effectively used in making scientifically informed management choices and help to further inform related conservation priorities and trade decisions. However, the maps produced should be interpreted with caution as there is no best transferable SDM for all species and predictions differ with varying modelling assumptions. Also, FIS infested material could arrive to any other vulnerable port or transportation destination, thus additional simulations for specific scenarios based on actual points of entry are still needed. The outputs will benefit Canada's forest resources ecologically and economically as the mid-range projected annual loss to industry for individual FIS are: US\$16M for ALB, US\$625M for DED, US\$121M for the gypsy moth (Colautti et al., 2006) and US\$25M for SOD (Nelson et al., 2009). In the following chapter I address some of the SDM limitations by using a modified niche delineation approach and explore if the assumption of niche conservatism used in this chapter holds true by comparing FIS niches in their respective native and introduced ranges.

Chapter III: Assessing niche shifts and conservatism by comparing the native and post-invasion niches of major forest invasive species³

3.1 Introduction

In the previous chapter I have assumed that the FIS niches were conserved, which means that the native and nonnative niches of the FIS were no different. However, this assumption is not always true and invasives might evolve over time and modify their niches in order to match the available conditions in their respective invasive ranges. Thus, in this chapter I am extending the research to find if the focal FIS niches have been conserved during their invasion course.

The geographic range of a species results from the complex interaction of many biotic and abiotic factors (Peterson et al., 2012; Soberon & Peterson, 2005). Climatic conditions are considered to be major determinants of a species range (Stohlgren & Schnase, 2006). However, climate alone cannot always predict the distribution of a species as many species do not occupy all available habitats due to accessibility. Geographic barriers such as mountain ranges and oceans limited the migration of many species to new areas. With increased trade, anthropogenic movement of alien species has accelerated in the past century breaching these historic barriers and permitting the unprecedented movement of organisms around the globe (Seebens et al., 2018). As alien species are introduced to novel habitats, they are exposed to a variety of abiotic and biotic conditions that may (or may not) resemble their native range. Here, climate along with other range-limiting factors plays a key role in the future outcomes of these introductions, once human mediated dispersal and/or elimination of dispersal boundaries allows movement beyond the native range (Guisan et al., 2014; Jiménez-Valverde et al., 2011).

Ecological niche can be defined as a multi-dimensional environmental space within which a species can maintain its source populations (Hutchinson, 1978). The ecological niche can be further described as fundamental and realized niche. The fundamental niche represents the conditions where a species can live indefinitely, whereas realized niche represents only a portion

³ The content of this chapter has been adapted from:

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of fundamental niche where species actually exists under competition, dispersal limitations and other biotic interactions. Predicting the potential distribution or realized niche of invasive species has received increased attention. Species distribution models (SDMs) have become a popular tool to investigate and predict the potential distribution of a new invader. SDMs rely on matching environmental conditions available in species native and invasive range to predict the niche. Recent improvements in SDMs with increased availability of species occurrences and climatic data have led to a wider use for investigating species climatic niche evolution during an invasion (Fitzpatrick et al., 2007; Jiménez-Valverde et al., 2011).

However, using SDMs to predict invasive niches has recently come under scrutiny. SDMs are based on the assumption of niche conservatism - that species occupy similar niches in both their native and invasive ranges - which is supported by little evidence (Jiménez-Valverde et al., 2011; Peterson et al., 2012). Moreover, niche overlaps measured using SDMs are likely to vary depending on the extent and distribution of environmental gradients in the study area and potentially due to varying statistical assumptions and procedures related to model fitting (Broennimann et al., 2012).

Furthermore, invasive species may undergo evolutionary niche shifts through genetic drift or selection that can modify their environmental requirements to match the available conditions in invasive ranges (Stohlgren & Schnase, 2006), such that the niche of the invasive range may no longer resemble that of the native range. Given this, SDMs will not be able to precisely predict the potential range of an invasive species or the characteristics of the niche for invasive range distributions (Srivastava, 2019). Moreover, SDMs are primarily based upon species occurrence records in their native range to describe a new potential distribution and may highly underestimate where an invasive species could survive. SDMs based on native ranges would also fail due to their inability to predict the post introduction influences of adaptations, interactions and dispersal barriers within the invasive range (Tingley et al., 2014). Given these constraints, doubts can arise whether the calculated niche corresponds to the one occupied by the given invasive, hence leading to significant levels of uncertainty regarding the outcomes of the assessed niche shifts (Araújo & Peterson, 2012). Thus, exploring niche shifts between native and invasive ranges may offer additional insights that might be useful in understanding range expansion and invasion potential of invading species (González-Moreno et al., 2015).

To address the criticisms leveled at SDMs for predicting niche space, the ordination method proposed by Broennimann et al. (2012) allows a direct comparison of the species environmental relationships within the environmental space and employs various maximization criteria to construct two dimensional representations of the niches using the associated environmental variables (Broennimann et al., 2012; Jongman et al., 1995). In addition, this method equally weighs all environmental variables and considers both species' geographic and environmental spaces. Moreover, the approach corrects the densities of known species occurrences by considering the available environmental space and correcting for sampling biases.

I used the ordination method to evaluate and contrast post invasion realized niche shifts across diverse populations of two insects (sirex woodwasp [WW], *Sirex noctilio* (Fabricus); (Asian longhorned beetle [ALB], *Anoplophora glabripennis* (Motschulsky) and two pathogens (sudden oak death [SOD], *Phytophthora ramorum* Werres; Dutch elm disease [DED], *Ophiostoma ulmi* (Buisman) Melin & Nannf. and *O. novo-ulmi* Brasier) which are currently occupying new ranges. I also analyzed the effects of differences in choice of variables (all versus selected) in evaluating climatic niche features for these focal FIS.

All four focal FIS pose significant threats to tree health in their invasive ranges (Hamelin & Roe, 2019; Lantschner & Corley, 2015) and pose continuing risk of spread to new areas (Roe et al., 2019). In the following I examine if the introduced invasives occupy similar environmental conditions in their invasive ranges when compared to their native populations. I also calculated how stable the niche is, determined if the species niche is expanding/evolving over time, and evaluated if the entire area defined by the niche has been invaded yet in each introduced range to better understand the niche dynamics of the selected species. I predict that sirex populations will show shifts in their niches and some degree of evolution. There seem to be two primary groupings (European and unknown source) of the strains that have become invasive and they seem to respond to biocontrols differently. These groups may also have different responses to temperature. Sirex causes more damage in the southern hemisphere than in the northern hemisphere which may have multiple causes (hosts, biological controls, and climate). The introduced ALB populations will show shift in their niches possibly due to alterations in their host preferences and variations in climatic profiles, given the more northern populations in Europe and that the invaded range does not go as far south in latitude as it does in China. Also, infested areas may represent a small part

of potentially suitable areas. Similarly, SOD populations are very likely to show shift in their niches due to shifts in their hosts and may expand their niche in the invasive ranges. The SOD pathogen is known to have a broad host range, but host jump can result in new outbreaks, as the outbreak on larch in Europe. The other big driver could be climate, as climate change could turn current inhospitable climates into disease-conducive climates. DED populations could show niche evolution due to expansion of the host and climate change. Also, some DED vectors are more efficient transmitters of the pathogen and can intensify outbreaks.



Figure 13 Geographical distribution of sirex woodwasp (WW), Asian longhorned beetle (ALB), sudden oak death (SOD) and Dutch elm disease (DED). Native ranges for each invasive are shown in green. Since the origin of Dutch elm disease is not known I assume them to be native to Asia for the purpose of comparison.

3.2 Research objectives

The key objectives of this research chapter are:

- 1) To compare post invasion realized niche shifts across diverse populations of major FIS.
- 2) To analyze the effects of differences in choice of variables in evaluating climatic niche features for representative FIS.

3.3 Methods

3.3.1 Occurrence data

An occurrence database was compiled for WW, ALB, SOD and DED from various sources, including (1) Records provided by the Canadian Food Inspection Agency (CFIA); (2) Global Biodiversity Information Facility database, an online database for species occurrences; (3) Centre for Agriculture and Bioscience International (CABI) invasive species compendium and (4) Scientific articles and maps (Figure 13) (Srivastava et al. 2020; Jung et al. 2020; Zahiri et al. 2019). I used Google Earth (Google Inc 2020) to obtain proxy coordinates for records lacking geographic coordinates. In order to generate geographically unique occurrences and account for potential sampling bias I applied a buffer of 5 km around each record using spThin R package (Aiello-Lammens et al., 2015). Considering dispersion abilities of the representative species a minimum convex polygon around the occurrences with an added dispersion distance of 1 degree was applied to define their geographic background in their respective regions. Following backgrounds were considered for each invasive: (1) WW- Eurasia (native, n = 116), North America (NA, n = 12), South America (SA, n = 12), South Africa (SF, n = 11) and Oceania (Australia + New Zealand), n=33 (2) ALB- Asia (native, n=149), Europe (EU, n=23) and North America (NA, n=26) (3) SOD-Indochina (native, n = 8), North America (native, n = 45) and Europe (EU, n = 53) (4) DED-Asia (native, n = 10), Europe (EU, n = 105) and North America (NA, n = 209).

3.3.2 Climate data

19 bioclimatic variables were obtained from the WorldClim database version 1.4 (http://www.worldclim.org/) (Hijmans et al., 2005), averaged for the 1950–2000 period at a spatial resolution of 2.5 arc minutes and were masked to match the extent of each species distribution. Following Broennimann et al. (2012), I evaluated niche features of the focal species among their

invasive ranges after calibrating them on their respective geographical regions. The selection of the best set of range-limiting uncorrelated climatic variables for each of the representative species was made using the R package "MaxentVariableSelection" (Jueterbock et al., 2016). The best set of variables for WW and ALB included five variables, for SOD four and seven for DED.

Table 4 Climatic variables for niche analyses of selected forest invasives selected using the R package "Maxen tVariableSelection" (Jueterbock et al., 2016).

Variables	WW	ALB	SOD	DED	Variable Details
Bio1	~	~		~	Annual Mean Temperature
Bio2	~				Mean Diurnal Range
Bio3				~	Isothermality
Bio4		~	~		Temperature Seasonality
Bio5					Max Temperature of Warmest Month
Bio6		~			Min Temperature of Coldest Month
Bio7	\checkmark			\checkmark	Annual Temperature Range
Bio8					Mean Temperature of Wettest Quarter
Bio9					Mean Temperature of Driest Quarter
Bio10					Mean Temperature of Warmest Quarter
Bio11		~		\checkmark	Mean Temperature of Coldest Quarter
Bio12					Annual Precipitation
Bio13		~			Precipitation of Wettest Month

Bio14	\checkmark	\checkmark	~	Precipitation of Driest Month
Bio15	\checkmark	\checkmark	~	Precipitation Seasonality
Bio16				Precipitation of Wettest Quarter
Bio17				Precipitation of Driest Quarter
Bio18				Precipitation of Warmest Quarter
Bio19		\checkmark	~	Precipitation of Coldest Quarter

3.3.3 Measuring climatic niche shifts

I used the environmental principle components analysis (PCA-env) method proposed by Broennimann et al. (2012) to test for shifts in the realized niches of focal species after their introduction into their invasive ranges. This method allowed me to compare the environment conditions available to a species within a region with its observed locations and calculate the available environment space which was defined by the first two axes from the PCA. By applying a kernel smoothing function to occurrence densities this method corrects for potential sampling biases by considering available environmental space within the entire background.

I compared the climatic conditions available for each species within their invasive ranges to those found within the native range. My approach followed Silva et al. (2016) where they created occurrence density models while correcting for the available environmental conditions for the studied species and quantified niche overlap using Schoener's D index (Schoener, 1970), which varies from 0 (no niche overlap) to 1 (when the niches are identical. I then used this metric to test for niche equivalency and similarity. The niche equivalency test compares the observed niche overlap with the estimated overlap when occurrences are randomly reassigned to both backgrounds. The species occurrences were randomized in both backgrounds and Schoener's D was recalculated 100 times to produce a null distribution of overlap scores which was then compared with the observed value (Warren et al., 2008). The niche equivalency test used exact

locations of species and didn't take into account the entire available space, whereas the niche similarity test considered differences in the surrounding environment conditions available across the species distributional area (Aguirre-Gutiérrez et al., 2015). The test examined if the observed overlap between the compared niches is different from the overlap between the observed niche in one range and randomly selected niches in the other range. I thus measured niche similarity between each pair of ranges by comparing the overlap of one range with randomized occurrences on the background conditions of the other $(1 \rightarrow 2)$, keeping the original number of occurrences and vice versa $(2 \rightarrow 1)$. The rejection of niche similarity hypothesis signifies that the environmental conditions occupied by the species in the invasive range are more similar to the environmental conditions occupied in the native range than would be expected by chance (overlap between native and invasive niche is larger than random expectation) (Strubbe et al., 2015). Hence, a *p*-value >.05 signifies niches that are less similar than expected by chance (Manzoor et al., 2020). I have used niche similarity test here to assess niche shifts and conservatism. For detailed information on niche similarity test readers are referred to Broennimann et al. (2012) and (Strubbe et al., 2015).

In order to provide more insight into the niche dynamics of the representative species I also calculated how stable the niche was, determined if the species niche is expanding/evolving over time, and evaluated if the entire area defined by the niche has been invaded yet. Niche stability and expansion (= 1-niche stability) measure the proportion of occupied environmental space in the introduced range that is overlapping and non-overlapping, respectively, to that of the native range. To determine if the non-native niche was completely invaded the proportion of native range that doesn't overlap with the invasive range was calculated. I used the package ecospat (Cola et al., 2017) in R (R Development Core Team 2020) to obtain the proportion of climatic niche in each comparison as proposed by Guisan et al. (2014). The R code for the PCA-env was modified from Broennimann et al. (2012) and Silva et al. (2016) to perform the analysis. To assess the impact of variable selection on the niche analysis, I compared the results obtained using the complete set of climatic variables (n=19) to the best set of range-limiting uncorrelated climatic variables. I discussed variations in the climatic niches of the focal species in the direction $1 \rightarrow 2$ (only considering native versus invasive ranges).

3.4 Results

The selected set of climatic variables for each study species explained more than 75% of the variance in environmental conditions (Table 4). In contrast, the complete set of variables explained less than 75% of the original environmental variation for all four species (Figure 14-17). When I compared these two datasets, selected vs complete, I found that they produced different proportions of niche overlaps and other studied metrics, where the selected set of variables provided results that were closer to the observed species occurrences. Hereafter, I present only the results generated using the selected variable sets but provide details for each dataset in the provided tables (Table 5-8) for direct comparison.

Sirex woodwasp

All introduced populations of WW showed low niche overlap (0.01-0.19, Table 5) and were not similar to the native range (did not exhibit high similarity to the native range and showed variable niche overlap proportions that varied from 0.01 to 0.19 (Table 5). The overlap scores between the native and invasive ranges were very low for South America (0.01) and Africa (0.02). The WW populations in Africa and SA occupied more humid and colder environments than those found in the Australian and NA ranges. Whereas, the WW populations in Australia occupied warmer conditions compared to native and other invasive ranges of WW. Also, along with native populations the Australian populations preferred drier environments (Figure 14). Climatic niches of the invasive range (0.57-0.91) indicating that there is considerable niche range into which the populations could expand. However, there was no expansion and stability observed in the niches of the Oceania and NA populations when compared to the native range. Populations in African and SA ranges showed moderate niche expansion and stability (Table 5).

Table 5 Summary of niche test of sirex woodwasp between native range Eurasia (EUA) and invasive ranges Africa, Oceania, North America (NA) and South America (SA) using all and selected climatic variables. Bold values represent niche comparison values between native versus each introduced ranges $(1\rightarrow 2)$ whereas unbolded values represent comparisons between introduced ranges versus native range $(1\leftarrow 2)$. Significant p values ($\alpha = 0.05$) are represented by *.

Region	Variable	Overlap	Similarity test (p values, $\alpha = 0.05$)		Uninvaded		Expansion		Stability	
Africa	All	0.02	0.515	0.079	0.87	0.47	0.47	0.87	0.53	0.13
	Selected	0.02	0.624	0.099	0.57	0.31	0.31	0.57	0.69	0.44
Oceania	All	0.24	0.267	0.050*	0.54	0.26	0.26	0.54	0.74	0.46
	Selected	0.14	0.178	0.030*	0.70	0.00	0.00	0.70	1.00	0.30
NA	All	0.31	0.475	0.020*	0.49	0.00	0.00	0.49	1.00	0.51
	Selected	0.19	0.347	0.396	0.57	0.00	0.00	0.57	1.00	0.43
SA	All	0.04	0.356	0.089	0.85	0.63	0.63	0.85	0.37	0.15
	Selected	0.01	0.366	0.030*	0.91	0.57	0.57	0.91	0.43	0.09



Figure 14 Native and invasive climatic niches of sirex woodwasp in different regions along with variable factor maps. Multivariate climatic space was calculated using the PCA-env method. Results using all variables are shown in parts a and b whereas parts c and d shows the results obtained with selected variables. The solid and dashed lines delineate the niche occupied by the 50% densest population and all available climatic niche, respectively. Shadings correspond to the density of occurrences in each region. Green, orange, blue, purple, and red represent Africa (non-native), Oceania (non-native), North America (non-native), South America (non-native), and native range, respectively. Refer to table 4 for description on the coded climatic variables used in the analysis.

Asian longhorned beetle

ALB has a large geographic distribution within its native range, spanning from 21 to 45° N degrees of latitude (Figure 13), with multiple invasions within North America and Europe. The ALB niches are defined by five climatic variables (bio1, 4, 6, 11, 13; Table 1), four of which are related to temperature. The niche overlap with the native distribution ranged from 0.17 to 0.33 for the invasive ranges in NA and EU respectively (Table 6). The NA niche showed less niche overlap with the native niche than EU. The results show that the introduced populations in the EU occupy locations that are warmer and more humid than those found in NA (Figure 15). NA populations exhibited a climatic niche that was significantly more similar than expected by chance, to the native

range. However, EU populations did not exhibit niche similarity to the native range (Table 6). The lack of significant similarity between native and invasive ranges shows that these invasive ranges have different climatic features based on the best set of climatic variables than that observed in the native range despite having an overlap value of 0.33. Climatic niches of the invasive ranges of ALB showed high degrees of niche filling when compared to the native range (Table 6). However, I observed little to no expansion in the niches of EU and NA populations, and these invasive populations showed high niche stability.

Table 6 Summary of niche test of Asian longhorned beetle between native range in Asia and invasive range in Europe (EU) and North America (NA) using all and the selected climatic variables. Bold values represent niche comparison values between native versus each introduced ranges $(1 \rightarrow 2)$ whereas unbolded values represent comparisons between introduced ranges versus native range $(1 \leftarrow 2)$. Significant p values ($\alpha = 0.05$) are represented by *.

Region	Variable	Overlap	Similarity test (p values, $\alpha = 0.05$)		Uninvaded		Expansion		Stability	
EU	All	0.01	0.752	0.040*	0.97	0.00	0.00	0.97	1.00	0.03
	Selected	0.33	0.980	0.059	0.06	0.00	0.00	0.06	1.00	0.94
NA	All	0.01	0.960	0.040*	0.98	0.00	0.00	0.98	1.00	0.02
	Selected	0.17	0.010*	0.119	0.00	0.00	0.00	0.00	1.00	1.00



Figure 15 Native and invasive climatic niches of Asian longhorned beetle in different regions along with variable factor maps. Multivariate climatic space was calculated using the PCA-env method. Results using all variables are shown in parts a and b whereas parts c and d shows the results obtained with selected variables. The solid and dashed lines delineate the niche occupied by the 50% densest population and all available climatic niche, respectively. Shadings correspond to the density of occurrences in each region. Green, red, and blue colors represent Asia (native), Europe (non-native), and North America (non-native), respectively. Refer to table 4 for description on the coded climatic variables used in the analysis.

Sudden oak death

SOD has a broad geographic distribution in its invasive range in North America and Europe, but its native range was unknown until recently (Figure 13). The discovery of a very diverse population of the pathogen in South Asia makes that region a likely center of origin. Climatic niche analyses of SOD revealed different climatic preference of SOD in the invasive ranges as both introduced EU and NA populations had less similar niche to that of native range. I observed an overlap of only 0.9% in climatic niches of NA and native populations but 16% overlap between EU native populations (Table 7). The SOD populations in NA were exposed to more variations in temperature whereas those in EU were exposed to more variations in precipitation compared to the native range (Figure 16). Introduced populations occupied drier areas compared to the native range. Based on

the complete set of climatic variables SOD populations in the invasive EU range occupied colder environments than populations in native and NA range (Figure 16). Most of the available SOD niche (99%) was not yet invaded in NA and 58.5% of the niche remained uninvaded in the EU range. A high degree (77.3%) of niche expansion was observed in the NA range whereas a moderate degree (58%) of niche expansion was observed in the EU range. Both invasive ranges had low niche stability (Table 7).

Table 7 Summary of niche test of sudden oak death between native range Indochina (Vietnam) and invasive ranges Europe (EU) and North America (NA) using all and selected climatic variables. Bold values represent niche comparison values between native versus each introduced ranges $(1\rightarrow 2)$ whereas unbolded values represent comparisons between introduced ranges versus native range $(1\leftarrow 2)$. Significant p values ($\alpha = 0.05$) are represented by *.

Region	Variable	Overlap	Similarity test (p values, $\alpha = 0.05$)		Uninvaded		Expansion		Stability	
EU	All	0.357	0.168	0.267	0.044	0.234	0.234	0.044	0.766	0.956
	Selected	0.161	0.554	0.861	0.585	0.580	0.580	0.585	0.420	0.415
NA	All	0.262	0.188	0.010*	0.567	0.552	0.552	0.567	0.448	0.433
	Selected	0.009	0.267	0.950	0.989	0.773	0.773	0.989	0.227	0.011



Figure 16 Native and invasive climatic niches of sudden oak death in Indochina (Vietnam), Europe and North America along with variable factor maps. Multivariate climatic space was calculated using the PCA-env method. Results using all variables are shown in parts a and b whereas parts c and d shows the results obtained with selected variables. The solid and dashed lines delineate the niche occupied by the 50% densest population and all available climatic niche, respectively. Shadings correspond to the density of occurrences in each region. Red, blue and green colors represent Europe (non-native), North America (non-native) and Indochina (native) respectively. Refer to table 4 for description on the coded climatic variables used in the analysis.

Dutch elm disease

DED has a broad geographic distribution in its invasive range in North America and Europe. Its native range is believed to be Asia, where a close relative of the DED pathogen is found and is used here for the native range (Fig 13). DED niche overlap comparisons between the chosen 'native' and invasive ranges also showed different overlap proportions ranging from 0.18 to 0.49 for invasive ranges in NA and EU, respectively. The DED populations occupied drier and warmer conditions in NA than in the EU range. The NA populations also showed a shift towards colder

regions as compared to the ones in the EU range. Moreover, the populations in the native range were exposed to higher variation in precipitation than those found in the invasive ranges. However, invasive DED in both NA and EU occupied cooler environments than native populations. DED populations in all ranges preferred humid environments (Figure 17). Both EU and NA populations exhibited a realized climatic niche that was not significantly similar to the native range (Table 8). Climatic niches of the introduced ranges of DED showed highest degrees of niche filling when compared to the native range. However, expansion in the niches of EU (22%) and NA (57%) populations were observed. Also, the EU range was found to be more stable than NA

Table 8 Summary of niche test of Dutch elm disease between native range Asia and invasive ranges Europe (EU) and North America (NA) using all and selected climatic variables. Bold values represent niche comparison values between native versus each introduced ranges $(1 \rightarrow 2)$ whereas unbolded values represent comparisons between introduced ranges versus native range $(1\leftarrow 2)$. Significant p values ($\alpha = 0.05$) are represented by *.

Region	Variable	Overlap	Similarity test p values, $\alpha = 0.05$)		Uninvaded		Expansion		Stability	
EU	All	0.69	0.238	0.238	0.00	0.26	0.26	0.00	0.61	1.00
	Selected	0.49	0.347	0.307	0.00	0.22	0.22	0.00	0.78	1.00
NA	All	0.57	0.030*	0.010*	0.00	0.39	0.39	0.00	0.74	1.00
	Selected	0.18	0.089	0.307	0.00	0.57	0.57	0.00	0.44	1.00



Figure 17 Native and invasive climatic niches of Dutch elm disease in different regions along with variable factor map. Multivariate climatic space was calculated using the PCA-env method. Results using all variables are shown in parts a and b whereas parts c and d shows the results obtained with selected variables. The solid and dashed lines delineate the niche occupied by the 50% densest population and all available climatic niche, respectively. Shadings correspond to the density of occurrences in each region. Green, red, and blue colors represent Asia (native), Europe (non-native), and North America (non-native), respectively. Refer to table 4 for description on the coded climatic variables used in the analysis.

3.5 Discussion & conclusions

The selection of relevant climatic factors is critical when delineating the climatic niches of invasive species (Fourcade et al., 2018; Petitpierre et al., 2017), however when selecting climatic variables to assess niche shifts, multiple approaches have been used. A few researchers have selected all 19 bioclimatic variables found in the WorldClim database (Mairal et al., 2017; Silva et al., 2016) whereas several have chosen only variables considered relevant to assess the niche shift (Liang, Papeş, et al., 2018; Liang, Tran, et al., 2018; Quintero & Wiens, 2013a, 2013b). The commonly used approaches assess the correlation between variables and then chose a subset to avoid multicollinearity (Braunisch et al., 2013). However, relevant variables should additionally be

selected based on the underlying species' ecology (Petitpierre et al., 2017). In this study I demonstrate the importance of selecting relevant climatic variables when defining the climatic niches of invasive species (Austin & Van Niel, 2011). When I used the relevant variables for each species, I found different values for each studied niche feature, compared with the results generated using all climatic variables. The results generated using a subset of variables produced results that were close to known distribution of my focal species. My results suggest that using a complete set of bioclimatic variables for niche analysis may underestimate or generate a niche which can be misleading and further limit our understanding on accurate niche delineation of respective species. Further, inappropriate selection of variables might not produce robust niche models and could produce false information on habitat quality and relative importance of variables in defining the niche (Warren & Seifert, 2011; Zeng et al., 2016). Using a complete set of bioclimatic variables in niche mapping should not be recommended based on my results. Previously, other researchers have demonstrated the importance of variable selection in determining suitable ranges for species establishment (Cobos et al., 2019; Halvorsen et al., 2016; Warren & Seifert, 2011). Title and Bemmels (2017) also found that including more variables which are likely to have direct relevance on ecological or physiological processes of target species can substantially improve the performance of niche models. I recommend using a subset of variables that are biologically important to the target species and have been obtained by a rigorous selection method for the niche analysis. There are many powerful tools available to assist in the selection of the best set of variables for the niche analysis. Recently developed tools like kuenm (Cobos et al., 2019), MaxentVariableSelection (Jueterbock et al., 2016) or ENMeval (Muscarella et al., 2014) all offer rigorous processes of variable selection that might be useful in carrying out the analyses.

My test results of niche shifts can be explained by combined effects of environmental requirements (species ecology) and evolutionary changes allowing focal species to occupy newer areas and spread into novel environments. A species range can expand as a result of local adaptations including gene flow and dispersal (Medley, 2010). Moreover, frequent introductions from multiple sources could also produce novel genetic combinations through hybridization helping invasive to adapt in a new environment (Stohlgren & Schnase, 2006). A genetically hybridized superior population can utilize new environmental conditions as compared to their parents (Sheth & Angert, 2014). Also the founder effect could further help in rapid adaptations by expressing beneficial fitness-related alleles (Blows & Hoffmann, 2005).

The results show that all introduced WW populations have different environmental preferences and there may have been some evolution of the niche in the invasive ranges. The niche differences mirror the invasion history that was revealed through genetic analysis. The NA and Oceania populations originated primarily from Europe, the SA populations had multiple origins (including one that is still unknown) and the African populations had origins in SA, Oceania and the same unknown source as part of the SA populations. The indicated range expansion in the SA and African populations may simply be an artifact due to the lack of sampling some unknown source population in Eurasia that was indicated by the genetic analyses. The unknown range may expand the niche in the native range once discovered and that may coincide with the apparent range expansions. It should, however, not be forgotten that the WW invasion is continuing and complicated by the fact that a nematode that can sterilize female wasps and the symbiotic fungus the wasp larvae need to feed on also travel with it. In addition, there are different strains of both the fungus and nematode as well as some parasitoids that all can affect the realized niche and spread of the WW in invade areas (Slippers et al. 2015).

The WW results also suggested that there was a considerable proportion of the introduced niche that was not yet invaded. This agrees with the results of modeling the potential range of the WW using CLIMEX (Ireland et al. 2018). There are areas of suitable native or exotic pines in Australia, Brazil, and North America that the WW could still disperse into. If portions of these additional areas differ in climate from the already occupied niche, then the invaded niche may be underestimated as was suggested for the SOD invaded niches.

ALB occupies a large climatic niche within its native range. This niche spans at least 24 degrees of latitude, and area that is characterized by significant temperature gradients (Javal et al., 2019a). The smaller niches estimated for ALB in the invaded regions are likely based on the small, localized invasive populations. Invasive ALB populations are subjected to intensive eradication programs (Haack et al., 2010), aimed at limiting the dispersal and spread into surrounding habitat. As such, the distribution of ALB is intentionally limited to these small infestations and the niches estimated for this species may not reflect the true invasive potential of this species.

Temperature was a dominant environmental factor driving niche differentiation between climatic niches within these non-native habitats speaks to the plasticity within the ALB populations.

Invasive populations in North America and Europe occupy different niches, albeit niches that were encompassed, more or less, by the niche diversity within native range. ALB is known to be very plastic in its response to temperature (Keena & Moore, 2010), which suggests that new infestations may have the capacity to survive and establish in a range of habitats outside its native range. For example, ALB can survive in cool climates by altering the number of larval instars and requiring (Keena & Moore, 2010). This ability to adapt may also explain the niche expansion beyond the borders of the native range seen in the EU populations. Although ALB in the introduced ranges currently seem to have filled their niche, their ability to adapt could expand the niche if new introductions occur. However, since the ALB in both NA and EU are under eradication that has limited the natural spread potential beyond the areas where the introductions occurred. This likely has limited the realized niche, resulted in higher niche filling rates, and high niche stability as was observed in this study.

The large proportion of the SOD niche that is uninvaded in NA and Europe may indicate that the NA and EU populations are early in the invasion process and could disperse much more before reaching niche equilibrium. The SOD pathogen can disperse in two ways: via anthropogenic transport on plants and naturally via spores. The first means can lead to long-distance, even intercontinental transport. But the spores naturally disperse slowly through wind driven rain with about half of the new infections occurring within 100 m of already infested trees (Rizzo et al., 2005). Also, as the best set of climatic variables suggest, the pathogen has specific temperature and moisture requirements for infection that occur only seasonally and vary between years (Meentemeyer et al., 2004; Tooley and Kyde, 2005). New infections also require susceptible hosts to be close to the infected trees. Most models of SOD spread and potential range in invaded areas include a susceptible host layer for this reason (Magarey et al., 2007; Václavík and Meentemeyer, 2009; Cunniffe et al., 2016). Adding a host variable to the niche model could improve the niche characterization. However, it has been shown that trying to model the niche for SOD when it is in an early stage of invasion will tend to underestimate the true niche so this may have affected the results (Václavík and Meetenmeyer, 2012). The host range of this pathogen is still poorly understood and the recent host jump to Japanese larch was unexpected (Brasier & Webber, 2010). The results suggest niche evolution in the invasive ranges of SOD. This was also supported by a very high degree of niche expansion observed in both invasive populations of SOD and the fact that niche stability is very low. This could result from the pathogen being introduced into areas

with many new susceptible hosts and a less favorable or more variable climate so that rapid selection for the most viable fungal genotypes may have occurred. Another possibility exists, that the sampling of the native range is still limited and thus may be underestimating the true extent of the native niche and therefore the overlap with the introduced niches. Although my study did not address subspecific niche adaptation, this could be done in the future. There are in fact three lineages of SOD in the Pacific Northwest and British Columbia and some of the lineages diverged as long as 1M years ago (Grünwald et al., 2019; Dale et al., 2019). It is possible that there are two different areas that make up the NA niche 50% zone which could suggest that there may be different genotypes with different niches.

The lack of similarity between native and introduced ranges of DED shows that the populations in the introduced ranges have different environmental preferences and adaptations than those observed in the chosen 'native' range. This could be caused by the presence of an entirely different species of the pathogen in Asia compared to the ones present in North America and Europe. The climatic niches in the invasive ranges of DED showed the highest degrees of niche filling compared to the native range possibly due to limited sampling of the pathogen in the presumed native range (Brasier, 1990). The niche expansion in North America and Europe could be linked to the differences in the fungal pathogen adaptation, the observed hybridization among the subpopulations of the pathogen and the availability of highly susceptible host species (Brasier, 2000, 2001; Brasier & Mehrotra, 1995; Hessenauer et al., 2020). Brasier (2000) has described the expansion of the Dutch elm disease outbreak (the second pandemic) following the appearance of a second species, O. novo-ulmi, that had optimum growth temperature (22C) lower than that of the original pathogen, *O.ulmi* (27.5-30°C); it is likely that *O. novo-ulmi* is better adapted to cooler climates than *O. ulmi* which is considered to be better adapted to subtropical climates (Brasier & Mehrotra, 1995; Stipes et al., 1981).

Most of my representative invasives were far away from reaching niche equilibrium and this finding was based completely upon observed species locations (realized niche). I know my results disregard the important biotic processes that may have delineated the species niche. Also limited samples from native and invasive ranges may have underestimated the actual distribution ranges of the invasives and hence the results obtained from this study should be assessed with caution. Additional observation data and information on physiological requirements of invasives derived

from genomics from both native and introduced ranges would be useful to better understand and predict the behavior of the representative invasives in their respective newly introduced ranges. The information on climatic niche expansion and other important niche characteristics can prove to be a useful cost-effective tool in managing and monitoring representative invasives future spread and currently infested areas.

General conclusions

4.1 Summary of key results

This dissertation had following three key objectives:

• Identify current applications of SDMs and review the benefits and challenges of using SDMs to estimate, and spatially project, invasion risk.

• Map FIS potential distribution, dispersal and prediction uncertainty and propose a framework to produce robust pest risk maps.

• Compare post invasion realized niche shifts across diverse populations of FIS.

These above listed objectives were independently addressed in three research chapters as detailed below.

Chapter 1 provided an in-depth literature review on correlative species distribution models, particularly in reference to forest invasive species. The chapter discussed various application areas of SDMs. It was found that the SDMs are being applied to answer wide range of questions in the fields of ecology and biogeography. Particularly it was shown that the key applications of SDMs were to characterize niche and ecological requirements of species, map species potential distribution, conservation and policy making, impacts of climate change or human footprint on species distribution, risk assessment and testing of ecological theory. Moreover, Chapter 1 found that the use of SDMs have evolved continually over the past decade particularly in the areas of climate change, risk mapping, analyzing species evolution and range shifts. It was found that the use of SDMs in invasion ecology is very recent and is gradually increasing. The chapter provided a detailed discussion on benefits and challenges of using SDMs for invasive species management. Specifically, issues around building a robust correlative SDM were discussed. This chapter also outlined potential benefits and associated challenges of using SDM to estimate, and spatially project, invasion risk. It was shown that SDMs are very effective tool in the fields of ecology and conservation biology and are accompanied with multiple benefits. However, challenges are linked in constructing SDMs. It was found that the challenges were linked with model building processes and uncertainties were associated with the modeled distributions. It was shown that the major challenges of using SDMs were related to transferability, niche characterization, biotic

interactions, species dispersal and uncertainty which were more relevant in the case of invasives. Best practises were also discussed under each challenges and suggestions were made in order to create more robust and accurate models. Throughout the thesis I have argued that in order to create an effective pest risk map, the risk modeler must incorporate strong ecological baseline assumptions for the accurate assessments of the invasion risk.

Chapter 2 brought the best practices and suggestions made in chapter 1 into a working framework and demonstrated its effectiveness in producing more accurate and ecologically relevant predictions. It was demonstrated that SDM's default settings were not effective and the performance of models were found to be improved by incorporating the suggested best practices. Evidence suggested that selection of background data, tuning of model parameters, choice of relevant predictors and sampling correction led to more accurate models and better transferability. In addition, it was demonstrated that the inclusion of human influence index, to account for FIS dispersal and human footprint, increased the overall accuracy of the FIS model while significantly contributing to each FIS model. Suitable areas where focal FIS can spread and eventually colonize once they get established at the chosen initial entry point were discovered along with environmental factors affecting their suitability distributions.

As discussed in the background section and in Chapter 1 that a major challenge of using SDMs for invasive species is that they don't include dispersal limitations of the species and often assume dispersal to be either absent or unlimited. It was shown that FIS specific dispersal traits can be effectively included in the distribution projections. And as a result, it was found that including FIS dispersal limited the range shift of the focal FIS. In the chapter it was made evident that an invasive SDM must include dispersal in order to highlight actual areas at risk of invasion.

The methodology presented in chapter 2 addresses model parameterization, selection of predictors, inclusion of dispersal and representation of prediction uncertainty together in a workflow. The risk assessment framework presented in chapter 2 is easy and allows early assessment of pest risk via integrating species specific dispersal traits. In general, these findings demonstrate that SDMs for invasive species, require a very careful construction and must address biotic interactions along with species biology and dispersal.

Chapter 3 investigated niche shifts and conservatism for the selected FIS. As discussed in the second chapter and in the background section that SDMs are based on the assumption of niche conservatism which seldom applies to invasive species. Analysis presented in chapter 2 have assumed the notion of niche conservatism to be true, but the occurrences from nonnative regions were taken into consideration in order to account for any additional information that invaisves in nonnative ranges might contain. However, FIS specific niche characteristics in both native and nonnative ranges were not compared, and thus whether the focal FIS niches were conserved, experienced shifts or whether they evolved in their invaded ranges were unknown. Thus, chapter 3 explored the niche similarities or dissimilarities of focal FIS by matching the overlap between respective native and introduced ranges in an environmental space. Moreover, Chapter 3 further explored the methodology of comparing niches and analyzed the impacts of variable selection on the estimated niches. Chapter 3 discovered that the variable selection impacted the delineation and overlap of each studied niche. Whereas, the subset of climatic variables selected from the first two PCA-environment axes explained more variance in environmental conditions than the complete set of climatic variables for all four species. It was also shown that most focal species showed niche shifts and further incomplete occupation of available niche within their invaded ranges. It further demonstrated that the proportion of niche overlap between the native and invasive ranges, varied with species. Chapter 3 demonstrated that exploring niche characteristics between native and introduced ranges offers additional insights that will be useful in understanding range expansion and invasion potential of non-native species.

4.2 Innovations of the research

This dissertation provided key innovations for designing SDMs for mapping invasion risk of forest invasives:

• The novel best practices to improve SDMs were outlined in Chapter 1 and the following chapters validated that their inclusion improves the accuracy of the models and accordingly forecasts the invasion risk. A novel framework for FIS risk assessment has been presented in chapter 2 and 3 and it was shown in both the chapters that model development and predictor section significantly affected the modeled outcomes. The presented methods form a standard for producing risk maps using SDMs.

- Chapter 2 provided new insights into the ongoing need of invasive SDMs to address dispersal limitations of the species. The chapter brought together the elements of FIS specific dispersal abilities and their respective modeled distributions. The novel method allowed to simulate FIS spread from a hypothesized entry point for a set of anticipated future climate change conditions, while integrating species specific genetic traits and dispersal barriers. This novel methodology enables distribution modelers to forecast invasive species spread while incorporating the dispersal capabilities of the species under changing landscape and climate conditions.
- Chapter 2 utilized a novel approach for visualizing uncertainty in species distribution models.
 This approach provided an effective representation of uncertainty with respect to input data in MaxEnt models.
- In order to find ways to model habitat suitability of a new incoming FIS for which almost negligible to very few observation data are available, a methodology was tested to replace the FIS presence data with that of its host. It was shown that by using the presence locations of the FIS host, information on potential areas of FIS establishments can be obtained. This approach provides risk assessors the ability to develop SDMs for less surveyed as well as for recently arrived FIS.
- This thesis provided new information with respect to focal FIS distributions, preferred climates, spread patterns, impacts of climate change on their range expansion and specific niche characteristics in their native and nonnative ranges. This information will help the decisionmakers towards management around these selected FIS.

4.3 Key limitations

My thesis presents advances towards a better understanding of spatial models for use in invasion ecology in particular reference to forests invasive pests. The methodology presented to develop pest risk maps is robust and easy despite there are few limitations and challenges.

In chapter 1, I have limited myself to issues related to model transferability, biotic interactions along with dispersal limitations (local and regional) and uncertainty, which appeared especially relevant in the case of invasive species. However, I have excluded other important aspects to consider such as autocorrelation amongst predictors, extent and resolution of the study area,

variable selection, pseudo-absence generation procedures and model evaluation which might also be useful to consider.

Challenges associated with the data are identified in the chapters 2 and 3. Sampling bias and inadequate FIS observation samples from native and invasive ranges may have underestimated the actual distribution ranges of the invasives. Additionally, lack of data from invasive ranges may have failed to capture FIS local adaptations and associated evolutionary niche shifts. In chapter 2, I have used SDMs to predict invasive niches. However, the approach has recently come under scrutiny due to the underlying assumption of niche conservatism which is supported by little evidence (Jiménez-Valverde et al., 2011; Peterson et al., 2012). Moreover, the estimated niches are likely to vary depending on statistical assumptions and procedures related model building and fitting.

To model the species niches, I have used coarse resolution climatic grids of 10 km and 5 km due to the data limitations. However, this resolution might not be adequate to completely capture species biological differences in the considered ranges. Moreover, the approach presented to model potential distribution of FIS only measured the realized niche, which is a subset of fundamental niche where the species is not absent due to biotic competition. Hence in this work the fundamental niche of the FIS remains unknown.

I have produced FIS dispersal maps assuming the focal FIS will enter through selected ports. However, the FIS infested material could arrive to any other vulnerable port or transportation destination other than Vancouver and Toronto, thus additional simulations for specific scenarios based on actual points of entry are still needed.

The methods proposed in chapters 2 and 3 disregard the important biotic processes that may have delineated the species niche. Additional observation data and information on physiological requirements of invasives derived from genomics from both native and introduced ranges would be useful to better understand and predict the behavior of the representative invasives in their respective newly introduced ranges.

SDMs are primarily based upon species occurrence records in their native range to describe a new potential distribution and may highly underestimate where an invasive species could survive.

SDMs based on native ranges would fail due to their inability to predict the post introduction influences of adaptations, interactions and dispersal barriers within the invasive range (Tingley et al., 2014). Similarly, the modelled areas in the invaded range that do not match the conditions in the native niche could be interpreted as shifts due to evolution or adaptation. However, these areas may also represent landscapes which would are part of the species' fundamental niches in their native environments, but which have not been documented due to their absence as a result of other factors such as competition, predation, host distribution, etc. Distinguishing these two patterns, to assign differences in niche occupancy between the native and invaded range implies based on a mechanism, seems difficult with this data. Due to the above stated limitations the results obtained from this study should be assessed with caution.

4.4 Future directions

- One of the key inputs to the SDMs is species occurrence data. For invasive species, often the occurrence data is inadequately available for the purpose of developing SDMs. Moreover, the available records occasionally lack georeferencing and adequate sampling. This insufficiency limits the performances of SDMs. Hence, much efforts are required towards data collection, frequent updates and accessibility in the future. It is recommended to allow more collaborative projects aimed at sharing and open distribution of knowledge and data on invasives. In the future, citizen science may contribute to enrich the invasives database, followed by genomics led invasive identification and data transfer to species distribution modelers.
- Currently, species distribution models lack processes to address species dispersal both at local and at regional scale. Dispersal is a key ability of a species that governs its spread and distribution potential. SDMs ignoring dispersal abilities of FIS might find it hard to differentiate between potentially suitable and potentially colonizable habitat. This increases the risk of misrepresentation of actual areas at risk of invasion and will trigger over valuation of survey and management costs. It is recommended that in future, the development of SDMs is such that it can address dispersal at both local and regional scales.
- Human-mediated dispersal, most notably along the transportation routes serve as a vector for many invasives, both at the pre and post introduction stages. Primary introductions often occur as a result of long-distance dispersal events such as international travel, trade, shipping, etc.

Whereas, secondary spread occurs on much smaller scales (e.g. landscape) and result from natural events or human activities. Currently, most spatial models disregard to include the processes at secondary levels of spread (e.g. cars, local transport, recreation, etc.). In future, there is scope to develop a spatial model that can simulate species spread while addressing both primary and secondary spread.

- Most of the niche-based models ignore important biotic processes of invasive species such as species interactions, local adaptations, etc. These important biotic processes play a key role in shaping a species niche and thus SDMs lacking these processes might not accurately predict the species niche. This inability of SDMs to include biotic processes might be lacking due to lack of any straightforward approach to include all the processes together. In future development of a model to simulate invasive spread by including all important biotic processes is warranted.
- In chapter 3, I have compared niches of DED and SOD at species level. However, there are differences present at sub species level for these pathogens. In future, work could be done in order to address subspecific niche adaptations of both DED and SOD.
- My work in chapter 3 shows that some of the focal FIS show preferences to novel environments in non-native range that might be due to genetic drifts or selection. If its genetic drift which is responsible to allow the organism to persist in the new environment, then the related genes must have been present in the source population. This can also be then relating to the regions of native niche that are fundamental niches, but not realized niches. Thus, it might be useful to carry research to answer the question "can the novel niches occupied in the invaded landscape identify parts of the fundamental niche in the native landscape that are not occupied?". Also, the ordination method proposed here can be used in combination with a vector analysis to identify directional trends in what the population is doing in the invaded landscape (i.e. its moving into dryer areas, more diverse areas, areas with shorter or longer growing seasons, etc.). This could be an interesting way to explore tools for identifying the characteristics in a species that makes it a good invader.
- Throughout the thesis I have highlighted the potential of SDMs for their use in management of invasive species. As prevention of invasives is considered the most cost-effective approach (Hulme 2009), the maps produced from this study will serve as a guide for prioritizing survey areas and directing the required provisions for focal invasives survey and necessary

management actions. It is recommended that the maps produced here should be used for setting up quarantines and cross border inspections in order to keep these threatening FIS away from getting into areas of high invasion risk. Areas at risk were identified in this thesis, if focal FIS were to establish in areas around port of Vancouver and Toronto. In future management and preventive actions related to these FIS must take place in these identified areas in order to ensure effective early detection and rapid response to these invaders. Recommendations are made to replace the hypothesized point of entry with actual FIS point of entry (when available) to simulate actual dispersal path of FIS. This work presents an opportunity for pest risk assessors to use the pest risk framework to inform related risk management decisions.

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Appendix-I

Evaluation summary of FIS models using TSS, correct classification rates, omission error and sensitivity metrics. The worst performing model (type iv) is highlighted with a horizontal across line for comparison purposes.









Asian longhorned beetle

0.800

Without

file

Correction Sampling Bias



Sudden oak death
Appendix-II

Potential distribution of selected FIS in current and future climate change scenarios.









CCSM4-RCP8.5 (2050)











HADGEM2-ES-RCP2.6 (2050)

HADGEM2-ES-RCP4.5 (2050)

MIROC5-RCP4.5 (2050)

HADGEM2-ES-RCP8.5 (2050)



MIROC5-RCP8.5 (2050)



Current

3,800 7,600 Km



MIROC5-RCP2.6 (2050)

Asian longhorned beetle



Sudden oak death

Appendix-III



(a) Predicted potential distribution of selected FIS in their respective distributional area. Higher probability (red colors) represent areas suitable for FIS. Zero probability or lower probability (dark green) indicates areas less suitable.



(b) Prediction uncertainty for the modelled FIS distributions. Higher uncertainty (red colors) represent highly uncertain areas with low confidence in modelled predictions whereas, lower uncertainty (dark green) indicates areas having low prediction uncertainty with higher confidence.

Appendix-IV

(a) Relationships between environmental predictors and the probability of the presence of FIS: Red curves show the mean response and blue margins are ± 1 SD calculated over 10 replicates. (b) Jackknife test for AUC of individual environmental variable importance (blue bars) relative to all environmental variables (red bar) for the MaxEnt model. Values shown are averages over 10 model runs. Temperature values are *10.

Asian longhorned beetle





(b)

Dutch elm disease





(b)



Sudden oak death





AUC

(b)

Appendix-V

Table: Comparing dispersal limited to unlimited FIS dispersal projections under climate change conditions. Here numbers represent total number of cells colonized under each scenario.

(a) Asian gypsy moth

	Infestation point- Vancouver port			Infestation point- Toronto port			Unlimited dispersal		
GCM/Sc enario	ccsm4	hadgem2 es	miroc5	ccsm4	hadgem 2es	miroc5	ccsm4	hadgem 2es	miroc5
rcp26	1507	1711	1625	4708	4943	4767	13627	13616	13027
rcp45	1543	2148	2256	4975	5027	4940	13340	13682	13129
rcp85	1748	2347	2457	5010	5149	5087	13916	13507	13122

(b) Asian longhorned beetle

	Infestation point- Vancouver port			Infestat port	ion point- 7	Foronto	Unlimited dispersal		
GCM/Sc enario	ccsm4	hadgem2 es	miroc5	ccsm4	hadgem2e s	miroc5	ccsm4	hadgem2e s	miroc5
rcp26	71	76	68	2482	2497	2446	6743	6848	6545
rcp45	75	82	72	2528	2539	2613	7019	7715	7237
rcp85	76	91	79	2567	2587	2663	7782	8560	7386

(c) Dutch elm disease

	Infest port	ation point- To	oronto	Unlimited dispersal			
GCM/Scenari o	ccsm 4	hadgem2es	miroc5	ccsm4	hadgem2es	miroc5	
rcp26	1555	1533	1552	6743	6848	6545	
rcp45	1568	1580	1568	7019	7715	7237	
rcp85	1595	1601	1622	7782	8560	7386	

(d) Sudden oak death

	Infestation port	on point- Vano	couver	Unlimited dispersal			
GCM/Scena rio	ccsm4	hadgem2es	miroc5	ccsm4	hadgem2es	miroc5	
rcp26	877	777	893	1165	977	1060	
rcp45	822	679	848	1060	944	1095	
rcp85	669	500	759	1032	911	1035	

Appendix-VI

FIS dispersal limited distributions under different climate change scenarios and two hypothesized infestation points-

AGM (Infestation point- Vancouver port)



Dispersal restricted future distribution of AGM under GCM-CCM4 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of AGM introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of AGM under GCM-HADGEM2ES and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of AGM introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of AGM under GCM-MIROC5 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of AGM introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.

AGM (Introduction point- Toronto port)



Dispersal restricted future distribution of AGM under GCM-CCSM4 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of AGM introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of AGM under GCM-HADGEM2ES and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of AGM introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of AGM under GCM-MIROC5 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of AGM introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.

ALB (Introduction point- Vancouver port)



Dispersal restricted future distribution of ALB under GCM-CCSM4 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of ALB introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of ALB under GCM-HADGEM2ES and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of ALB introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of ALB under GCM-MIROC5 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of ALB introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.

ALB (Introduction point- Toronto port)



Dispersal restricted future distribution of ALB under GCM-CCSM4 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of ALB introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of ALB under GCM-HADGEM2ES and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of ALB introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of ALB under GCM-MIROC5 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of ALB introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.

DED (Introduction point- Toronto port)



Dispersal restricted future distribution of DED under GCM-CCM4 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of DED introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of DED under GCM-HADGEM2ES and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of DED introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of DED under GCM-MIROC5 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of DED introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.

SOD (Introduction point- Vancouver port)



Dispersal restricted future distribution of SOD under GCM-CCM4 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of SOD introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of SOD under GCM-HADGEM2ES and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of SOD introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.



Dispersal restricted future distribution of SOD under GCM-MIROC5 and RCP 2.6, 4.5 and 8.5 climate change scenarios. Color gradient from blue to grey represents the first 10 years of the simulation time frame when colonization first occurred, the light grey to light yellow color gradient represents the next 10 years followed by orange and rose color gradients (years 2031-2050). Dark red pixel indicates the hypothesized point of SOD introduction while the green pixels represent suitable areas that were not colonized due to dispersal limitations.

Appendix-VII

AGM life history parameters and associated references

AGM is a potent invader with more than 600 known hosts. AGM females are capable of flight and can lay eggs on human-made objects.

- *Generations per year Univoltine- one generation per year (Elkinton & Liebhold, 1990)*
- Dispersal
 - Adult females disperse and spread their population naturally by sustained flight and wind-borne dispersal of first instars (M. A. Keena, Côté, Grinberg, & Wallner, 2008).
 - Attracted to lights at night (Montgomery & Wallner, 1988; Schaefer & Strothkamp, 2014)
- Dispersal Distance
 - Frequent long distance dispersal flights (average less than 1 km to max range of 20-40 km) (Iwaizumi, Arakawa, & Koshio, 2010; M. A. Keena et al., 2008)
 - Russian females may fly distances up to 100 km and eastern Siberian females seen crossing mountain ranges in large groups during outbreaks (Rozhkov and Vasilyeva 1982)
 - Egg masses in Japanese cities found within 1 km of forests(Liebhold, Turcáni, & Kamata, 2008).
 - Average flight distance of 1 day old Chinese females in 8 hours on flight mills was 5.65 km and maximum was 10.67 km (Yang, Luo, & Shi, 2017)
- *Reproductive capacity,*
 - Producing an average of 600 to 1000 eggs per egg mass (USDA)
- Distribution
 - Found throughout temperate Asia. Usually east of the Ural Mountains into Far East Russia, through most of Japan, China and Korea. It is not found east of the Himalayan range in India (USDA)

- Critical temp.
 - AGM populations may struggle in regions experiencing longer periods of temperatures ≥ 30°C and survival rate is highest between 15and 25°C (Limbu et al., 2017).

ALB life history parameters and associated references

- Sex ratio
 - 1-1:14 male female (Bancroft & Smith, 2005)
 - 1:1 male-female (Trotter, Talbot Trotter, Pepper, Davis, & Vazquez, 2019)
 - Other papers use only the females to model spread since she drives the establishment of new infestations
- Generations per year
 - *Temperature dependent*
 - Haack 2010
 - (*M. A. Keena & Moore, 2010*)
 - (Faccoli & Gatto, 2016)
 - (Favaro, Wichmann, Ravn, & Faccoli, 2015)
 - *Not strictly univoltine (one year); may take multiple years to develop*
 - (M. A. Keena & Moore, 2010; Trotter & Keena, 2016) (in Finland may take 10+ years)
 - (Straw, Tilbury, Fielding, Williams, & Cull, 2015)
 - 3 years for Paddock Woods
 - (Kappel, Talbot Trotter, Keena, Rogan, & Williams, 2017)
 - Do not use the Newtonian Cooling model to estimate within tree temps may not accurately reflect temps within tree
 - But estimated that in northern states will take minimum 2-3 years to complete development, some areas up to 5-6 years
- Dispersal Distance
 - Frequent short distance dispersal flights (<1.5km)
 - (Javal, Roux, Roques, & Sauvard, 2018)

- Tendency to remain on and reinfest natal tree
 - Haack 2010
- Dispersal occurs when tree host quality deteriorates
 - Sawyer 2007
- *Rare long distance flights (<1.5km)*
 - Human mediated transport likely more significant at farther distances
 - (Fournier & Turgeon, 2017)
- \circ ~10km (modeled and based on graph)
 - Trotter 2018
- \circ Longest single sustained flight on flight mill = 4006m; median = 247.6m
 - Javal 2018
- *Lifetime dispersal for a female = 14060m; median=3964m*
 - Javal 2018
- Spread rates
 - in England in one stand, mean rate of population spread 29.3m/year
 - (Straw, Fielding, Tilbury, Williams, & Cull, 2016)
 - Jersey City spread 50m/year
 - Sawyer et al. 2004
 - New Jersey spread 2,4-3.2km in 5-6years
 - Sawyer et al. 2010
 - Italy spread 2x2km in 5 years
 - *Favaro et al. 2013*
- Probability to disperse
 - \circ 55% of tethered test flights = no flight
 - Javal 2018
 - <50% took flight in a number of laboratory experiments, esp females
 - (*Melody A. Keena*, 2018)
- Critical temps
 - \circ 10.2C egg hatch
 - Temperature developmental model -(Trotter & Keena, 2016)
 - Adult emergence in spring after 400-degree-days (10C threshold)

- (*Smith, Tobin, Bancroft, Li, & Gao, 2004*)
- Dispersal ceases below 15°C
 - *(Keena 2018)*
- Habitat preferences
 - Edge preference
 - (*Williams, Lee, & Kim, 2004*)
 - (Shatz, Rogan, Sangermano, Ogneva-Himmelberger, & Chen, 2013)

DED biology and vector life history

DED is vectored by several species of bark beetle: Hylurgopinus rufipes (native), Scolytus multistriatus (introduced - Europe), and Scolytpus schevyrewi (introduced - Asia).

- Surprising lack of dispersal information for above three species
 - (Harwood, Tomlinson, Potter, & Knight, 2011)
- Dispersal Kernel
 - (*Harwood et al.*, 2011)
 - DED vectors
 - Negative exponential kernel of 20km (15-40km)
 - Experts estimate max dispersal = 12.88km
 - Most dispersal within 500m of host
 - Median dispersal distance of 150m for a negative square power law function for incorporating radial dispersal
 - Probability of 0.002 for dispersal >12.88km
 - Combined beetle and firewood kernel of 3:1 beetle:firewood movement gives a reasonable pattern of spread in early stages of epidemic
- *History of DED in UK*
 - (Tomlinson & Potter, 2010)
- Review of factors influencing flight in bark beetles (Jones, Shegelski, Marculis, Wijerathna, & Evenden, 2019)
- Bark beetles (= Scolytinae) contain vectors of DED
- Flight capacity vs dispersal distinct
 - *Capacity = physiological ability to fly*
 - *Dispersal = capacity + imapct of external factors (e.g. environment)*
 - Long distance dispercal characterized by above canopy flight carried by wind (e.g. Mountain pine beetle dispersal over Rocky Mountains; 30-100km/day via wind)
- Dispersal distance
 - mean for beetles ranges from 500m to 6km; max distances can be >25km, but this is a long thin tail, bulk of the pop is short distance
- Fat-tailed dispersal kernel needed to capture potential for bark beetles to disperse long distances
- *Min temp for flight initiation in bark beetles range from 10.6C 21C; mean = 15.6C*
- Dispersal distance
 - *Mark recapture 38% pop close to release site, 52% within 400-600m from release site (Strobel & Lanier, 1981)*
 - 5-6km dispersal (Wolfenbarger & Jones, 1943)
 - Mark recapture 1km (Pines & Westwood 2008)
 - 400-600m dispersal (Wollerman, 1979)

SOD biology and vector life history parameters and associated references

There are no known vectors of SOD other than humans but any organism that can move soil is potentially a vector of SOD.(Grünwald et al., 2012, 2019; Kliejunas, 2010; David M. Rizzo, Garbelotto, & Hansen, 2005)

- Dispersal
 - Long range spread of disease through sporangia and chlamydospores, chlamydospores can survive for a week at a constant temperature of 55°C.
 - Natural dispersal of SOD is by movement of plant material, waterborne and soilborne chlamydospores, and by waterborne, soilborne and wind-blown rain

containing sporangia.(David M. Rizzo & Garbelotto, 2003; David M. Rizzo et al., 2005)(Grünwald et al., 2019)

- Dispersal distance
 - Splash dispersal-propagules can travel up to 60 cm above infested surfaces (Kuske, 1983).
 - Local spread <1 km (ecological (Condeso, Emiko Condeso, & Meentemeyer, 2007; Ellis, Václavík, & Meentemeyer, 2010)and genetic (Mascheretti, Croucher, Kozanitas, Baker, & Garbelotto, 2009; Mascheretti, Croucher, Vettraino, Prospero, & Garbelotto, 2008))
 - Most inoculum remains within 10 m of the host (Davidson, Wickland, Patterson, Falk, & Rizzo, 2005)
 - *Maximum dispersal distance < 8 km during rare storm events (apsnet.org).*
 - Number of trees infected was higher on public lands that were open to recreation than on adjacent lands lacking public access and higher human population densities within 50 km increased chances of fungal infection (Cushman et al., 2008).
- Effects of temperature and moisture on growth and sporulation
 - Fungal growth occurs 10-31°C (Tooley, Browning, Kyde, & Berner, 2009)
 - Exposure to temperatures over 30°C decreases survival and a few minutes at 40°C kills the fungus (Browning, Englander, Tooley, & Berner, 2008)
 - Sporangia production occurs over the temperature range of 16-22°C (Englander, Browning, & Tooley, 2006)
 - A dew period of as little as 1 hour was enough for fungal development but moisture for 24-48 hours is required for maximal disease development in the laboratory (Tooley et al. 2009)
 - Most clonal hyphal colonies can survive 24 h exposure to -5 C and some can withstand -25 C for 24 h. (Browning et al. 2008).
- Distribution
 - SOD is distributed only in Europe and parts of North America, with three identified clonal lineages (EU1, NA1 and NA2), named for the continent where

they were first found, followed by a number indicating the order of discovery (Grünwald et al., 2009)

- Habitat
 - Coastal forest types (David M. Rizzo & Garbelotto, 2003; D. M. Rizzo, Garbelotto, Davidson, Slaughter, & Koike, 2002), moist and moderate climates (Rizzo et al., 2005).

Appendix-VIII



Figure: DED potential distribution predictions in novel environment (Canada) obtained from (a) a complex (default) MaxEnt and (b) a simple (tuned) MaxEnt model. Canadian DED occurrences are overlaid on suitability surface for visual comparison of the outcomes.



Figure: AGM potential distribution predictions in novel environment (Canada) obtained from (a) a complex (default) MaxEnt and (b) a simple (tuned) MaxEnt model. Canadian EGM occurrences are overlaid on suitability surface for visual comparison of the outcomes.

Appendix-IX



Figure: Ulmus americana (DED host) potential distribution predictions in novel environment (Canada) obtained from a tuned MaxEnt model.



Figure: DED potential distribution predictions in novel environment (Canada) obtained from a tuned MaxEnt model.