BUILDING AN ARC IN THE ANTHROPOCENE: APPLYING PRINCIPLES OF ENVIRONMENTAL RESILIENCE TO IMPROVE SINGLE-SPECIES CONSERVATION PLANNING IN AN ERA OF CLIMATE CHANGE

by

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One for the people who still fight for the earth…

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Abstract

Habitat loss and fragmentation have precipitated a mass extinction. Therefore, maintaining a functionally connected habitat network is an effective response to biodiversity loss. However, climate change poses challenges for conservation planning, as areas that are protected for unique biodiversity values may not retain those values in the face of shifting temperature and precipitation regimes. Furthermore, range shift predictions can be notoriously uncertain, and planning efforts that seek to achieve broad species representation are unlikely to confer sufficient protection to individual species. In this thesis, I addressed 2 key limitations that challenge single-species conservation planning: variable reliability of presence-only species distribution models (SDMs) and uncertainty of conservation plans developed for an era of climate change. Specifically, I performed 3 studies that investigated (1) parameterization choices in Maximum Entropy (Maxent) presence-only modeling, (2) the use of resilient topographic features as covariates in models, and (3) strategies to reduce uncertainty in conservation planning.

In the first paper, I investigated the unresolved issues of sample bias and choice of environmental covariate subset in Maxent, the most popular presence-only SDM algorithm, in order to improve the reliability of model predictions. I found that spatially filtering species occurrence data (a sample bias correction strategy) reduced model complexity when environmental covariates were selected using reverse stepwise elimination; however, changing the bias correction strategy had a limited effect on model results overall. Conversely, using alternative subsets of environmental covariates led to non-trivial differences in model outputs.

In the second paper, I developed landscape-scale Maxent models for 3 at-risk migratory forest landbirds in the province of Nova Scotia, Canada: the Rusty Blackbird (*Euphagus carolinus*), the Olive-sided Flycatcher (*Contopus cooperi*), and the Canada Warbler (*Cardellina canadensis*). One objective of this research was to investigate whether topographic covariates, which may be considered more resilient to the effects of climate change, can be used alongside forest covariates to predict bird occurrence. Topographic covariates were found to have moderate to strong predictive power in all bird models. As topography (1) should be relatively unaffected by a changing climate and (2) helps regulate the structure and composition of forest habitat, I posited that topographic covariates may be useful in identifing areas that are more likely to support the persistence of species over the long term as climate changes.

In the third paper, I proposed a novel approach to single-species conservation planning that (1) targets individual species which may be missed by more general planning strategies, while also (2) contributing towards the maintenance of overall biodiversity in an era of climate change. Specifically, the proposed approach combines elements of predictive modeling and an existing resilience-based conservation planning strategy known as “conserving nature’s stage” (CNS) to delineate climate-resilient refugial habitat and reduce uncertainty in conservation plans.

LIST OF ABBREVIATIONS USED

ACCDC	Atlantic Canada Conservation Data Center
AUC	Area Under the Curve
AIC_c	Akaike's Information Criterion corrected for small sample sizes
BM	Background Manipulation
cAUC	Calibrated AUC score
CAWA	Canada Warbler
CNS	Conserving Nature's Stage
D2W	Depth to Water-table
DEM	Digital Elevation Model
ESRI	Environmental Systems Research Institute
FID	Forest Inventory Database
GCM	Global Climate Model or Global Circulation Model
GIS	Geographic Information System
HRW	High Roadside-bias Weight
LTP	Lowest Presence Threshold
LRW	Low Roadside-bias Weight
Maxent	Maximum entropy modeling
MaxSS	Maximum Specificity and Sensitivity threshold
MBBA	Maritime Breeding Bird Atlas
NAD	North American Datum
NSDNR	Nova Scotia Department of Natural Resources
NSTDB	Nova Scotia Topographic Database
OSFL	Olive-sided Flycatcher
RUBL	Rusty Blackbird
SDM	Species Distribution Model
SF	Spatial Filtering
SF+BM	Spatial Filtering and Background Manipulation
SF+TG	Spatial Filtering and Target Group background manipulation
SPSS	Statistical Package for the Social Sciences
STD	Standard Deviation

TG	Target Group background manipulation
TPI	Topographic Position Index
UTM	Universal Transverse Mercator
10PT	10% Presence Threshold

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CHAPTER 1: INTRODUCTION

Life on Earth is the product of 3.5 billion years of natural selection (Taylor et al, 2009), a period which gave rise to a spectacular array of biodiversity. However, the 21st century world is much changed from that which fostered life's humble beginnings. Today, humans are the evolutionary force that dominates the landscape (Wagler, 2011). Indeed, half of the planet's surface has been modified by human activities; less than 25% of ice-free land can be considered wild (Sanderson et al, 2002; Hooke & Martin-Duque, 2012); and between 20-40% of potential primary production has been appropriated by humans (Hooke & Martin-Duque, 2012). Geologists call this state of affairs the "age of the anthropocene" (Zalasiewicz et al., 2011), and it is an age in which industrial societies are monopolizing biotic energy flow, use over half of all accessible fresh water, and move more soil and sediment than all natural processes combined (McDaniel & Borton, 2002; Cruzen, 2002; Lewis, 2006, Wagler, 2011).

There is much agreement among ecologists that the collective impact of human activities has pushed the planet towards a sixth mass extinction (Thomas et al., 2004; Ceballos et al., 2015), on par with previous cataclysmic events such as that which killed the dinosaurs. While estimates about the overall severity of the current event are varied, recent publications report that the background extinction rate has accelerated between 100 and 1000 times over the past few centuries and predict that future rates could exceed pre-human levels 10,000 fold (Millennium Ecosystem Assessment MEA, 2005; Wagler, 2011; Ceballos, 2015). The causes of biodiversity loss are varied, although in terrestrial systems the primary driver is habitat fragmentation and destruction (Sala et al., 2000; Wagler, 2011), the negative effects of which are exacerbated by climate change. Therefore, unless significant action is taken to connect, protect, and/or restore large tracts of resilient habitat, the accelerated rate of species loss is expected to continue, which will lead to concurrent declines in ecosystem services that species provide (Luck et al., 2003; Dobson et al., 2006).

1.1 Conservation planning in an era of climate change

Given the critical importance of habitat availability to biodiversity conservation, maintaining a functionally connected network of high quality habitat reserves has been cited as one of the most effective responses to species loss (Rubio & Saura, 2012). As a signatory to the Convention on Biological Diversity, Canada has committed to protecting 17% of terrestrial land and freshwater by 2020 (Environment and Climate Change Canada, 2016). However, this target was primarily based on political (not scientific) rationale, and more recent scientifically-based reports have estimated that at least 50% of land should be set aside to ensure that biodiversity conservation efforts are effective (Noss and Cooperrider, 1994; Boreal Leadership Council, 2003; Locke, 2014). Achieving ambitious habitat protection targets is clearly challenged by accelerating human population growth and the need to satisfy the competing interests of many stakeholders. Indeed, by the end of 2015, only 10.6% of Canada's terrestrial land-base had been granted protected status (Environment and Climate Change Canada, 2016). Furthermore, large protected areas (which confer the greatest benefits to biodiversity conservation) are not evenly distributed; they are mostly found in the northern parts of the country (where ecological productivity is limited) due to the lack of land-use conflicts that typically characterizes high latitudes (Andrew et al., 2011; Environment and Climate Change Canada, 2016).

Traditionally, systematic conservation planning efforts, including in Canada, have often sought to prioritize areas with high endemic species richness or sets of areas with broad species representation. However, these strategies assume that ecosystems are stationary and that habitat which is suitable today will remain so in the future (Lawler et al., 2015). In an era of climate change, altered temperature and precipitation regimes are predicted to cause species' distributional ranges to shift and/or contract in geographic space (Beier & Brost, 2009; Anderson & Ferree, 2010); indeed, for some species, significant range shifts have already been observed, and more extensive shifts are expected to occur over the next century (Schloss et al., 2011; McClure et al., 2012; Lawler et al., 2015).

In recent decades, ecologists and planners have recognized that more robust strategies for conservation system design are needed, and new approaches that address climate change are now being actively developed, refined, and applied. Conservation planning efforts typically fall into 2 broad categories: (1) fine-filter, which target individual rare and at-risk species as well as specific hotspots of diversity; and (2) coarse-filter, which target representative examples of communities and ecosystems and seek to protect tracts of habitat that are large enough to support viable populations of suites of species (Noss, 1987; Hunter et al., 1988; Beier et al., 2015). In attempting to mitigate the effects of climate change on biodiversity, fine-filter strategies typically employ climate-envelope modeling for the species of interest (Beier et al., 2015), whereby habitat models created using current climatic conditions are projected onto predictions of future climatic conditions (e.g. based on global circulation models and potential emissions scenarios) to better understand how the location and extent of habitat will change over time (Stralberg et al., 2015). Habitat models are in turn derived from species distribution models (SDMs), which use a correlative approach to quantify the niche of a species and develop spatial predictions of species' distributions under a given set of environmental conditions.

Conversely, a coarse-filter strategy that has been proposed as a way to account for climate change is known as "conserving nature's stage" (CNS). This strategy was developed according to scientific understanding of the biotic response to rapid warming that occurred at the start of the Holocene (Hunter et al., 1988; Anderson et al., 2012). During this period, relatively few extinctions occurred (Gill et al., 2015), likely due to (1) micro-refugias that retained pockets of suitable climate (i.e. areas where the *in situ* climate state experienced on the ground differed from the regional average; Dobrowski, 2010), which allowed small populations to persist in place (Keppler et al., 2012) and (2) a lack of dispersal barriers, which allowed species to move in response to climatic shifts. In brief, CNS seeks to represent a diverse but connected array of resilient abiotic features, such as landforms and geological types, which will not be affected by altered temperature and precipitation regimes and are thus said to comprise the "stage" upon which ecological and evolutionary processes take place (Beier et al., 2015; Gill et al., 2015). CNS also encourages a focus on topographically diverse areas (e.g. comprising different elevations and aspects), which tend to feature more diverse microclimates and thereby provide greater opportunities for refugial populations of species to persist as climate changes (Anderson et al., 2012).

However, both the aforementioned fine-filter and coarse-filter strategies have weaknesses. For example, both the SDMs and future climate predictions that underlie fine-filter climate envelope models suffer from uncertainty, which can be severe in many cases, leading some to question whether the noise exceeds the signal when this strategy is used (Stralberg et al., 2015). Furthermore, comprehensive absence data, which can only be obtained through rigorous, systematic field sampling, is lacking for many species, especially for depleted, rare, and/or cryptic species that tend to need conservation attention the most (Elith et al., 2011). A lack of absence data necessitates the use of "presence-only" datasets in the creation of SDMs. Unfortunately, presence-only datasets (e.g. museum records, herbarium records, observations from citizen science projects such as breeding bird surveys, etc.) almost invariably comprise undesigned, opportunistic, or purposive observations obtained from multiple sources of varying integrity. Therefore, these datasets tend to be severely impacted by sample bias, which can significantly confound model results.

Conversely, CNS was primarily developed to promote the maintenance of general biodiversity, not to protect specific species, communities, or ecosystems (Anderson et al., 2012); thus, the ability of CNS to conserve individual taxa is limited. Indeed, the strength of the relationship between abiotic features and species' distributions varies greatly (Beier et al., 2015) and, for mobile vertebrate species especially, biotic (i.e. floristic) factors tend to predict habitat suitability more directly (Franklin, 2009). Therefore, even proponents of CNS suggest that it should be complemented by fine-filter strategies which target species that are likely to be missed in a coarse-filter approach (Lawler et al., 2015).

1.2. Research goals and objectives

In this thesis, I sought to address some of the limitations in current fine-filter approaches to landscape-scale conservation planning in a context of climate change. Specifically, I sought to refine, improve, and extend habitat delineation and prioritization strategies for individual at-risk species that might not receive sufficient protection under conservation strategies that target biodiversity more generally. To achieve this objective, I performed numerous modeling and conservation planning exercises with the goals of (1) improving the reliability of presence-only SDMs, both in terms of parameterization choices (chapter 2) and predictions of future habitat (chapter 3); and (2) reducing the risk associated with the implementation of SDM results (i.e. habitat maps) in real-world conservation plans (chapter 4).

The research performed herein focused on specific taxa from a vulnerable species group, migratory forest landbirds. Specifically, I targeted the Rusty Blackbird (*Euphagus carolinus*), the Olive-sided Flycatcher (*Contopus cooperi*), and the Canada Warbler (*Wilsonia canadensis*). Therefore, a secondary goal of this thesis was to contribute spatial information to conservation planning for these at-risk landbirds in Nova Scotia.

1.3. Conservation significance of study species and study area

Between 1970 and 2010, migratory bird populations declined by 12% in Canada and by 13% in the Canadian Maritimes (Bird Studies Canada, 2012). Nova Scotia (45° N, 63° W) is a Maritime province of southeastern Canada that contains key sites along the Atlantic Flyway, including the easternmost extent of breeding habitat for the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler. On the breeding range, ongoing, spatially extensive changes to forest habitat comprise the most serious threats to migratory landbirds (Westwood et al., 2015). However, climate change compounds these threats by further reducing available habitat (e.g. through sea-level rise or wetland drying); by affecting the timing and route of migrations, thereby causing a phenology mismatch between the time when birds arrive on the breeding grounds and peak resource availability (Marra et al., 2005; Visser & Both, 2005); and by increasing competition with resident birds for the breeding resources that remain (Ahola et al., 2007; Kirby et al., 2008).

The Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler are listed under Canada's Species at Risk Act (9S. C. 2002, c. 29) and the Nova Scotia Endangered Species Act (S. N. S. 1998, c. 11). Since the 1960s, all 3 of these birds have suffered steep population declines, particularly in Canadian Maritime provinces. Nonetheless, in recent years, research interest and conservation concern surrounding these species have increased, and international research and conservation consortiums have been founded to protect them (e.g. the Rusty Blackbird Working Group, the Canada Warbler Conservation Initiative). There have also been greater efforts by both governmental and non-governmental organizations to target the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler in conservation planning and management initiatives (Westwood, 2015).

1.4. Summary of research chapters and their contributions

Chapters 2, 3, and 4 are stand-alone research papers that include independent sub-goals and self-contained introduction, methods, results, and discussion sections (summarized in greater detail below). However, note that because these chapters were written to be stand-alone, there is some redundancy in the information they present (e.g. in descriptions of the study area and study species). A final concluding chapter (5) presents a synthesis discussion, which pays particular attention to the implications of the research findings in the context of conservation planning in an era of climate change.

Chapter 2 comprises a methods study in which I explored ways to optimize maximum entropy (Maxent) modeling, the most widely used presence-only modeling technique. Here, the specific objectives were to (1) investigate the effects that 2 unresolved modeling issues, sample bias and choice of covariate subset, have on Maxent model outputs; and (2) determine which parameterization choices best address these issues to yield more accurate and reliable model results. Results from this work were used to guide the parameterization of landbird SDMs in chapter 3.

Chapter 3 comprises a Maxent modeling study in which landscape-scale SDMs were developed for the Rusty Blackbird, the Olive-sided Flycatcher, and the Canada Warbler in Nova Scotia. The objectives of this chapter were to (1) investigate whether topographic features, which are considered more resilient to the effects of climate change, can be used alongside biotic features to predict bird occurrence; (2) elucidate landscape-scale habitat requirements for the birds of interest at the easternmost extent of their breeding range; and (3) identify the most valuable conservation areas for these birds in the province of Nova Scotia.

Finally, chapter 4 presents a novel single-species (fine-filter) conservation planning strategy that targets specific at-risk species while also benefitting more general (coarse-filter) conservation goals. Specifically, the proposed strategy aims to (1) reduce the uncertainty associated with the delineation of core conservation habitat for the target species by combining the results of multiple SDMs produced using different techniques and at different scales; and (2) increase the climatic resilience of the overall landscape to support general biodiversity. The application of the proposed strategy was demonstrated through a conservation planning exercise in which high value conservation habitat for the Olive-sided Flycatcher was identified in the province of Nova Scotia. These habitat patches were then prioritized according to landscape resilience scores, which were in turn defined according to permeability and topographic complexity (using methods adapted from Anderson et al., 2012).

The research performed in this thesis should be of practical and theoretical interest to 2 fields: species distribution modeling and conservation planning. Findings from the methods study (chapter 2) provide practical, user-friendly suggestions that can be applied to improve the reliability of Maxent SDMs. Results of chapter 2 also contribute to the ongoing discussion about what constitutes best practices in presence-only species distribution modeling, a topic that currently remains controversial. Conversely, the SDMs developed in chapter 3 help elucidate landscape-scale habitat requirements for the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler in the easternmost extent of their breeding range and also delineate key conservation sites for these vulnerable species in Nova Scotia. Moreover, the SDM results of chapter 3 highlight the potential utility of topographic covariates in predicting species occurrence, which may help conservation planners identify habitat patches that are characterized by greater resilience against climate change. Finally, the novel conservation planning strategy proposed in chapter 4 can be applied to benefit specific at-risk species while also increasing the resilience of the overall landscape. In this way, the proposed strategy, while fine-filter in nature, should also support coarse-filter conservation goals in the face of climate change.

In an era of climate change, it is impossible to guarantee the indefinite persistence of any specific species. Nonetheless, it is my hope that the research conducted in this thesis will be useful in helping migratory forest landbirds and other irreplaceable elements of biodiversity survive the age of the anthropocene a little bit longer.

CHAPTER 2: MAXIMIZING THE UTILITY OF MAXENT: INVESTIGATING THE IMPACT OF SAMPLE BIAS CORRECTION STRATEGY AND CHOICE OF COVARIATE SUBSET ON PRESENCE-ONLY SPECIES DISTRIBUTION MODELS

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Abstract

Presence-only species distribution models (SDMs) have become widely used tools in environmental research and conservation management. Of all presence-only SDMs, maximum entropy (Maxent) is the most popular. However, over the past decade, rapid growth in the application of these tools has greatly outpaced corresponding methodological refinements to guide and standardize their use. As a result, many previously published empirical Maxent models have been criticized as unreliable or erroneous. In recent years, however, researchers have begun to address the need for a stronger set of best practices to improve presence-only modeling applications in earnest. We sought to contribute to this conversation by investigating the unresolved issues of sample bias and choice of environmental covariate subset in Maxent. Specifically, we used data from 1 virtual species (sampled at 2 bias intensities) and 1 real species (the Canada Warbler, *Cardellina canadensis*) to compare the efficacy of several commonly applied sample bias correction strategies: (1) spatial filtering (SF), (2) single species background manipulation (BM), (3) a combination of SF and BM (SF+BM), (4) modified target group background manipulation (TG), and (5) a combination of SF and TG (SF+TG), under a variety of conditions. For this, we ran multiple series of trials in which covariates were selected using either reverse stepwise elimination or *a priori* knowledge. Taken together, our findings suggest that, when reverse stepwise elimination is used, datasets should (at a minimum) be spatially filtered, as this tends to result in the selection of fewer covariates, thereby reducing model complexity. The combination SF+BM strategy may provide further marginal improvements in model results when the overall distribution of presence-points is sufficiently dense or exhibits severe spatial clustering. However, choice of bias correction strategy appears to be less important when covariates are selected according to *a priori* knowledge alone. Indeed, differences across all bias correction strategies were small and relatively inconsequential when the same covariates were used to train models. In contrast, using a less appropriate covariate to train presence-only SDMs led to pronounced effects in model outputs, which could lead to significant consequences for conservation and environmental management.

Keywords: Species distribution modeling, sample bias, covariate selection, reverse stepwise elimination

2.1 Introduction

Species distribution models (SDMs) seek to elucidate relationships between species' occurrence or abundance at known locations and the environmental or spatial attributes that characterize those locations. These tools have greatly increased in prominence since the 1980s, when parallel advances in statistics, physical geography, and geographic information systems (GIS) allowed for more sophisticated and realistic models to be built (Elith & Leathwick, 2009). Today, SDMs are considered standard tools in the conservationist's toolbox and are applied to support a variety of ecological goals, including to help guide reserve design, predict the effects of climate change on biodiversity, and test biogeographical hypotheses about species' responses to their environment (Franklin, 2009a).

Of the many SDM algorithms that have been applied by researchers and conservationists, maximum entropy modeling (Maxent) is among the most widely used. Indeed, the seminal paper which first introduced Maxent to the field of ecology (Phillips et al., 2006) was cited more than 3000 times in the ensuing decade. Maxent compares environmental conditions at point locations where a focal species has been observed to those of background locations (where presence is unknown). The resulting model is generated by calculating the probability distribution of environmental covariates which most closely matches that of the overall landscape while still meeting data moment constraints imposed by the species' occurrence locations themselves (Elith et al., 2010; Merow et al., 2013). (In other words, the mean, variance, covariance, etc., of environmental covariates at predicted presence locations must match those of observed species locations.) Notably, Maxent is a 'presence-only' technique, meaning that absence data are not required to generate predictions (Phillips et al., 2006). The popularity of Maxent can be attributed to (1) an algorithm which is fairly robust to small sample sizes and modest locational errors, (2) strong predictive performance compared with other presence-only techniques, and (3) a freely available software package that is particularly easy to use (Elith et al., 2010; Merow et al., 2013).

On the one hand, the advent of presence-only techniques such as Maxent has been a boon for ecology and conservation, creating opportunities for previously existing data, such as that from museums, government databases, or citizen science projects (e.g. breeding bird atlases), to be used in new and scientifically meaningful ways. In so doing, presence-only methods can preclude the need for rigorous and time-consuming field studies, which can be prohibitively expensive, particularly for rare and/or cryptic species that tend to need conservation work the most (Elith et al., 2011). On the other hand, presence-only SDMs are typically considered less robust than their presence-absence counterparts, partly because the exponential growth in the application of these tools has rapidly outpaced the development of standardized methodologies to guide their use. Maxent SDMs, which have frequently been criticized for adopting default software parameters with little or no justification (Merow et al., 2013), are particularly notorious in this regard.

Of outstanding methodological questions challenging Maxent and other presence-only SDMs, sample bias is among the most commonly cited concerns (e.g. Kramer-Schadt et al., 2013; Yackulic et al., 2013; Boria et al., 2014). This is because presence-only datasets almost invariably comprise a collection of undesigned, opportunistic, or purposive observations obtained from multiple sources of varying integrity (Franklin, 2009b). Indeed, Yackulic et al. (2013) reported that 87% of all empirical Maxent models published between 2008 and 2012 were likely to suffer from sample bias. Furthermore, in the vast majority of Maxent models examined by Westwood (2016), sample bias was either unreported or incorrectly characterized.

Another outstanding challenge in presence-only modeling involves choosing the most appropriate set of environmental covariates with which to build the model. This issue is non-trivial, as the true set of ecological factors influencing a species' distribution is rarely known (Synes & Osborne, 2011), and as the choice of covariates can greatly influence the predictive performance of SDMs. For example, Synes & Osborne (2011) generated competing models to forecast the future distribution of a threatened bird species under the influence of climate change. They found that using alternative sets of environmental covariates led to much greater uncertainty in model predictions than did applying different climate change or emissions (e.g. environmentally conscious world versus status quo) scenarios.

Fortunately, however, findings such as those of Synes & Osborne (2011) and Yackulic et al. (2013) have highlighted the need for a stronger set of best practices to guide presence-only modeling applications, and many researchers are now actively working to standardize modeling methodologies (see Guisan et al., 2013; Westwood, 2016). We sought to contribute to this conversation by performing experiments to investigate the outstanding issues of sample bias and choice of covariate subset in Maxent. In so doing, we had 3objectives. The first was to compare several commonly used bias correction strategies to determine which yields the most accurate spatial predictions (i.e. maps of relative habitat suitability) under a variety of conditions. Specifically, the bias correction strategies we considered were (1) spatial filtering (SF), (2) manipulating background data so that it contains the same spatial bias as the species occurrence dataset (i.e. background manipulation; BM), (3) using a 'target group' (TG) to select background data, (4) a combination of SF and BM (SF+BM), and (5) a combination of SF and TG (SF+TG). Our second objective was to determine whether any of the 6 bias correction strategies is able to improve covariate selection when a reverse stepwise elimination process is used. The third and final objective was to determine which has a greater impact on model outputs: sample bias correction strategy or choice of covariate subset.

To address these research objectives, we applied the various bias correction strategies in 4 series of trials, in which Maxent models were trained using (1) occurrence points from either virtual species datasets (sampled at 2 bias weightings) or a real Canada Warbler (*Cardellina canadensis*) dataset as well as (2) covariates that had been selected according to *a priori* knowledge or a reverse stepwise elimination process. Virtual species SDMs were assessed by AUC, by comparing the predicted suitability surface to the 'true' suitability surface, and by examining the accuracy of selected covariates and response curves. Real species (Canada Warbler) SDMs were evaluated using variants of AUC and by considering the ecological realism of models.

To the best of our knowledge, this is the first study to examine the interplay between sample bias correction strategy and covariate selection. Insights from this study should help researchers and conservation practitioners who use Maxent in their work make more appropriate methodological and parametrization choices, thereby improving the reliability of SDM predictions. Findings from the current study should also interest the growing number of researchers working to refine and optimize a methodological framework to guide presence-only modeling efforts.

2.2 Methods

2.1.1 Study area

Our study area was Nova Scotia (45° N, 63° W; Figure 2.1), a Maritime province in southeastern Canada that is characterized by a modified continental climate and exhibits a wide (though not extreme) temperature range, ample precipitation (particularly in winter and fall), and great variability in daily weather conditions (Nova Scotia Museum of Natural History, 1996a). With a total area of 52,939 km^2 (Statistics Canada, 2014), Nova Scotia contains a diverse array of landscapes and an abundance of wetlands, lakes, and rivers (Nova Scotia Museum of Natural History, 1996b). The province is characterized by gently rolling topography, and elevation ranges from 0 - 520 m above sea level, with the highest elevations found in Cape Breton. Nova Scotia belongs to the Acadian Forest Ecozone and has a mixed-forest species composition, though conifers dominate in many areas, particularly where drainage is impeded (Rowe, 1972; Neily et al., 2005). Recently, efforts to model habitat for songbirds (including the Canada Warbler) (e.g. chapter 3 of this thesis; Westwood, 2016) and other at risk species (Snaith & Beazley, 2004; Cameron et al., 2013) have been focused in Nova Scotia.

2.2.2 Data and workflow

The workflow and analytical framework employed to address our 3research objectives was modified from Fourcade et al. (2014) and involved 4 series of Maxent modeling trials (Table 2.1, Figure 2.2). Trial series 1 and 2 were conducted to address our first research objective: compare commonly used bias correction strategies and determine whether any of them yields more accurate mapped predictions of habitat suitability. Specifically, trial series 1 involved training Maxent models with virtual species datasets (sampled at 2 bias weightings) and the 4 “true” environmental covariates that were used to synthesize them. In trial series 2, models were trained using real species data and pre-defined sets of either 5 (i.e. ‘depth to water-table’ (‘D2W’), ‘distance to wetland’, ‘distance to coniferous stand’, ‘distance to deciduous stand’, and ‘distance to stand with dead material) or 6 (i.e. all of these as well as ‘distance to clear-cut) covariates, chosen according to a literature review and findings of a previous landscape-scale modeling study conducted for the Canada Warbler in Nova Scotia (Westwood et al., 2015).

Trial series 3 and 4 were conducted in support of our second research objective: determine whether any of the bias correction strategies shows a superior ability to facilitate accurate covariate selection when reverse stepwise elimination is employed. For this, in trial series 3, Maxent models were trained using virtual species data (sampled at 2 bias weightings) and sets of covariates that were selected using a reverse stepwise elimination process (described in section 2.2.4). In trial series 4, covariates were also selected through reverse stepwise elimination, but real species (Canada Warbler) data was used.

Our third and final research objective − determine whether sample bias correction strategy or environmental covariates used in model training have a greater impact on SDM results − was also addressed using models that were generated in trial series 2 (i.e. real species data + pre-defined sets of 5 or 6 covariates).

Over subsequent sections, the following is described: (1) preparation of environmental covariates and species’ occurrence datasets (2) sample bias correction strategies evaluated in comparative analyses, (3) reverse stepwise elimination, and (4) model evaluation.

2.2.3 Dataset preparation

Environmental covariate data. Environmental covariates used to train Maxent models included 4 themes: topography, characteristics of forest vegetation, access to water, and anthropogenic disturbance (base layers were obtained from the Nova Scotia Department of Natural Resources; NSDNR); however, the subsets of covariates employed in each of the 4 trial series varied slightly (Table 2.2). All data preparation was performed using tools in ArcGIS 10.2.2 software (Environmental Systems Research Institute [ESRI], 2014). Environmental covariates were prepared as a stack of ASCII files with the same projection (NAD 1983 UTM Zone 20), spatial extent, and cell size (i.e. resolution; 150m^2). Following this, Spearman correlation coefficients were calculated for each pair of covariate data layers using SPSS 21 (IBM Corp, 2013). When the Spearman's r value was ≥|0.6|, 1 of the covariates in the pair was dropped from further analysis. After removing highly correlated layers, 14 environmental covariates were available for input into Maxent (Table 2.1; See Appendix A for a more detailed description of GIS layers and their preparation).

Synthesis and biased sampling of virtual species data. Trial series 1 and 3 employed virtual species data, which was synthesized using the niche synthesis method developed by Hirzel et al. (2001). Specifically, we generated a series of 'niche response functions' (i.e. the species' responses to a set of ecogeographical or environmental features) for 4 covariates: 'distance to coniferous stand', '% crown closure', 'topographic position index' ('TPI'), and 'distance to agriculture'. These response functions were then weighted and combined according to Eq. 1 to synthesize a virtual habitat suitability surface:

$$(1) \qquad \mathrm{H} = \frac{1}{\sum_{i=1}^{n} W_i} \sum_{i=1}^{n} w_i H_i + \varepsilon \qquad ,$$

where H is the overall suitability score of a raster cell; H_i is the partial suitability score of the *i*th niche coefficient; w_i is the weight assigned to that partial suitability score; and ε is a random error term between -0.05 and 0.05 (Hirzel et al., 2001). The virtual habitat suitability surface (truth map, hereafter) represents the "true" intrinsic preferences of the virtual species and was used to evaluate the quality of our predictive Maxent models. The covariates and associated response functions that were used to create the truth map are listed in Table 2.3.

To generate virtual presence points from the truth map, a virtual distribution map was synthesized by (1) adding a random value between -0.2 and 0.2 to each cell of the truth map to introduce stochasticity to the data; and (2) selecting a presence threshold to convert the continuous values of this stochastic truth map into a binary presence/absence map (distribution map, hereafter) (Hirzel et al., 2001). We used a threshold of 0.9 in order to yield a distribution map in which approximately 25% of cells were classified as 'suitable'. Following this, we randomly generated 5000 virtual presence points in suitable cells (i.e. cells where $H \geq 0.9$).

To simulate roadside bias, which commonly affects presence-only datasets (Fourcade et al., 2014), we weighted virtual species presence points in such a way that points closer to roads were more likely to be sampled than points farther away. We then subsampled 25% and 5% of the 5000 weighted virtual presence points to generate datasets with low roadside weight (LRW; 1250 presence points) and high roadside weight (HRW; 250 presence points), respectively (Figure 2.3) (Fourcade et al., 2014). The subsampling procedure was repeated 5 times (at each roadside weight) in order to obtain 5 replicates of both HRW and LRW datasets.

Real species data. For trial series 2 and 4, we constructed real species presence-only models using occurrence data for the Canada Warbler (*Cardellina canadensis*), a neotropical passerine migrant of conservation concern that breeds in Nova Scotia and shows a facultative preference for forested wetlands, but is also common in wet, shrubby forests in the eastern part of its range (Reitsma et al., 2010). The Canada Warbler selects nest sites on or near the ground that are concealed by thick understory and forages for insects in shrubs or the lower branches of both coniferous and deciduous trees (Goodnow and Reitsma, 2011).

Presence points for the Canada Warbler were obtained from the Atlantic Canada Conservation Data Center (ACCDC, 2014), and primarily comprised records from the Maritime Breeding Bird Atlas (MBBA) database (2006-2010 surveys), but also included observations made by other individuals or research groups. We removed duplicate points and low-resolution data (i.e. observations where birds were not guaranteed to be less than 150 m away from the recorded coordinates), which left 412 presence points available for input into Maxent modeling software (Figure 2.4).

2.2.4 Sample bias correction strategies

As controlling for sample bias is critical in building a robust SDM, we compared the efficacy of the different bias correction strategies under a variety of conditions, represented by the 4 series of Maxent modeling trials. Specifically, the bias correction strategies we considered were: spatial filtering (SF), background manipulation (BM), a combination of both SF and BM (SF+BM), a modified target group (TG) strategy, and a combination of both SF and TG (SF+TG). The SF, BM, and SF+BM correction strategies were applied on both virtual and real species (i.e. Canada Warbler) datasets, and the TG and SF+TG strategies were applied on Canada Warbler data alone, due to the lack of a suitable target group for virtual species data. The application of bias correction strategies are described in greater detail over the following sections.

Spatial filtering (SF). One of the most common and simple sample bias correction strategies is SF, a technique which attempts to reduce or remove the spatial structure of occurrence data by imposing a minimum distance between presence points (Franklin, 2009b). We used a threshold of 1 km and, when the distance between a pair (or set) of points fell below this threshold, the point(s) nearer to a road was removed (Mahon et al. 2014). SF reduced the Canada Warbler dataset to 312 presence points, LRW datasets to between 1188 and 1199 presence points, and HRW datasets to between 244 and 249 presence points. (Note that the number of presence points among spatially filtered LRW and HRW datasets varied slightly because the number of points that were within 1 km of each other in the unfiltered 5 LRW and 5 HRW datasets also varied.)

Background manipulation (BM). Manipulating background data can be an effective way to distinguish real ecological signals from noise (Phillips et al., 2009). Recall that Maxent generates predictions by comparing the distributions of environmental covariates at observed species locations with those of the overall landscape. The landscape is in-turn defined by covariates at 10,000 "background points" (Phillips & Dudik, 2008). Under default settings these points are collected at random; however, more recent versions of Maxent software allow the user to provide specifications dictating where and how frequently background points are selected for model training through the use of a "bias grid" (i.e. a GIS layer which defines the relative sampling frequency of background points throughout the entire study area). In this way, the landscape can be characterized with similar spatial bias as that exhibited by presence points, thereby factoring out the sample bias in occurrence data (Phillips & Dudik, 2008; Phillips et al., 2009).

To create such a bias grid, we generated a kernel density map of presence points for each occurrence dataset using the 'Kernel Density with barriers' tool in the 'Homerange tools' extension for ArcGIS (Beyer, 2004). For this, we applied a kernel radius of 10 km, and raw bias grid values were normalized between 1 and 20 (Elith et al., 2010; Fourcade et al., 2014), wherein areas located near higher densities of presence points had a higher probability of being used to characterize the background landscape.

Target Group Background Manipulation. For trial series 2 and 4, which used Canada Warbler data, we also created a second bias grid using occurrence points from a target group (TG). The target group is a large group of related taxa of which the focal species is a part (i.e. all birds in this case). Therefore, for the TG bias correction strategy, rather than use presence points from the focal species alone, the bias grid was created using presence points from all passerine bird observations in Nova Scotia contained in ACCDC and MBBA databases.

2.2.5 Reverse stepwise elimination

In trial series 3 and 4, to compare the ability of the various bias correction strategies to facilitate accurate covariate selection, we generated models using covariates selected through a reverse stepwise elimination process. For this, an initial model was first trained using the full set of candidate covariates (Table 2.2), which comprised 14 covariates for the Canada Warbler and 13 covariates for the virtual species. (We did not include 'distance to deciduous stand' in reverse stepwise elimination for the virtual species as our virtual species was designed to nest in coniferous trees, and this habitat preference would likely be known in a real world conservation application. All other covariates considered for the Canada Warbler and the virtual species were the same.) After running an initial model, the covariate that contributed the least to predictive power (according to permutation importance score; Yost, 2008; Baldwin, 2009) was removed from subsequent model iterations. This procedure was repeated until a single variable remained, yielding a set of 'n' candidate models, where n = the number of covariates included in the initial run. Of these, the most parsimonious model was identified using Akaike's Information Criterion (corrected for small sample sizes; AIC_c), which was calculated using a Perl-script developed for Maxent by Warren and Seifert (2011).

2.2.6 Model evaluation

The accuracy and reliability of models created in each of the 4 trial series were evaluated and compared. Specifically, for trial series 1 and 3 (i.e. trials that employed virtual species data), our comparison included 1 uncorrected model (i.e. with no bias correction strategy applied) and 3 corrected models (i.e. using SF, BM, or SF+BM) for each of the 5 LRW and 5 HRW datasets: a total of 4 models x 10 virtual species datasets (i.e. 20 LRW and 20 HRW models) per trial series. For trial series 2 and 4 (i.e. trials that employed real Canada Warbler data), this included 1 uncorrected model and 5 corrected models (i.e.

using SF, BM, SF+BM, TG, or SF+TG): a total of 6 real species models per trial series (Table 2.1).

Virtual species models were evaluated in 3ways. First, we assessed the accuracy of covariate selection. Specifically, for both trial series 1 and trial series 3, we compared the shape of predicted response curves to the true response curve shapes. For trial series 3 (in which covariates were selected using reverse stepwise elimination) we also examined how closely the selected covariate subsets matched the set of 4 true covariates that were used to synthesize the virtual species.

Second, we assessed the accuracy of spatial predictions output by each of the virtual species models by calculating Schoener's D, a measure of niche overlap (Schoener, 1968). In other words, we used Schoener's D scores to determine how closely each of the predicted suitability surfaces resembled the truth map. Schoener's D calculates the similarity between a pair of surfaces by comparing normalized habitat suitability scores of all intersecting cells across the entire study area (Eq. 2) (Warren et al., 2010). The Schoener's D index ranges from 0 (no overlap) to 1 (identical models) and was calculated using the ENMTools extension for Maxent (Warren et al., 2008; Warren et al., 2010):

$$(2) \qquad D(p_{x,}p_y) = 1 - \tfrac{1}{2}\textstyle\sum_i |\, p_{x,i} - p_{y,i}| \quad ,$$

where $p_{x,i}$ and $p_{y,i}$ are normalized suitability scores for grid cell i on surfaces X and Y.

Similarly, the ΔD indicator (Eq. 3) is used to standardize and describe the difference in Schoener's D scores between uncorrected and corrected models (Fourcade et al., 2014). We used ΔD values to compare the ability of each correction strategy to reduce the effects of sample bias and improve spatial predictions of habitat suitability:

$$(3) \qquad \Delta D = (D_{\text{corrected}} - D_{\text{uncorrected}}) / (1- D_{\text{uncorrected}}) \ .$$

Finally, we evaluated the discriminatory power of models by calculating the probability that a randomly selected presence point has a higher suitability score than a randomly selected absence point using AUC (Elith et al., 2006; Fourcade et al., 2014), which was calculated in SPSS. AUC scores also range from 0 (no power to discriminate between presence and absence/background) to 1 (perfect discriminatory power). A score of 0.5 indicates that model predictions are no better than random.

To determine the AUC of virtual species models, we generated 10,000 absence points in cells on the virtual distribution map where $H < 0.9$. We also calculated the ΔAUC indicator (Fourcade et al., 2014) to quantify improvements in AUC score conferred by each bias correction strategy. As with ΔD, the ΔAUC measure standardizes differences between control and corrected models:

$$(4) \qquad \Delta AUC = (AUC_{corrected} - AUC_{uncorrected}) / (AUC_{unbiased} - AUC_{uncorrected}) \qquad ,$$

where $AUC_{unbiased}$ is the AUC score calculated for the truth map.

For real species (Canada Warbler) trials (trial series 2 and 4), we evaluated the ecological realism of models by assessing how well covariates and their response curves reflected known habitat preferences of the species, determined according to a literature review and a previously published model (Westwood et al., 2015). To assess Canada Warbler models quantitatively, we used variants of AUC (calculated in Maxent using random background points). (Note that using Schoener's D to evaluate the quality of Canada Warbler models would not be reasonable as the 'true' habitat suitability surface cannot be known for real species presence-only datasets.) Specifically, to evaluate model fit, we calculated the difference between AUC_{train} and AUC_{test} scores (AUC_{diff} hereafter). (Overfit models tend to predict training data well and test data poorly; Warren & Seifert, 2011.) Both AUC_{train} and AUC_{test} scores are reported as the average across 10 cross-validated model runs.

To evaluate the discriminatory power of real species models, we used AUC_{test} scores calibrated using a null geographic model (calibrated AUC; cAUC, see Supplementary

Material), as proposed by Hijmans (2012). Models were calibrated in this way to account for residual spatial auto-correlation among presence points, which can artificially inflate AUC scores when absence data is unavailable (Lobo et al., 2008; Veloz, 2009; Jiminez-Valverde, 2011). Finally, for trial series 2, to determine whether changing bias correction strategy or covariate set had a greater impact on model outputs for the Canada Warbler, we used Schoener's D to assess the similarity of predicted habitat suitability surfaces generated using different covariate sets and different bias correction strategies.

2.3. Results

In this study, we used data from 1 virtual species and 1 real species to investigate the issues of sample bias and choice of covariate subset in Maxent. Over subsequent paragraphs, we first discuss the characterization of sample bias in virtual species occurrence datasets and then discuss the results of Maxent modeling trials as they pertain to the research objectives of this study: (1) the ability of the various bias correction strategies to yield accurate, mapped predictions of habitat suitability , (2) the ability of the various bias correction strategies to facilitate accurate covariate selection when reverse stepwise elimination is used, and (3) the influence of bias correction strategy versus covariate subset on model outputs.

2.3.1 Characterization of sample bias in virtual species occurrence datasets

All uncorrected virtual species models showed a decrease in AUC score compared to the unbiased model (i.e. AUC of truth map: 0.895), with HRW data causing a larger decrease than LRW data (Figure 2.5). Furthermore, when trained using the same occurrence dataset, uncorrected models in trial series 3 (i.e. models trained using covariates selected by reverse stepwise elimination) always had a lower AUC score than their counterparts in trial series 1 (i.e. models trained using the 4 "true" covariates). Nonetheless, reductions in AUC score were similar in magnitude for all uncorrected models. Schoener's D values confirmed that habitat suitability surfaces predicted by uncorrected models always deviated from the truth map; however, as with AUC, deviations were similar in magnitude (Figure 2.5).

2.3.2 Ability of bias correction strategy to yield accurate, mapped predictions of habitat suitability (trial series 1 and 2)

Trial series 1, virtual species data. While quantitative metrics were similar for all uncorrected and corrected models in trial series 1 (i.e. models trained using the 4 “true” covariates), some patterns did emerge, and these were particularly evident when examining ΔD values (Figure 2.6, Table 2.4). Specifically, when LRW data was used, the SF+BM strategy yielded the most accurate spatial predictions (i.e. the predicted suitability surface was most similar to the truth map) for 4/5 models (Appendix B). Results for HRW datasets were less conclusive; however, when considering average scores across 5 replicate datasets, SF yielded the greatest improvement in Schoener’s D in trial series 3. Results for AUC, which describe models’ discriminatory power, were more variable and often contradicted results obtained for Schoener’s D (Figure 2.6, Table 2.4). For models that were generated using both LRW and HRW data, on average, the BM strategy yielded the greatest improvement in AUC score (i.e. ΔAUC). However, according to the ΔD metric, the BM strategy actually reduced the accuracy of mapped habitat suitability predictions compared to the uncorrected model.

Trial series 2, real species data. In trial series 2, which used Canada Warbler data and pre-defined sets of covariates, the TG strategy yielded the highest $\mathrm{AUC}_{\mathrm{test}}$ and lowest $\mathrm{AUC}_{\mathrm{diff}}$ scores for both the 5 (i.e. ‘distance to stand with dead material’, ‘distance to coniferous stand’, ‘distance to deciduous stand’, ‘distance to wetland’, and ‘D2W’) and 6 (also including ‘distance to clear-cut’) covariate models, and the BM strategy yielded the 2nd highest and 2nd lowest such scores, respectively (Figure 2.7, Table 2.5). However, according to the cAUC metric, for both the 5 and 6 covariate models, the SF strategy provided the best results, and SF+BM provided the 2nd best results (Figure 2.7, Table 2.5).

2.3.3 Ability of bias correction strategy to facilitate accurate covariate selection when reverse stepwise elimination is used (trial series 3 and 4)

Trial Series 3, virtual species data. For LRW datasets, the choice of bias correction strategy did not seem to greatly affect the accuracy of covariate selection, as covariates included in uncorrected, SF, BM, and SF+BM models were similar. In brief, the 4 environmental covariates that were truly important to the virtual species (‘distance to coniferous stand’, ‘% crown closure’, ‘distance to agriculture’, and ‘TPI’) were selected in all 20 models that employed LRW data and reverse stepwise elimination (i.e. 3 corrected models & 1 uncorrected model x 5 replicate LRW datasets) (Appendix B).

Although all 20 LRW models in trial series 3 correctly identified the 4 true variables, many of these LRW models selected erroneous covariates as well (i.e. covariates which were not used to synthesize the virtual species), and some erroneous covariates were selected more frequently than others. Specifically, 15/20 models trained using an LRW dataset contained erroneous covariates. Of these, the 2 that were selected most frequently were ‘distance to clear-cut’ (present in 12 models) and ‘distance to scrubland’ (present in 7 models). Conversely, some covariates were never selected erroneously (Appendix B).

Furthermore, for models trained using HRW data in trial series 3, the number of covariates that were selected when spatially filtered data was used (models in which the SF or SF+BM bias correction strategy was applied) was always equal to or less than the number of covariates included in counterpart models that used unfiltered data (i.e. uncorrected and BM models), and additional covariates were always erroneous. Uncorrected models as well as models built using the SF, BM, and SF+BM bias correction strategies each failed to select ‘TPI’ for 2/5 HRW datasets; however, the other 3 true environmental covariates were always correctly selected. (Appendix B).

As with the LRW models developed in trial series 3, many HRW models contained erroneous covariates, and certain erroneous covariates were included more often than others. For example, ‘distance to clear-cut’ and ‘distance to stand with dead material’ were both present in 4/9 HRW models that contained erroneous covariates. Interestingly, for both LRW and HRW virtual species datasets, in all but 2 cases, whenever a covariate showed a permutation importance score of <5%, it was erroneous (data not shown).

Finally, for all models in trial series 3 (and also in trial series 1), response curves for 3 of the 4 covariates that were actually important to the species (‘TPI’, ‘distance to coniferous forest’, and ‘% crown closure’) were similar to the expected shape (Figure 2.8). However, the shape of the response curve for ‘distance to agriculture’ did not match expectations. Specifically, the truth map was synthesized in such a way that habitat suitability improved as distance from an agricultural area increased from 0 m to 1500 m and remained constant thereafter. While modeled response curves for this covariate correctly showed an improvement in habitat suitability as distance from agriculture increased to 1500 m, when the distance exceeded this threshold, habitat suitability began to decrease once again. This trend was observed in all virtual species trials, but was especially pronounced when models were trained using HRW datasets (Figure 2.8).

Trial Series 2, Real Species data. In trial series 4 (which employed reverse stepwise elimination), using unfiltered Canada Warbler data always led to more covariates being selected than when spatially filtered data was used. In other words, uncorrected models or models in which the BM or TG bias correction strategies were applied always included more covariates than models in which the SF, SF+BM, or SF+TG strategies were applied. However, all Canada Warbler models in trial series 4 included: ‘distance to deciduous stand’, ‘distance to coniferous stand’, ‘distance to clear-cut’, ‘distance to wetland’, and ‘depth to water-table’ (‘D2W’). Furthermore, ‘D2W’ and ‘distance to clear-cut’ were ranked as the 1st and 2nd most important covariates (i.e. according to permutation importance score), respectively, in all cases except the SF+TG strategy (where ‘distance to clear-cut’ was 2nd and ‘D2W’ was 3rd). Summaries of Canada Warbler models generated using reverse stepwise elimination are provided in Table 2.6. The full results of Canada Warbler reverse stepwise elimination trials are provided in Appendix C.

For Canada Warbler models, while response curves for most of the frequently selected covariates matched known habitat preferences of the species, the response-curve for ‘distance to clear-cut’ was somewhat suspect (Figure 2.9). Specifically, this response curve indicates that habitat within or at the edge of clear-cuts is highly suitable, but suitability rapidly decreases outside of these areas and continues to decrease, albeit at a slower rate, thereafter. A similar pattern was also observed in virtual species’ response curves when ‘distance to clear-cut’ was erroneously included in models (Figure 2.10).

2.3.4 Influence of bias correction strategy versus covariate subset on model outputs (trial series 2)

Comparing Schoener’s D scores across models built using different covariate subsets as well as different bias correction strategies would produce uninterpretable results. Therefore, to address our third research objective, we instead compared Canada Warbler models generated in trial series 2 that were (1) built using the same set of 5 covariate (‘D2W’, ‘Distance to wetland’, ‘Distance to coniferous stand’, ‘Distance to coniferous stand’, and ‘Distance to stand with dead material’) or 6 covariate (all of these and also ‘Distance to clear-cut’) subsets but different bias correction strategies, or (2) built using the same bias correction strategy but different sets of covariates (i.e. the pre-defined sets of 5 or 6 covariates listed above). Results of these evaluations are presented in Table 2.7.

Across all of these pairwise comparisons, Schoener’s D scores were never lower than 0.8988. Nonetheless, models produced using competing sets of covariates but the same bias correction strategy were almost always less similar than models produced using the same covariate set but a different bias correction strategy (Table 2.7). The only exceptions to this trend involved SF+BM models. Specifically, the Schoener’s D score between the SF+BM model built using 5 covariates and the SF+BM model built using 6 covariates was 0.9402, which was higher than the Schoener’s D score between SF+BM and TG models built using 6 covariates (0.9236), SF+BM and TG models built using 5 covariates (0. 9358), and SF+BM and uncorrected models built using 5 covariates

(0.9308). (Schoener’s D scores were higher than 0.9402 for all other pairwise combinations involving SF+BM models.)

However, although all Schoener’s D scores were relatively high in trial series 2 (Table 2.7), a visual examination of habitat suitability surfaces output by Canada Warbler models built using alternative subsets of 5 or 6 covariates (i.e. with or without ‘distance to clear-cut’) revealed several obvious qualitative discrepancies in large areas of suitable and unsuitable habitat. Conversely, areas of discrepancy were much less clear when comparing models built using the same covariate subset but different bias correction strategies (Figure 2.11).

Specifically, a visual examination of predicted habitat suitability surfaces in trial series 4 revealed that models which included ‘distance to clear-cut’ classified a large area in southern Nova Scotia as unsuitable habitat for the Canada Warbler (Figures 2.11 and 2.12). This same area was predicted to be suitable by models that did not include ‘distance to clear-cut’. Similarly, models that included ‘distance to clear-cut’ classified a much greater proportion of northwestern Nova Scotia as unsuitable than models that did not include ‘distance to clear-cut’.

2.4. Discussion

In this study, we used data from 1 real and 1 virtual species (sampled at 2 bias weightings) to investigate how bias correction strategy and choice of covariate subset impact accuracy and uncertainty in Maxent SDMs. A virtual species approach allows model outputs to be compared with a known “truth”, making it easier to distinguish the effects of subjective decisions made by the modeler from those of data-related factors (Miller, 2014). However, because the virtual reality is much less complex than a real-world ecosystem, we opted to strengthen our analysis by conducting trials with a real Canada Warbler presence-only dataset as well. In addition, though SDM accuracy can be affected by a variety of bias types, we simulated roadside bias as this is the type to most commonly affect presence-only datasets (Kadmon et al., 2004). Indeed, most of the

Canada Warbler data used in the current study had been obtained along roadside point counts. Furthermore, of the 4 bias types studied by Fourcade et al. (2014), roadside bias was found to be most difficult to rectify.

2.4.1 Uncertainty associated with model evaluation metric

Though it is the most commonly used evaluation metric in SDM studies, AUC has been widely criticized as, among other things, it tends to reward models that have been over-fit (Lobo et al., 2008). When calculated using background data instead of absence data, AUC becomes even less reliable (Veloz, 2009; Jimenez-Valverde, 2012). Indeed, the well-documented pitfalls of AUC were evident in the results of the current study, whereby the most complex models (i.e. models trained using the largest number of environmental covariates) consistently received the highest AUC_{train} and AUC_{test} scores (Table 2.6, Appendix B). Therefore, when analyzing results of this current study, we chose to rely on alternative evaluation metrics as much as possible. Specifically, for virtual species trials, we focused on Schoener's D results, and for Canada Warbler trials we focused on cAUC and AUC_{diff} scores. For both virtual and real species, we considered the accuracy of covariate selection, response curve shape, and the ecological realism of habitat suitability surfaces output by Maxent.

2.4.2 Ability of bias correction strategy to yield accurate, mapped predictions of habitat suitability (trial series 1 and 2)

For all trial series, quantitative metrics were calculated to evaluate the quality of models produced when each of the various bias correction strategies was applied. However, in determining which bias correction strategy showed a superior ability to yield accurate, mapped predictions of habitat suitability (i.e. research objective 1), we primarily considered results from trials series 1 and 2 (i.e. models trained using the same subset of covariates selected according to *a priori* knowledge). In trial series 3 and 4, the effects of different bias correction strategies would be difficult to disentangle from the effects of different covariate subsets.

For virtual species models in trial series 1, ΔD scores suggest that, on average, SF+BM and SF alone produced the most accurate spatial predictions (i.e. produced a habitat suitability surface that most closely matched the truth map) for LRW and HRW data, respectively (Table 2.4; Figure 2.6). For Canada Warbler models in trial series 2 (which involved pre-defined sets of covariates chosen according to *a priori* knowledge) SF and SF+BM achieved the highest and 2nd highest cAUC scores, respectively, for both the 5 and 6 covariate models; however, these same strategies showed the worst AUC_{diff} scores (Table 2.5; Figure 2.7).

Findings from trial series 1 and 2 provide some limited evidence to indicate that, when the covariate subset used to train competing models is the same, applying the SF or SF+BM bias correction strategy can slightly improve the accuracy of mapped predictions of habitat suitability. Nonetheless, for most of the 40 virtual species models (20 LRW and 20 HRW models), the improvements in Schoener's D and cAUC scores conferred by the use of SF and SF+BM were minor. Furthermore, other quantitative metrics (e.g. AUC_{diff} in trial series 2) suggested that alternative bias correction strategies (e.g. the TG strategy) can generate more accurate mapped predictions of habitat suitability, thereby contradicting results of Schoener's D and cAUC. Based on these conflicting findings, we cannot definitively recommend one bias correction strategy over another. Rather, the optimal bias correction strategy likely varies according to data-related factors (e.g. density and/or distribution of occurrence points, etc.). Even so, all else being equal, the choice of bias correction strategy does not appear to greatly influence mapped model results.

2.4.3 Ability of bias correction strategy to facilitate accurate covariate selection when reverse stepwise elimination is used (trial series 3 and 4)

Several important conclusions can be drawn regarding the efficacy of bias correction strategies when reverse stepwise elimination is applied. Firstly, no single bias correction strategy showed an especially superior ability to accurately identify important environmental covariates (i.e. the 4 true covariates were selected in all LRW models and in most HRW models, regardless of the bias correction strategy that was applied; and, for Canada Warbler models, the same covariates were assigned high importance scores across bias correction strategies). However, in trial series 4, Canada Warbler models built using spatially filtered data (SF, SF+BM, and SF+TG models) always included fewer covariates than counterpart models built using unfiltered data (i.e. uncorrected, BM, and TG models) (Table 2.6). In trial series 3, HRW models built using spatially filtered data never included more covariates than counterpart models built using unfiltered data, and when unfiltered HRW models included a greater number of covariates than their spatially filtered counterparts, the additional covariates were always erroneous (Appendix B). Clearly, spatially filtering data (with or without the application of an additional correction strategy) prior to performing reverse stepwise elimination led to a reduction in model complexity when sample bias was more severe. However, in terms of response curve shape, although all LRW and HRW models that employed reverse stepwise elimination correctly included ‘distance to agriculture’, no bias correction strategy was able to recover the true response curve shape. This distortion was especially severe in HRW datasets (Figure 2.8).

Therefore, when reverse stepwise elimination was used, there was a clear trend in which spatially filtering occurrence data (with or without the use of an additional bias correction strategy) tended to improve model quality by reducing the number of covariates used to train models and thereby reducing model complexity.

Secondly, our study provides some limited evidence to suggest that, when the density of presence points across the study area is high (i.e. LRW datasets, Figure 2.3, center panel), the accuracy of reverse stepwise elimination may be further improved by manipulating the selection of background data so that the probability of including an area in the background sample is defined according to the density of surrounding presence points after spatial filtering is performed (i.e. the SF+BM strategy). Indeed, considering all bias correction strategies, SF+BM came closest to identifying the true subset of covariates in

4/5 LRW datasets, and for 2 of these datasets, SF+BM led to perfect covariate selection (i.e. only the 4 true covariates were selected; no erroneous covariates were included). Although for the 5th LRW dataset the SF+BM model included the greatest number of erroneous covariates, all 5 SF+BM models created using LRW data nonetheless yielded the highest Schoener's D scores, regardless of the number of covariates that were used to train them. SF+BM may also be useful if the species dataset is relatively sparse but contains clusters of occurrence points that are significantly more dense in some areas than others, as was the case for the Canada Warbler dataset (Figure 2.4). However, given the conflicting results between AUC_{diff} and cAUC scores in trial series 4, evidence to support the application of SF+BM on this type of data is less strong.

In the case of the HRW virtual species dataset (Figure 2.3, right panel), in which points suffered from roadside bias but did not exhibit much clustering, applying the BM strategy in addition to SF was less useful, even reducing model accuracy compared to when SF alone was used. Note that, as this dataset contained a low point density across the entire study area, applying a 1 km spatial filter on HRW datasets only resulted in a loss of 1 to 6 points. However, all bias grids used for the BM strategy caused areas near the highest density of presence-points to be selected as background data 20 times more frequently than areas near the lowest density of presence-points, regardless of whether the true range of density values was small or large. Therefore, applying the SF+BM strategy on the HRW dataset likely assigned more importance to some background areas than was warranted. It is possible that less extreme differences in sampling probability weights would have provided different results.

2.4.4 Influence of bias correction strategy versus covariate subset on model outputs (trial series 2)

Though results from the current study suggest that, under certain conditions, some sample bias correction strategies are more effective than others, in trial series 1, 3, and 4, uncorrected, SF, BM, and SF+BM models (as well as TG and TG+BM models for the Canada Warbler) all yielded similar habitat suitability surfaces and showed similar quantitative scores. Conversely, evidence from Canada Warbler models in trial series 2 (i.e. models built with and without ‘distance to clear-cut’) suggests that the choice of environmental covariates can have more pronounced and consequential effects on model results than the choice of bias correction strategy (Figure 2.11, Table 2.7). For these models, Schoener’s D overlap scores were almost always higher in pairwise comparisons between models built using the same covariates but different bias correction strategies than they were in pairwise comparisons between models built using different covariates but the same bias correction strategy (Table 2.7). The critical importance of training models with covariates that are appropriate and reliable has been noted by others as well (Araujo & Guisan, 2006; Williams et al., 2012).

Additionally, though all models achieved relatively high Schoener’s D overlap scores (range: 0.8988 – 0.9815), a visual assessment of predicted habitat suitability surfaces revealed that training a model with poorly chosen covariates can lead to spatial patterns in modeled results which have consequences for conservation planning that are more severe than quantitative evaluation metrics suggest. As shown in Figures 2.11 and 2.12, alternative models built using 6 or 5 covariates (i.e. generated with or without ‘distance to clear-cut, respectively) yielded substantially different predictions in the southern and northwestern parts of Nova Scotia.

Indeed, our results demonstrate that not all environmental covariates have equally impactful consequences on model predictions. Rather, the degree to which sample bias confounds model results depends on the spatial distribution of covariate values (Varela et al., 2013). The especially strong confounding effects of ‘distance to clear-cut’ can likely be explained by the fact that all datasets used in this study exhibited roadside bias, and clear-cuts are typically located near logging roads (many of which are contained in the provincial ‘Roads and Rails Network’ file; Nova Scotia Geomatics Center, n.d.). Conversely, covariates that do not correlate with distance to roads should not seriously confound results output by models created in this study. Recall that, in trial series 3 (which employed virtual species data and reverse stepwise elimination), certain erroneous covariates were selected more frequently than others (with ‘distance to clear-cut’ being selected most often among these), while other covariates were never selected erroneously. Furthermore, although Canada Warbler models in trial series 4 were trained using different subsets of covariates (but nonetheless all contained 'D2W', 'distance to wetland', 'distance to clear-cut', 'distance to coniferous stand', and 'distance to deciduous stand'), there were no obvious discrepancies in the habitat suitability surfaces they output.

While the true habitat suitability surface cannot be known for real species presence-only SDMs, we suspect that, in trial series 3 (i.e. models trained using real Canada Warbler data and the same pre-defined set of either 5 or 6 covariates), spatial predictions were more accurate when the covariate 'distance to clear-cut' was not included in model training. We acknowledge that some previous research has reported a slight, positive correlation between Canada Warbler density and timber-harvested areas (Westwood et al., 2015), likely due to the bird's preference for a dense shrub layer and early seral habitat. Therefore, the results of models that included 'distance to clear-cut' are unlikely to be completely erroneous. However, there is evidence to suggest that the importance of this covariate as well as the Canada Warbler response to it has been greatly exaggerated in our study. Firstly, the shape of the response curve for 'distance to clear-cut' indicates that relative habitat suitability is highest at 0 m from clear-cuts, rapidly decreases with distance, and remains constant thereafter (Figure 2.9, 2nd panel from left). When response curves for this same covariate were modeled using LRW and HRW virtual species data, similar trends were observed (Figure 2.10), even though this covariate was not used to synthesize the virtual species. Secondly, a qualitative visual assessment revealed that our mapped results were more similar to those of Westwood et al. (2015) (who developed SDMs using a high quality presence-absence dataset) when 'distance to clear-cut' was not included in model training (data not shown). Finally, the areas in southern and northwestern Nova Scotia that were classified as unsuitable for the Canada Warbler when 'distance to clear-cut' was included in model training fall within 'tier 1 matrix forest blocks' (defined by The Nature Conservancy), which delineate contiguous, resilient forest ecosystems that are large enough to support a variety of biota (including neotropical migratory birds such as the Canada Warbler) and ecological processes (Figure 2.12).

2.5. Recommendations and conclusions

After being relatively ignored for years, methodological challenges in presence-only species distribution modeling have begun to receive serious attention in the SDM literature (Guisan et al., 2013; Fourcade et al., 2015; Westwood, 2016). However, no two studies have approached the same challenge in exactly the same way (e.g. different areas of interest, study species, parameterization choices, data resolutions, etc.) and, as a result, findings have often been contradictory. The lack of consensus is not surprising. Even within the current research, different conclusions can be drawn depending on which evaluation metric is considered. Inconsistency among evaluation metrics has been observed in previous work as well (e.g. Synes & Osborne, 2011; Fourcade et al., 2014) and highlights yet another source of uncertainty for presence-only SDMs. Despite this, by considering multiple types of evidence in tandem (i.e. habitat suitability maps, response curve shapes, and trends in quantitative results), the current comparative study can still provide valuable recommendations for researchers and conservation practitioners who apply presence-only SDMs in their work.

Firstly, our findings highlight the fact that quantitative metrics cannot substitute a well-reasoned qualitative assessment of modeled relationships and suitability surfaces, as was noted by Austin (2007) and others (Elith & Leathwick, 2009). This is especially true when absence data is unavailable. For example, as mentioned, results in trial series 2 (Canada Warbler data + pre-defined sets of covariates) varied depending on whether AUC_{diff} or cAUC was considered. Furthermore, no quantitative evaluation metric used in this study provided an indication that the Canada Warbler models created in trial series 4 (using reverse stepwise elimination), all of which included ‘distance to clear-cut’ as the second most important covariate (Table 2.6), could be a cause for concern. Only by considering the ecological realism of Maxent outputs (i.e. response curves and relative habitat suitability surfaces) did the errors in models become clear. As Yackulic et al.

(2014) pointed out, the user friendly nature of Maxent software has sometimes allowed well-intentioned conservationists to build models without the requisite biological and/or statistical understanding of assumptions underlying them. Had Canada Warbler models from trial series 4 that included 'distance to clear-cut' been used to inform management decisions, there could have been negative consequences for bird conservation.

Secondly, while bias correction strategies did tend to yield marginal improvements in prediction accuracy compared to uncorrected models, no correction strategy was universally superior, and no correction strategy was able to adequately address the problem of sample bias when inappropriate environmental covariates were used. Conversely, when models were trained with identical covariates, changes in predicted suitability surfaces were highly comparable across correction strategies, a phenomenon which was reported by Verbruggen et al. (2013) and Fourcade et al. (2014) as well. These findings are not overly surprising, as multiple researchers (e.g. Anderson & Gonzalez Jr., 2011; Fourcade et al., 2014) have presented evidence to suggest that (1) there is unlikely to be a "silver bullet solution" for the problem of sample bias, and (2) no single correction strategy can consistently provide superior results across all datasets and bias types.

Nonetheless, although consensus has not yet been reached, some patterns are emerging. Namely, results of several studies have suggested that, at a minimum, presence-only datasets should be spatially filtered (e.g. Kramer-Schadt et al., 2013; Boria et al., 2014; Fourcade et al., 2014.), The current study also recommends spatial filtering, especially when reverse stepwise elimination is employed to select covariates. In addition to SF, we found limited evidence to suggest that, if the spatial distribution of presence-points is sufficiently dense or highly clustered, manipulating background data so that areas located near higher densities of presence points have a greater likelihood of being included in the background sample may further improve model results (i.e., the SF+BM strategy). However, because evidence to support the application of this strategy was less strong, modelers should carefully consider whether SF+BM is warranted, even if the spatial distribution of presence points in a species occurrence dataset is dense or exhibits clustering. Both SF and SF+BM offer practical advantages to modelers in that they can be easily and generally applied in a GIS without any additional knowledge of sampling method or effort distribution (Boria et al., 2014). Nonetheless, if time constraints are not limiting, we suggest that best practices in SDM research should include employing multiple bias correction strategies (i.e. including and in addition to SF and SF+BM) and comparing the alternative results they produce. The model that shows the greatest ecological realism and/or the strongest predictive power can then be retained to guide conservation planning initiatives or other applications.

The third conclusion to arise from this study is that altering the subset of environmental covariates used to train the model usually led to more pronounced and consequential differences in model outputs than did changing the bias correction strategy. This finding is alarming in light of the fact that no bias correction strategy was able to reduce the importance of ‘distance to clear-cut’ in real species reverse stepwise elimination trials, which caused Canada Warbler models to predict that forests that were deemed to be of high ecological quality (by the Nature Conservancy) were very unsuitable for this bird. Nonetheless, despite the fact that training a model with an inappropriate environmental covariate appears to have graver consequences for real-world ecological applications than does applying a sub-optimal bias correction strategy, covariate selection has received less attention in the modeling literature than other methodological challenges which affect presence-only SDMs.

In the field of species distribution modeling, there are longstanding disagreements about the relative importance and utility of using statistical methods versus expert selection to choose model covariates. Austin (2007) provided general guidelines, stating that the most optimal covariate subset will have direct ecological relevance to the species of interest but will have also been reduced through some sort of statistical analysis. However, explicit information about ecological factors that directly affect species’ distributions in a given area is typically unavailable, and equally plausible subsets of environmental covariates often exist (Synes & Osborne, 2011). In addition to reverse stepwise elimination, there are many ways that a modeler can attempt to identify the most robust set of environmental predictors (e.g. see Synes & Osborne, 2011), including forward stepwise selection, principal component analysis, or informed (but subjective) decision making based mostly on *a priori* knowledge of species' ecology. Just as there is unlikely to be a single "silver bullet" solution for the problem of sample bias, there may be no single best method of choosing environmental covariates. Nonetheless, it is possible that some approaches consistently outperform others, and studies that succeed in identifying the most promising approaches could fill a research gap and greatly benefit the field of presence-only species distribution modeling.

For many years, the rapid growth of presence-only SDMs outpaced corresponding refinements in methodology. While some improvements have now been achieved, particularly in terms of sample bias, further progress remains to be made. Nonetheless, when modeling habitat and investigating species' distributions in geographic and environmental space, the most important things a modeler can do to ensure the quality of their SDM is to ground parameterization choices in ecological theory as much as possible and ensure that model outputs have strong ecological realism. This practice will remain important regardless of future progress towards more standardized methodologies to guide model parameterization and workflow.

2.6 Tables and figures

Table 2.1: Summary of the 4 species distribution modeling trial series, including their associated research objective(s), the species datasets and covariate subsets that they used, and the number of models that were generated and compared in subsequent evaluations.

Trial series	**Relevant objective**	**Species occurrence dataset**	**Covariate subset**	**Number of models generated**
1	Investigate which bias correction strategy can yield the best mapped predictions of relative habitat suitability (*Objective #1*)	Virtual species (5 LRW & 5 HRW datasets)	Pre-defined set of 4 “true” covariates	40 models, as follows: 1 uncorrected model + 3 corrected models for each of the 5 LRW and 5 HRW datasets
2	Investigate which bias correction strategy can yield the best mapped predictions of relative habitat suitability (*Objective #1*) Investigate whether bias correction strategy or covariate subset has a greater impact on model outputs (*Objective #3*)	Real species (Canada Warbler dataset)	Pre-defined sets of 5 and 6 covariates	6 models, as follows: 1 uncorrected model + 5 corrected models
3	Determine whether a given bias correction strategy better facilitates reverse stepwise elimination (Objective #2)	Virtual Species (5 LRW & 5 HRW datasets)	Selected using reverse stepwise elimination	40 models, as follows: 1 uncorrected model + 3 corrected models for each of the 5 LRW and 5 HRW datasets
4	Determine whether a given bias correction strategy better facilitates reverse stepwise elimination (Objective #2)	Real Species (Canada Warbler dataset)	Selected using reverse stepwise elimination	6 models, as follows: 1 uncorrected model + 5 corrected models

Table 2.2: Environmental covariates used in model training. All covariates were considered in reverse stepwise elimination trials for the Canada Warbler. Conversely, the virtual species synthesized for this study only makes use of coniferous trees, and this habitat preference would typically be known to field ecologists. Therefore ‘distance to deciduous stand’ was not considered in virtual species reverse stepwise elimination trials.

Topographic covariates	**Covariates representing characteristics of forest vegetation**	**Covariates representing access to water**	**Covariates representing anthropogenic disturbance**
Topographic position index†	2nd story height	Distance to wetland	Distance to clear-cut‡
Depth to water-table‡	% crown closure†	Distance to river or lake	Distance to agriculture†
Solar insolation	Distance to coniferous stand†‡		
	Distance to deciduous stand‡ *(**considered in real species trials only)*		
	Distance to all-height stand		
	Distance to scrubland		
	Distance to stand with dead material‡		

† This covariate was also 1 of the 4 “true” covariates used to train virtual species models in trial series 3.

‡ This covariate was also 1 of the 5 or 6 covariates (chosen according to *a priori* knowledge) used to train real species models trial series 4.

Table 2.3: Environmental covariates as well as associated weights and response function types used to synthesize the virtual species. A qualitative description of virtual species habitat preferences is also provided.

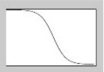
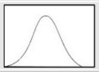
Variable	**Weight**	**Response Function**	**Description**
Topographic position index (TPI)	1	Logistic increasing 	Uplands more suitable than lowlands
Distance to coniferous stand	3	Logistic decreasing 	Habitat more suitable near coniferous stands
% Crown closure	2	Gaussian 	Habitat most suitable in areas with 60% crown closure
Distance to agriculture	1	Linear truncated 	Habitat suitability improves as distance from agriculture increases from 0 – 1.5 km; constant thereafter

Table 2.4: Average change in virtual species model performance (according to ΔD and ΔAUC scores) associated with each sample bias correction strategy in trial series 1 and 3. Values were calculated against uncorrected models and represent the mean of 5 replicate runs. Largest improvements are highlighted in bold. Note that some combinations of bias weighting and bias correction strategy resulted in a performance decrease compared with uncorrected models.

	SF	**BM**	**SF+BM**
Δ D			
Trial series 1: LRW data	0.0054	0.0098	**0.0154**
Trial series 1: HRW data	**0.0047**	-0.0042	0.0010
Trial series 3: LRW data	0.0037	0.0026	**0.0103**
Trial series 3: HRW data	**0.0192**	0.0028	0.0082
Δ AUC$_{test}$			
Trial series 1: LRW data	-0.0270	**0.027**	0.000
Trial series 1: HRW data	-0.0128	**0.0556**	0.0256
Trial series 3: LRW data	-0.0272	**0.0544**	0.0204
Trial series 3: HRW data	**0.1469**	0.0781	0.0406

Table 2.5: Performance of real species models in trial series 2 according to various AUC-based metrics. (Upper) Results from models trained using 5 covariates and (lower) results from models trained using 6 covariates. Results are reported as the mean of 10 cross-validated runs.

Bias Correction Strategy	**AUC**$_{train}$	**AUC**$_{test}$	**AUC**$_{diff}$	**cAUC**
Uncorrected	0.7408 +/- 0.004	0.7139 +/- 0.0293	0.0269	0.4831
SF	0.7244 +/- 0.0059	0.6927 +/- 0.0527	0.0317	0.5649
BM	0.7414 +/- 0.005	0.7169 +/- 0.0387	0.0245	0.04886
TG	0.7438 +/- 0.0043	0.7194 +/- 0.0407	0.0244	0.4886
SF+BM	0.7267 +/- 0.0059	0.6864 +/- 0.0512	0.0403	0.5585
SF+TG	0.7237 +/- 0.0069	0.6937 +/- 0.0603	0.03	0.5535

Bias Correction Strategy	**AUC**$_{train}$	**AUC**$_{test}$	**AUC**$_{diff}$	**cAUC**
Uncorrected	0.7667 +/- 0.0027	0.738 +/- 0.0163	0.0287	0.5072
SF	0.7463 +/- 0.0055	0.7126 +/- 0.0535	0.0337	0.5848
BM	0.7645 +/- 0.0037	0.736 +/- 0.313	0.0285	0.5059
TG	0.7677 +/- 0.0047	0.7398 +/- 0.0426	0.0279	0.509
SF+BM	0.745 +/- 0.0056	0.7017 +/- 0.0521	0.0433	0.5738
SF+TG	0.7434 +/- 0.0063	0.71 +/- 0.0562	0.0334	0.5698

Table 2.6: Performance of real species models in trial series 4 according to various AUC-based metrics. Covariates included in each model (selected using reverse stepwise elimination) are also listed in order of greatest to least importance (according to permutation importance score). Quantitative results are reported as the mean of 10 cross-validated runs.

Bias Correction Strategy	**$\text{AUC}_{\text{train}}$**	**AUC_{test}**	**AUC_{diff}**	**cAUC**	**Covariates included in model**
Uncorrected	0.7879 +/- 0.0033	0.7506 +/- 0.0289	0.0373	0.5198	(1) Distance to wetland, (2) Distance to clear-cut, (3) Depth to water-table, (4) Distance to agriculture, (5) Distance to scrubland), (6) Distance to deciduous stand, (7) Distance to stand with dead material, (8) Percent crown closure, (9) Distance to coniferous stand
SF	0.7533 +/- 0.0047	0.7076 +/- 0.051	0.0457	0.5798	(1) Depth to water-table, (2) Distance to clear-cut, (3) Distance to coniferous stand, (4) Distance to wetland, (5) Distance to deciduous stand, (6) Percent crown closure, (7) Distance to scrubland
BM	0.7869 +/- 0.0031	0.7448 +/- 0.0284	0.0421	0.5147	(1) Depth to water-table, (2) Distance to clear-cut, (3) Distance to wetland, (4) Distance to coniferous stand, (5) Distance to deciduous stand, (6) Distance to agriculture, (7) Distance to scrubland, (8) Distance to stand with dead material
TG	0.7914 +/- 0.004	0.7475 +/- 0.0313	0.0439	0.5167	(1) Depth to water-table, (2) Distance to clear-cut, (3) Distance to wetland, (4) Distance to agriculture, (5) Distance to scrubland, (6) Distance to coniferous stand, (7) Distance to deciduous stand, (8) Distance to stand with dead material, (9) Percent crown closure, (10) Distance to all height stand

Bias Correction Strategy	**AUC$_{\text{train}}$**	**AUC$_{\text{test}}$**	**AUC$_{\text{diff}}$**	**cAUC**	**Covariates included in model**
SF+BM	0.7362 +/- 0.0063	0.7021 +/- 0.0635	0.0341	0.5742	(1) Depth to water-table, (2) Distance to clear-cut, (3) Distance to wetland, (4) Distance to coniferous stand, (5) Distance to deciduous stand
SF+TG	0.7504 +/- 0.0058	0.7073 +/- 0.0422	0.0431	0.5671	(1) Distance to wetland, (2) Distance to clear-cut, (3) Depth to water-table, (4) Distance to coniferous stand, (5) Distance to deciduous stand, (6) Distance to stand with dead material, (7) % crown closure

Table 2.7: Schoener's D overlap between real species models built using (A) the same set of 5 covariates ('distance to stand with dead material', 'distance to coniferous stand', 'distance to deciduous stand', 'distance to wetland', and 'depth to watertable') but different bias correction strategies; (B) the same set of 6 covariates (as above, but with 'distance to clear-cut' added) but different bias correction strategies; and (C) the same bias correction strategy but competing covariate sets (i.e. the sets of 5 and 6 covariates listed above).

(A) Bias correction strategy used in 5 covariate Canada Warbler model	**Uncorrected**	**SF**	**BM**	**TG**	**SF+BM**	**SF+TG**
Uncorrected	1	0.9471	0.9742	0.9774	0.9446	0.9521
SF	x	1	0.9565	0.935	0.9815	0.979
BM	x	x	1	0.9667	0.9602	0.964
TG	x	x	x	1	0.9358	0.946
SF+BM	x	x	x	x	1	0.9798
SF+TG	x	x	x	x	x	1
(B) Bias correction strategy used in 5 covariate Canada Warbler model	**Uncorrected**	**SF**	**BM**	**TG**	**SF+BM**	**SF+TG**
Uncorrected	1	0.9402	0.9628	0.9705	0.9308	0.9392
SF	x	1	0.959	0.9277	0.9779	0.9727
BM	x	x	1	0.9544	0.9584	0.9585
TG	x	x	x	1	0.9236	0.9386
SF+BM	x	x	x	x	1	0.9733
SF+TG	x	x	x	x	x	1
(C) Canada Warbler model type (built with 5 and 6 variables)	**Control**	**SF**	**BM**	**TG**	**SF+BM**	**SF+TG**
Schoener's D	0.8988	0.9303	0.9206	0.9033	0.9402	0.9345

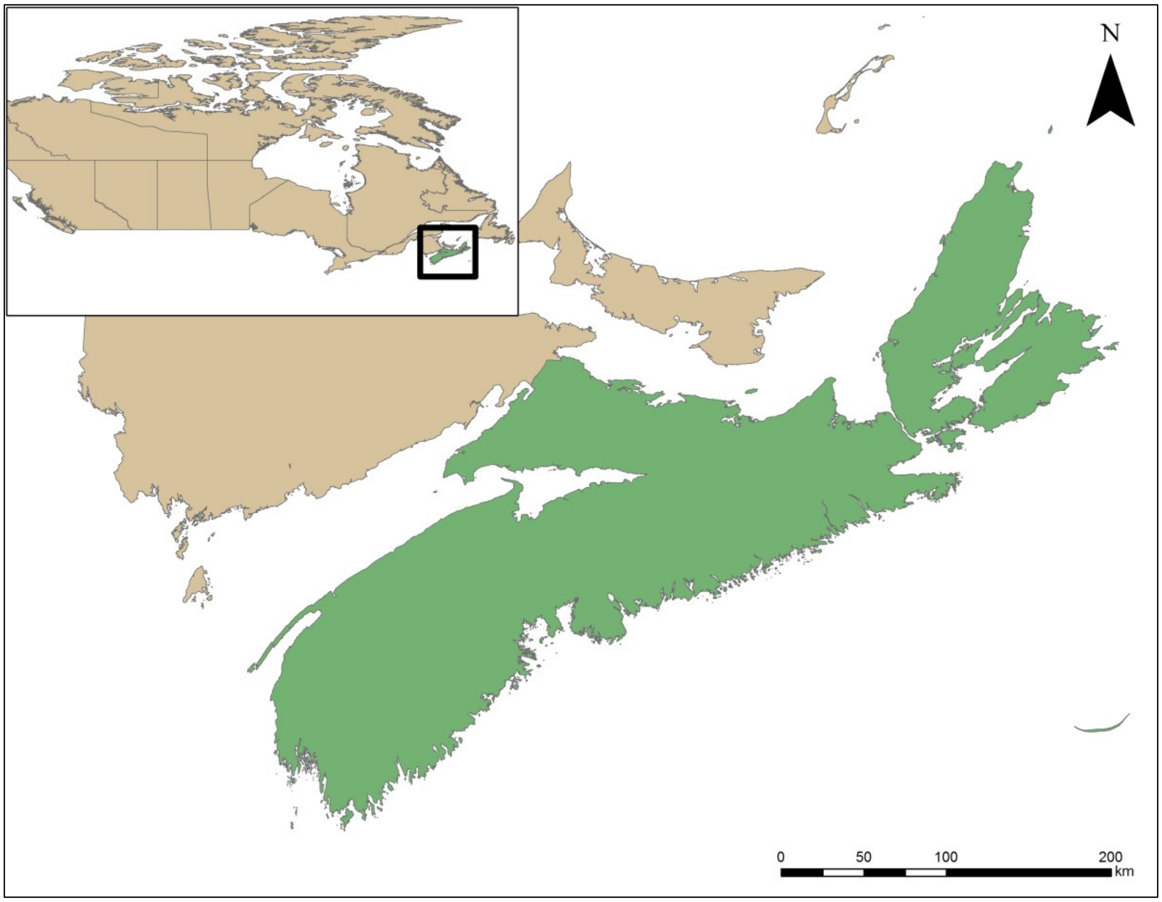


Figure 2.1: Nova Scotia (main map), a maritime province of Canada (upper left inset).

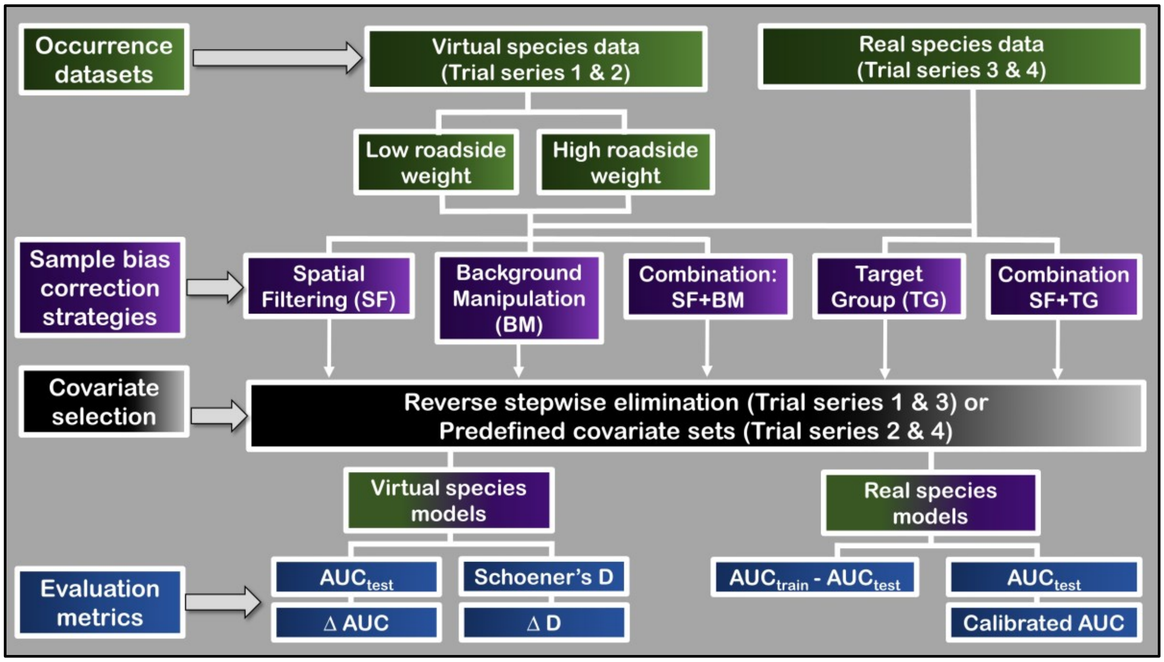


Figure 2.2: Workflow applied in comparative analysis to address outstanding methodological challenges in presence-only species distribution modeling. To determine whether a given bias correction strategy is able to yield more accurate mapped predictions of habitat suitability (objective #1), models were trained using environmental covariates chosen according to *a priori* knowledge + either virtual species data (trial series 1) or real species data (trial series 2). To determine whether a given bias correction strategies has a superior ability to facilitate accurate covariate selection when reverse stepwise elimination is employed (objective #2), models were trained using sets of covariates that were selected using a reverse stepwise elimination process + either virtual species data (trial series 3) or real species data (trial series 4). To determine whether sample bias correction strategy or environmental covariates used in model training have a greater impact on SDM results (objective #3), we again compared models created in trial series 2. Note that virtual species trials were performed on 5 replicate datasets sampled at a low roadside weighting (LRW) and on 5 replicate datasets sampled at a high roadside weighting (HRW). We also produced control models using uncorrected data (not shown). Model quality and accuracy were evaluated according to a qualitative assessment of ecological realism and with quantitative metrics based on AUC and Schoener's D statistics. AUC_{train} refers to the AUC score associated with training data; AUC_{test} refers to the AUC score associated with test data.

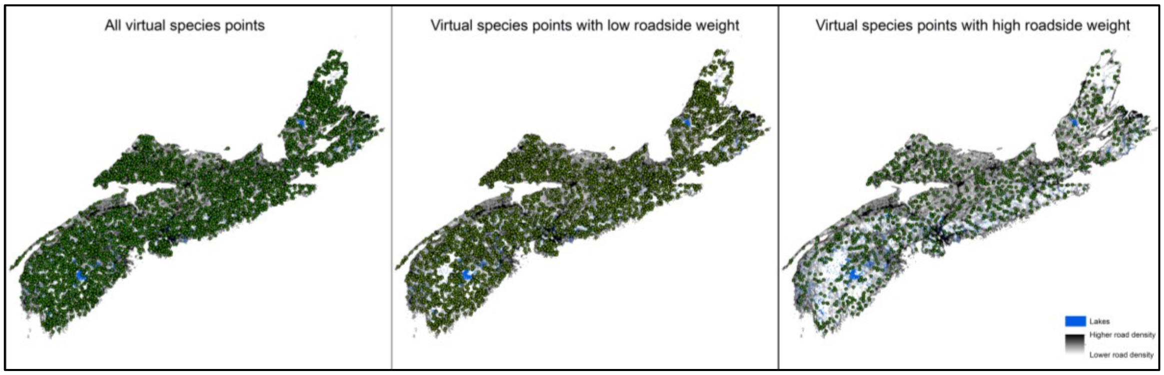


Figure 2.3: Virtual occurrence datasets generated using the niche synthesis method (Hirzel et al., 2001). (Left) All 5000 virtual species points; (center) virtual species points sampled at a low-bias weighting (LRW data); (right) virtual species points sampled at a high-bias weighting (HRW data). On the base map, darker areas denote higher road density and lighter areas denote lower road density (as calculated from the NSTDB 'Roads and Rails' network file; Nova Scotia Geomatics Center, n.d.); blue areas are lakes.

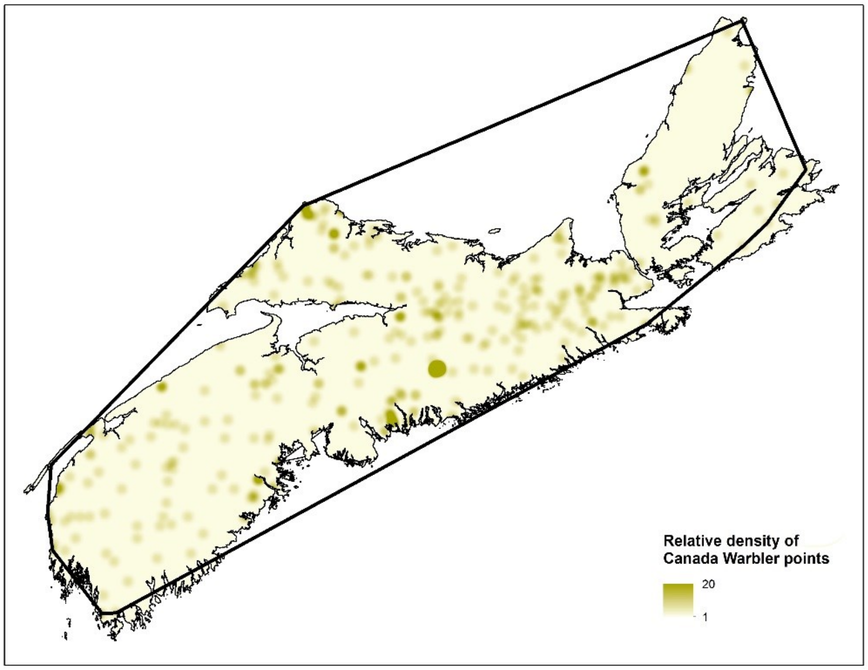


Figure 2.4: Relative density of presence points in the Canada Warbler dataset used by this study. The minimum convex polygon that encloses all points is also shown (black outline on map). Actual occurrence locations are not displayed due to the sensitive nature of data for at-risk species.

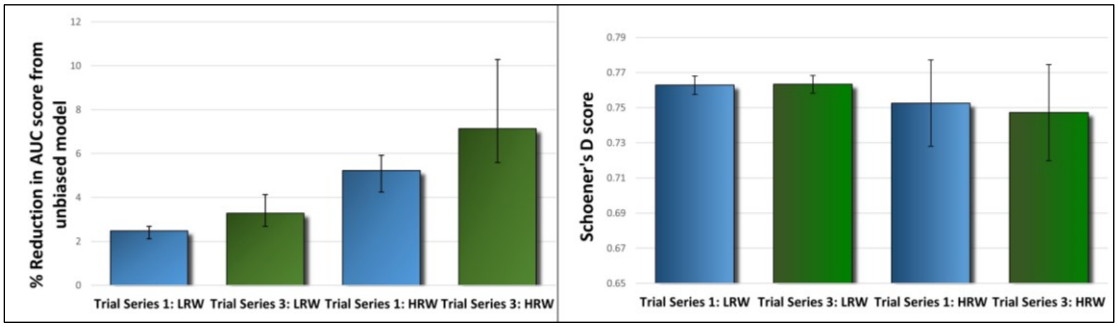


Figure 2.5: Effects of low- and high-bias weightings on uncorrected virtual species models according to quantitative metrics. (Left) Percent reduction in AUC score between biased models and the truth map (AUC of truth map: 0.895); error bars delineate full range of values. (Right) Schoener's D overlap between truth map and habitat suitability surfaces output by biased models; error bars denote standard deviation. In both graphs, each column summarizes results from 5 replicate runs.

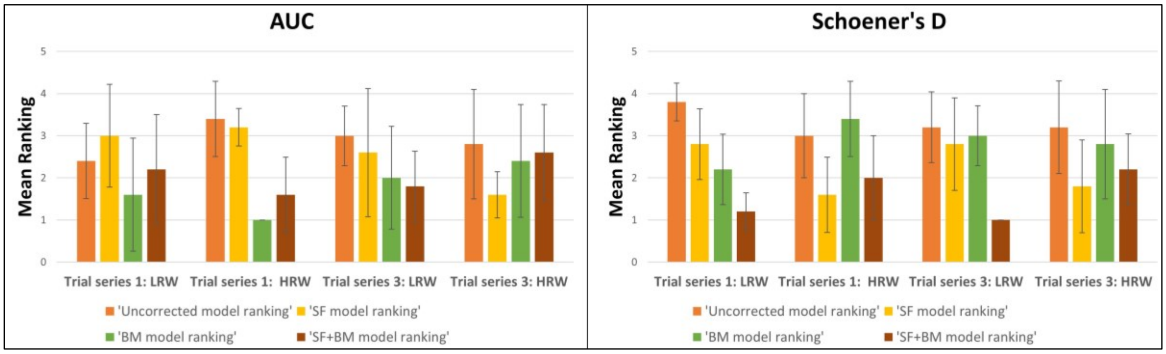


Figure 2.6: Average rank ± standard deviation of uncorrected (control), SF, BM, and SF+BM virtual species models in trial series 1 and 3 according to Schoener's D (left) and AUC (right) metrics. For both LRW and HRW data, results represent the average ranking of models generated using 5 replicate datasets.

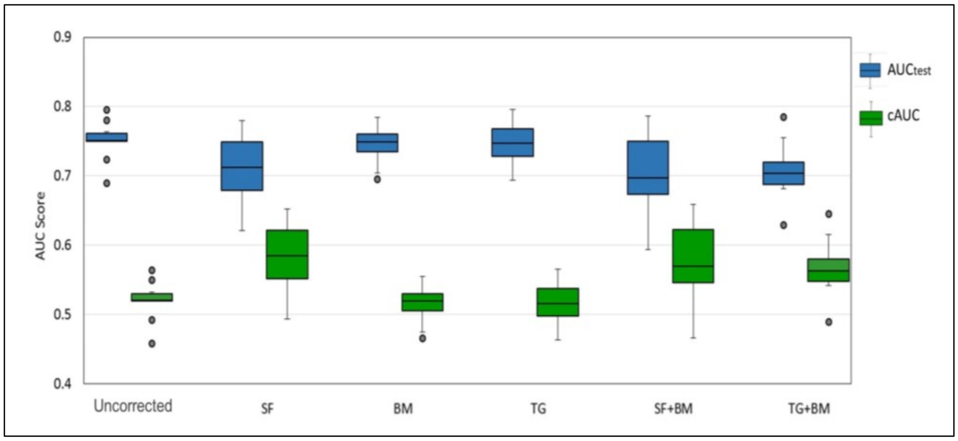


Figure 2.7: Boxplot showing $\mathrm{AUC}_{\mathrm{test}}$ and cAUC scores for real species models created using uncorrected data and the SF, BM, TG, SF+BM, and SF+TG bias correction strategies in trial series 2. Covariates used to train each model were identified using reverse stepwise elimination. Results represent the average of 10 cross-validated runs; error bars are standard deviation

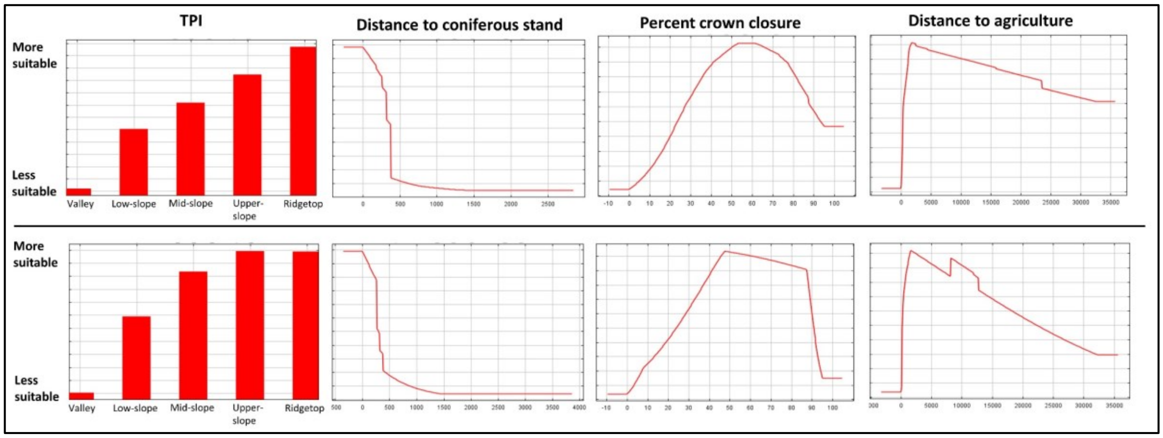


Figure 2.8: Example of response curves generated by virtual species models. (Upper row) Model generated using LRW data and the SF+BM correction strategy; (lower row) model generated using HRW data and the SF correction strategy. Note that the shapes of response curves generated by all virtual species models (in both trial series 1 and trial series 3) were similar to the ones shown in this figure. Numeric values on x-axes are all reported in meters

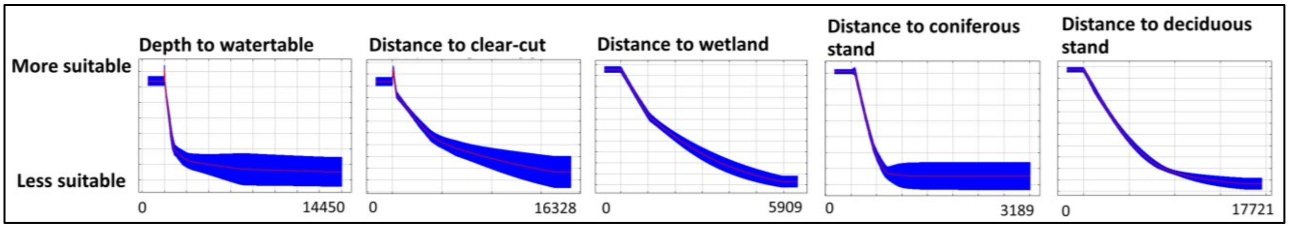


Figure 2.9: Example of response curve functions generated by Canada Warbler models. Response curves shown are for covariates selected by reverse stepwise elimination when the SF+BM correction strategy was applied. Note that these 5 covariates were selected regardless of which bias correction strategy was applied, and that their response curves were similar in all Canada Warbler models. Numeric values on x-axes are all reported in meters.

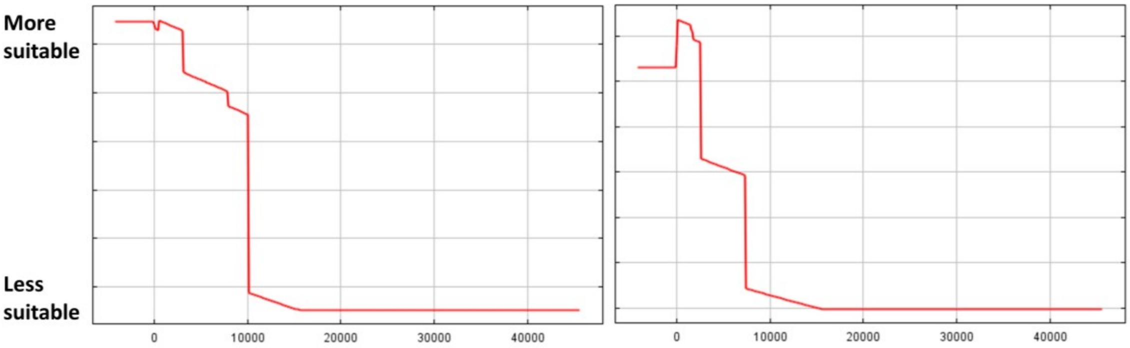


Figure 2.10: Example of response curve functions for the ‘distance to clear-cut’ covariate, output from models built using (left) spatially filtered LRW data and (right) spatially filtered HRW data. Note that the models that generated the above response curves had been trained using not only ‘distance to clear-cut’, but the 4 ‘true’ covariates that were actually important to the virtual species as well.

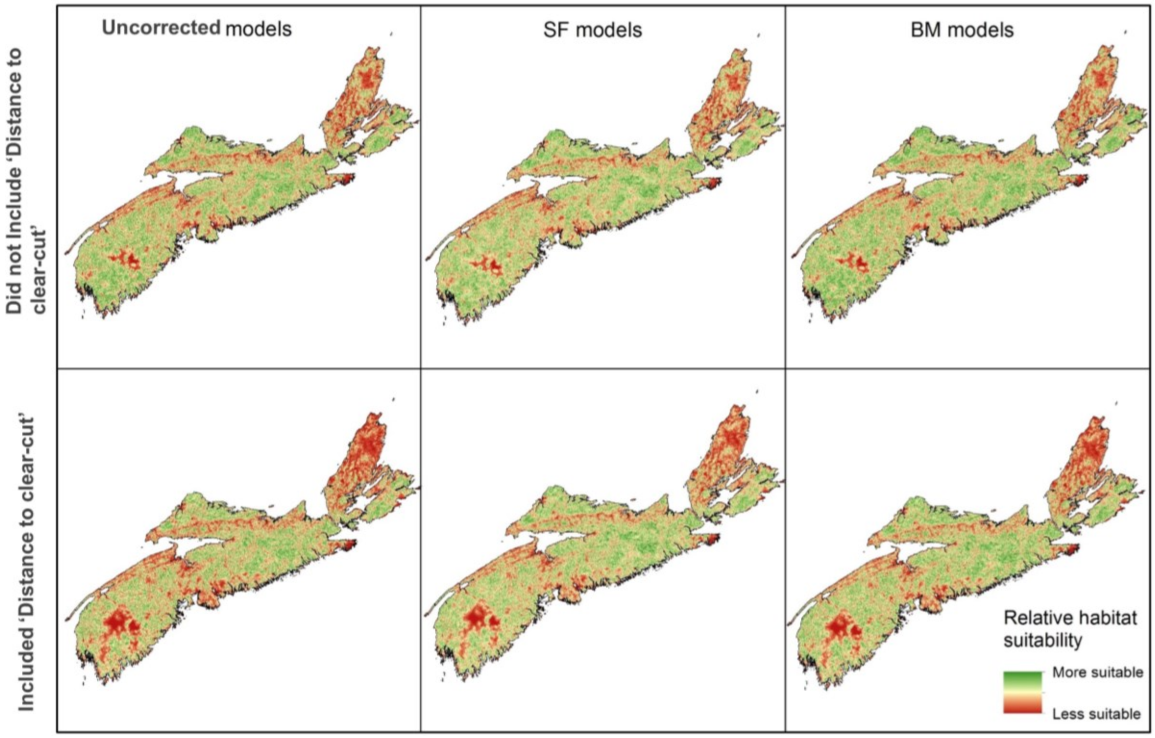


Figure 2.11: Relative habitat suitability surfaces generated by uncorrected and corrected (using the SF and BM strategies) real species (Canada Warbler) models produced using (upper row) 5 covariates (excluding 'Distance to clear-cuts') and (lower row) 6 covariates (including 'Distance to clear-cuts). Note that much larger discrepancies exist between models generated using the same bias correction strategy but different covariate subsets than between models generated using a different bias correction strategy but the same covariate subset.

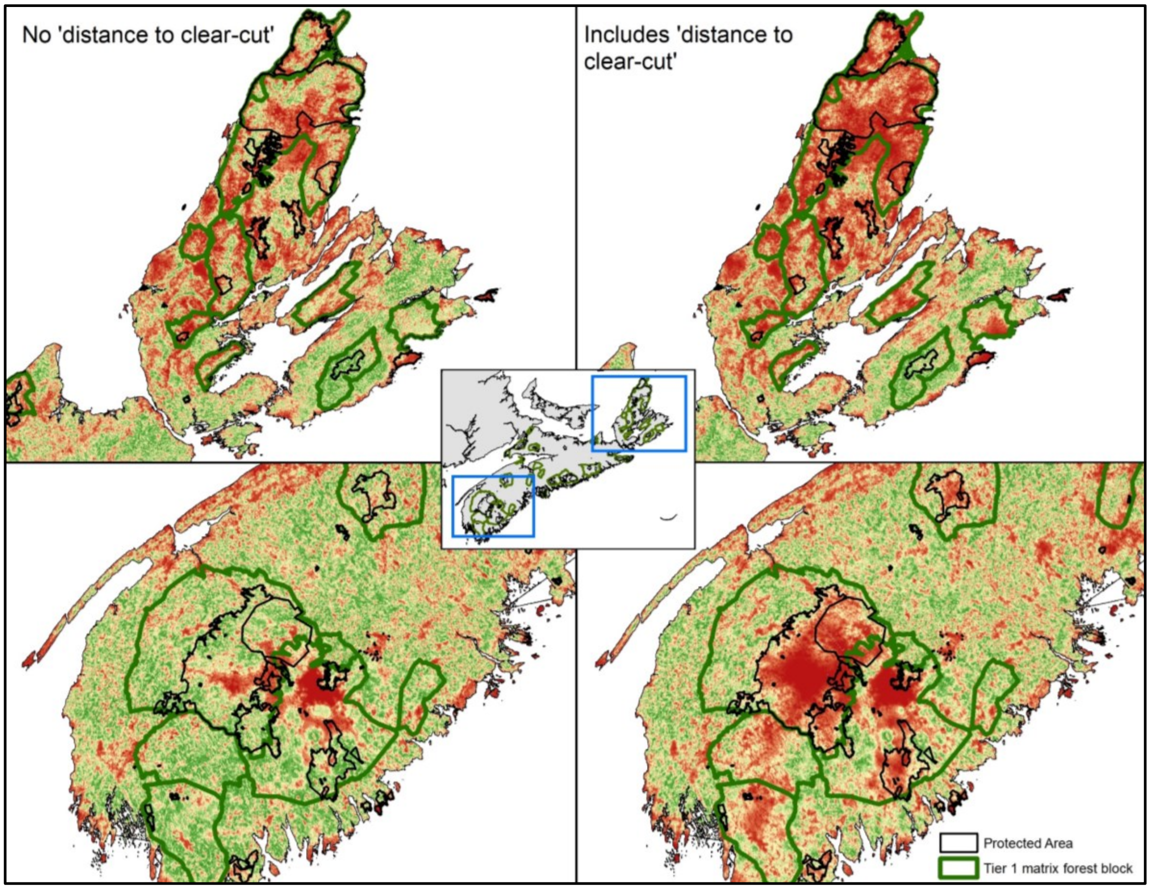


Figure 2.12: Habitat suitability surfaces for the Canada Warbler in northern and southern NS. (Left) habitat suitability surfaces output from the uncorrected real species models built in trial series 2 using the pre-defined set of 5 covariates (i.e. did not include 'distance to clear-cut'), and (right) habitat suitability surfaces output from the uncorrected real species model built using the pre-defined set of 6 covariates (included 'distance to clear-cut').

CHAPTER 3: USING TOPOGRAPHIC FEATURES TO HELP PREDICT THE SPATIAL DISTRIBUTION OF RESILIENT HABITAT FOR THE RUSTY BLACKBIRD, OLIVE-SIDED FLYCATCHER, AND CANADA WARBLER IN NOVA SCOTIA, CANADA: A MAXENT MODELING STUDY

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Abstract

Biodiversity is currently being lost at a rate that is unprecedented in modern history, and this challenge requires urgent conservation action. Maintaining a functionally connected network of high-quality habitat is considered one of the most effective responses to species declines; however, as a result of climate change, habitat patches which are currently suitable may not remain so in the future. Indeed, some taxa, such as migratory forest landbirds, are already undergoing climate-driven range shifts. Therefore, climate resilient habitat (i.e. habitat which is more likely to retain characteristic structures and functions in the face of changing temperature and precipitation regimes) is especially valuable from a conservation perspective. In this study, we performed maximum entropy (Maxent) modeling to delineate suitable breeding habitat in Nova Scotia, Canada, for 3 migratory forest landbirds: the Rusty Blackbird (*Euphagus carolinus*), the Olive-sided Flycatcher (*Contopus cooperi*), and the Canada Warbler (*Wilsonia canadensis*). In so doing, we employed a reverse stepwise elimination technique to help identify covariates that influence habitat suitability for the target species at the landscape-scale. This analysis considered both biotic covariates related to forest characteristics and abiotic covariates related to topographic control of landscape-scale moisture and nutrient accumulation. While previous modelers have sometimes frowned upon the inclusion of abiotic features in models, we posited that, as topography (1) should be relatively unaffected by a changing climate and (2) helps regulate the structure and composition of forest habitat, certain topographic features may be able to help identify areas that are more likely to support bird persistence over the long-term. Results of reverse stepwise elimination supported this assertion, as both forest and topographic covariates were identified as important predictors of relative habitat suitability for all birds. (However, the specific combination of covariates included in each model differed.) Our models also indicated that, for all 3birds, wet lowlands comprise particularly valuable habitat, and that this is especially true for the Rusty Blackbird and Canada Warbler. Finally, we found that, at present, suitable breeding bird habitat appears to be relatively abundant and well distributed in Nova Scotia, providing good opportunities for conservation.

Keywords: Species distribution modeling, Rusty Blackbird, Olive-sided Flycatcher, Canada warbler, topography, climate change, ecological resilience

3.1. Introduction

The earth is currently undergoing a human-induced mass extinction event in which species are disappearing at a rate not seen since the age of the dinosaurs (Wagler, 2011). Though a multitude of factors have contributed to this, habitat modification, fragmentation, and destruction are the most significant proximal causes (Millennium Ecosystem Assessment, 2005; Wagler, 2011). Accordingly, maintaining and restoring functionally-connected networks of high-quality habitat is considered one of the most effective responses to species loss (Noss, 1983; Rubio & Saura, 2012). However, due to increasing human population growth and the competing interests of many stakeholders, there are limits to the number of natural areas that can be restored and/or conserved. Therefore, identifying, prioritizing, and protecting habitat that can yield the greatest conservation benefit is critically important. Unfortunately, climate change renders the identification of optimal conservation lands more difficult, as changing temperature and precipitation regimes are likely to cause many habitat areas to become unsuitable for species that currently utilize them (Beier and Brost, 2010; Anderson and Ferree, 2010). Indeed, increased wetland drying, insect-induced tree mortality, and climate-driven range shifts have already been observed in the boreal region (Stralberg et al., 2015). Range shifts are especially problematic for conservation planning, as critical habitat and protected area designations are typically granted on a permanent basis. Therefore, from a land acquisition perspective, climate resilient habitat (i.e. climate refugia), which has a stronger likelihood of remaining suitable regardless of future climatic conditions, has especially high conservation value.

Though many taxa are under threat from anthropogenic activities, migratory birds face unique risks due to a dependence on habitat that spans multiple continents and the significant biological stresses associated with migration itself (Weisendaul, 2000). On the breeding range, spatially-extensive changes to forest habitat are believed to pose the greatest threat to migratory forest birds (Westwood et al., 2015). In addition, multiple studies have reported that this taxonomic group has already begun to undergo distributional shifts as a result of climate change (McClure et al., 2012; Nogués-Bravo et al., 2012).

Species Distribution Models (SDMs) use spatial occurrence data (i.e., point locations delineating where a species has been observed) to generate mathematical representations of species' distributions in environmental space (i.e., how species respond to environmental covariates), and these are in-turn used to predict species' distributions in geographic space (i.e., maps of relative habitat suitability) (Elith & Leathwick, 2009). SDM outputs typically include (1) response curve graphs which can provide ecological insight into species' habitat preferences and (2) maps delineating species' occurrence or abundance on a landscape. Over the past few decades, advances in the fields of statistics and geographic information systems (GIS) have allowed SDMs to emerge as useful tools for the delineation of high value habitat (Elith & Leathwick, 2009). Indeed, SDM techniques are now widely applied to guide conservation system design and identify suitable areas for ecological restoration.

The current study applied maximum entropy (i.e. using Maxent 3.3 software; Phillips et al., 2006) modeling and a reverse-stepwise elimination technique to build predictive, spatially-explicit models of breeding habitat in Nova Scotia, Canada, for 3 at-risk migratory forest landbirds: the Rusty Blackbird (*Euphagus carolinus*), the Olive-sided Flycatcher (*Contopus cooperi*), and the Canada Warbler (*Cardellina canadensis*). These species have suffered steep population declines, particularly in the eastern portion of their range (Environment Canada, 2014), and climate-driven range shifts have also been observed or predicted for each of these birds (McClure et al., 2012; National Audubon Society, 2014). Indeed, all 3 birds have been designated as at-risk under Nova Scotia's Endangered Species Act (S. N. S. 1998, c. 11) and are also listed under Canada's Species at Risk Act (S. C. 2002, c. 29). Nonetheless, although threats to these species have been recognized, efforts to develop regional predictive habitat models have thus far been very limited (but see Westwood et al., 2015).

In building the SDMs for the target bird species, we recognized that we were working in a context of climate change. Previous studies which have examined species distributions through a climate change lens have typically done so by predicting which areas will contain suitable habitat under some *future* climate scenario (or a range of future climate scenarios), wherein models created using current climatic conditions are projected onto predictions of future climatic conditions (e.g. based on global circulation models and potential emissions scenarios) (Franklin, 2009a; Stralberg et al., 2015). However, the uncertainty associated with this approach can be severe in some cases, leading some to question whether the noise exceeds the signal when such a strategy is used (Stralberg et al., 2015).

Therefore, rather than attempt to predict future range shifts, we sought to identify habitat patches that may be more resilient to the effects of climate change. Specifically, we attempted to identify potential climate refugia by building models using covariates which represent environmental processes and features operating at 2 levels of the ecological resilience hierarchy originally proposed by C. S. Holling (1986). Briefly, Holling's theory posits that ecosystem structures and functions are regulated by a limited number of biotic and abiotic environmental conditions hierarchically nested in space and time. In 1992, Holling extended this theory to describe the intersection between scale-dependent environmental processes and behavioural decisions made by a species in choosing habitat, noting that habitat selection strategies also vary according to spatial grain. Mackay and Lindenmayer (2001) further advanced Holling's work by defining critical structuring scales according to natural breaks in the distribution and availability of primary environmental resources that control biological productivity: heat, light, water, and mineral nutrients. Specifically, these structural scales are defined at global-, meso-, topo-, micro-, and nano-levels, and represent ever-finer spatial and temporal variation in the delivery of water and energy (Mackay and Lindenmayer, 2001). In line with this theory, the types of covariates that are scale appropriate for province-wide, landscape-scale SDM research are those that operate at the topo- (e.g., that describe regional topography) and micro- (e.g., that describe characteristics of forest stands) levels.

To date, SDM researchers have tended to frown upon the inclusion of abiotic topography in models, as the influence of such features over species distributions tends to be indirect, especially for mobile vertebrate taxa (Franklin, 2009b; Beier et al., 2015). Although topographic features have nonetheless been used to help predict species distributions in previous studies, such features have generally been employed as surrogates when mapped data representing important biotic features were unavailable. Nonetheless, the utility of abiotic topography in identifying climate resilient habitat has been noted as these features (1) have the ability to promote 'ecological memory', whereby ecosystems retain similar structures and functions following disturbance (Holling, 1992; Larkin et al., 2006) and (2) will generally not be affected by changing temperature and precipitation regimes (Anderson et al., 2012). Therefore, in building SDMs for the current study, we posited that a better understanding of how birds respond to hierarchically organized topo- and micro-level covariates can help identify habitat patches which are more likely to be resilient against the effects of climate change.

The SDMs developed herein are directly relevant to landscape-scale conservation planning in Nova Scotia and can be used to prioritize resilient bird habitat for land acquisition and/or conservation easement initiatives. Moreover, the reverse stepwise elimination process we employed helps elucidate important landscape-scale ecological associations that exist between these birds and their environment at the easternmost extent of breeding habitat. Therefore, our findings should also interest ornithologists working to develop a comprehensive understanding of habitat preferences for these species across the full extent of their range. Finally, our models highlight the ability of topographic covariates to help predict the relative suitability of breeding bird habitat, and theoretical evidence suggests that habitat located in areas which contain both favorable topography and favorable forest characteristics may be more climate resilient (Holling, 1986; Dobrowski, 2010). Therefore, while we acknowledge that it is impossible to guarantee the indefinite persistence of any species, we posit that the resilience-based approach to species distribution modeling presented here may be able to help promote the long-term persistence of a variety of terrestrial taxa, not just the landbirds considered in the current study.

3.2. Methods

3.2.1 Study area

Nova Scotia (~45° N, ~63° W; Figure 2.1), a maritime province of southeastern Canada, lies on the Atlantic migratory flyway and contains the easternmost breeding habitat of the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler. The province is characterized by a modified continental climate and exhibits a wide (though not extreme) temperature range, ample precipitation (particularly in winter and fall), and great variability in daily weather conditions (Nova Scotia Museum of Natural History, 1996a). With a total area of 52,939 km^2 (Statistics Canada, 2014), Nova Scotia contains a diverse array of landscapes and an abundance of wetlands, lakes, and rivers (Nova Scotia Museum of Natural History, 1996b). Land-use/land cover is mixed, and includes agriculture, intact and fragmented forests, coastal barrens, 2 cities (Halifax and Sydney), and a number of scattered towns (Agriculture and Agri-food Canada, 2015; Statistics Canada, 2016). The province is further characterized by gently rolling topography and elevations that range from 0 to 520 m above sea level, with the highest elevations occurring in the northeast of the province. Finally, Nova Scotia is situated within the Acadian Forest Ecozone and is characterized by a mixed-forest species composition, although conifers dominate in many areas, particularly where drainage is impeded (Rowe, 1972; Neily et al., 2005).

3.2.2 Study species

Three at-risk migratory forest landbirds were considered in this study: the Rusty Blackbird, the Olive-sided Flycatcher, and the Canada Warbler. Two of these species (the Olive-sided Flycatcher and Canada Warbler) are Neotropical migrants, and the third (the Rusty Blackbird) overwinters in the southeastern United States. All 3 species breed in Nova Scotia's forests (Bird Studies Canada, 2015). The Olive-sided Flycatcher often occurs adjacent to wetlands, likely taking advantage of edge habitat associated with these areas (Altman & Sallabanks, 2000; Committee on the Status of Endangered Wildlife in Canada [COSEWIC], 2007). The Canada Warbler shows a facultative preference for forested wetlands (Becker et al., 2012) and is also common in wet, shrubby mixed-wood forests (in the eastern part of its range; Environment Canada, 2015). Conversely, the Rusty Blackbird is a wetland obligate (Matsuoka et al., 2010). In terms of nesting, the Olive-sided Flycatcher prefers the mid-to-upper limbs of tall coniferous trees (Dixon, 1920); the Canada Warbler selects sites on or near the ground, concealed by thick understory (Goodnow and Reitsma, 2011); and the Rusty Blackbird often nests in dense patches of stunted conifers surrounded by a matrix of sparse canopy closure (Powell et al., 2010).

All 3 focal birds are insectivorous on their breeding grounds, although they make use of different foraging niches. Specifically, the Olive-sided Flycatcher hunts from elevated perches of trees or snags (COSEWIC, 2007); and the Canada Warbler forages on the ground, in shrubs, or in the lower branches of both coniferous and deciduous trees (Goodnow and Reitsma, 2011). Conversely, the Rusty Blackbird wades in shallow water, foraging primarily for aquatic macroinvertebrates (Matsuoka et al., 2010).

To develop Maximum Entropy (Maxent) SDMs for the 3 landbirds of interest, we prepared GIS layers comprising (1) species occurrence data (i.e., the response covariate, input as point locations of bird observations) and (2) environmental data (i.e., predictor covariates, input as raster layers which describe abiotic and biotic environmental conditions) in ArcMap 10.2.2 (Environmental Systems Research Institute [ESRI], 2014). Dataset preparation is briefly outlined in subsequent sections (and described in more detail in Appendix A).

3.2.3. Species occurrence data

Point observations for the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler were obtained from the Atlantic Canada Conservation Data Center (ACCDC), a

NatureServe Canada organization that maintains spatially accurate occurrence datasets for species of conservation concern (ACCDC, 2014). Data points primarily comprised records from the Maritime Breeding Bird Atlas (MBBA) database (2006-2010 surveys) but also included observations made by individuals and research groups. The ACCDC dataset contained observations made between 2005-2013 for the Olive-sided Flycatcher, between 2006-2013 for the Canada Warbler, and between 2006-2012 (as well as single sightings made in 1998 and 2001) for the Rusty Blackbird. The resolution of occurrence points in the ACCDC dataset varied from 3 m to 10 km. However, we removed points with a resolution >150 m (i.e. points where the bird was not guaranteed to be less than 150 m away from recorded coordinates), as these were considered too coarse for meaningful analysis. To reduce spatial autocorrelation among occurrence points, we applied a spatial filter with a distance threshold of 1 km (Franklin and Miller, 2009). When the distance between points was below this threshold, the point closest to a road was removed. After filtering, 136 Rusty Blackbird observations, 502 Olive-sided Flycatcher observations, and 312 Canada Warbler observations were available for modeling (Figure 3.1).

3.2.4. Environmental data

We created GIS layers to represent environmental processes and features operating at 2 levels of the ecological resilience hierarchy proposed by C. S. Holling (1986) and Mackay and Lidenmayer (2001): topo (i.e. covariates describing regional topography) and micro (i.e. covariates describing forest stand conditions). These are listed in Table 3.1 and summarized over subsequent paragraphs. The creation of these layers is described in detail in Appendix A (with the exception of the ‘landscape complexity’ layer, whose creation is described in chapter 4). The initial list of candidate covariates (Table 3.1) was established to reflect known ecological preferences of the target bird species. Specifically, candidate covariates were chosen through a literature review, personal communications with key experts (C. Staicer and C. Ferrari), the field experience of A. Westwood, and multiple tuning experiments (data not shown). Many of the candidate covariates we considered were also found to have predictive value for the target birds in nation-wide research by the Boreal Avian Modeling Project (Haché et al., 2014) and in research conducted by Westwood et al. (2015) in provincial parks of Nova Scotia and New Brunswick.

Environmental covariate layers were prepared as a stack of ASCII rasters with the same projection (NAD 1983 UTM Zone 20), spatial extent, and cell size (i.e., 150 m, to match the coarsest resolution of species occurrence data). To reduce the confounding effects of multi-collinearity on model outputs, Spearman correlation coefficients were calculated for each pair of covariates using SPSS 21 (IBM Corp, 2013), wherein a conservative threshold of |0.6| was adopted. When the Spearman's r value fell below this threshold, 1 of the covariates in the pair was dropped from further analysis. After removing correlated layers, 12 covariates were available for input into Maxent.

Topo-level covariates. Regional topography creates microclimates with variable temperature and moisture regimes (Anderson et al., 2012) and regulates the accumulation of water and soil nutrients on the landscape. These phenomena in-turn influence ecosystem vegetation (Mackay & Lindenmayer, 2001) and the ecological resilience of an area (Anderson et al., 2012). In this study, we used the Enhanced Digital Elevation Model (DEM) of Nova Scotia (Nova Scotia Department of Natural Resources [NSDNR], 2006), either alone or in conjunction with other base-layers, to derive a regional topographic position index (TPI) and a landscape complexity index. Conversely, the influence of topography on moisture availability was represented by the depth-to-watertable (D2W) layer (NSDNR, 2007a).

The TPI classifies landform position relative to the surrounding 'neighborhood' (i.e. local topographic position). Topographic position affects many biophysical processes, such as soil erosion and deposition, wind exposure, cold air drainage, and hydrological balance (Weiss, 2001). We created a TPI that distinguished among 5 different topographic positions (i.e., valleys, low-slopes, mid-slopes, up-slopes, and ridges) using methodology that was developed by Weiss (2001) and modified by Cooley (2014). (See Appendix A.)

Conversely, landscape complexity was defined according to Anderson et al. (2012) as the number of microclimates present in an area, which is in turn a function of landform variety, wetland density, and elevation range. More complex landscapes typically support greater biodiversity levels and promote climate resilience (Anderson et al., 2012). For this study, we built a 150 m^2 index delineating relative landscape complexity across Nova Scotia using methodology adapted from Anderson et al. (2012) and datasets provided by NSDNR (i.e. the provincial DEM [NSDNR, 2006] and the provincial wetland inventory [NSDNR, n.d.]). (See chapter 4.)

Finally, the 'D2W' layer describes where water is likely to flow and/or accumulate on a landscape and was found to be a strong predictor of focal bird habitat in research by Westwood et al. (2015). This layer was created by researchers at the University of New Brunswick using a digital elevation model (DEM) and mapped hydrographic data (NSDNR, 2007b).

Micro-level covariates. Micro-level covariates are believed to have a more direct influence on the suitability of songbird habitat and on the diversity of songbird communities than does topography (Franklin, 2009b). In this study, micro-level covariates were created to represent forest stand characteristics, including the vertical and horizontal distribution of canopy elements or patch types. Forestry data was obtained from the province-wide Forest Inventory Database (FID), which is distributed by NSDNR as a vector polygon layer. The FID is continually updated through aerial-photograph interpretation and describes land-use as well as the structure and composition of vegetation (NSDNR, n.d.). The full range of data collection years for the FID data used in the current study was 1988 to 2012, with most of the data collected between 2003 and 2012.

Specifically, we created layers which characterized mean canopy height and mean canopy density in each raster cell by averaging relevant polygon values (i.e. 1st story height and % crown closure) within 150 m*150 m areas. We then created 2 corresponding layers to characterize the heterogeneity of canopy height and canopy density by calculating the standard deviation of relevant polygon values within the same 150 m*150 m areas. To delineate the availability and distribution of cover types in the province, we measured the distance to coniferous and deciduous stands, respectively, using the 'Euclidean Distance' tool in ArcMap. Finally, to delineate the availability and distribution of key patch types, we measured the distance to all-height stands and the distance to stands with dead material.

3.2.5. Maximum entropy modeling

We used Maxent 3.3 software (Phillips et al., 2006) to model relative habitat suitability for the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler in Nova Scotia. Maxent is a widely used machine-learning SDM method that estimates the relative probability of species presence by comparing environmental conditions at occurrence points to those at 10,000 background points (i.e. locations where the species was not observed) (Elith et al., 2010a; Merow et al., 2013). In brief, Maxent predictions are generated by calculating the probability distributions of environmental covariates at species' locations which are most similar to those of the overall landscape (i.e. the maximum entropy distribution, as defined by the 10,000 background points) while still meeting constraints derived from the occurrence dataset itself. (In other words, the mean, variance, covariance, etc., of environmental covariates at predicted presence locations must match those of observed species locations.) (For a full theoretical and statistical explanation of Maxent, see Phillips et al. (2006), Edith et al. (2010a), or Merow et al. (2013).)

The maximum entropy approach was chosen because, due to the nature of the ACCDC dataset, presence/absence methods were not available to us, and Maxent has typically ranked among the top performing presence-only models (Elith et al., 2006). Maxent also has the additional advantages of being easy to use and relatively robust to small sample sizes and/or spatial errors in occurrence data (Elith et al., 2006; Merow et al., 2013). In developing Maxent models, we applied a regularization penalty (used to reduce over-fitting in machine-learning applications) of 1.5, as we noted that some covariate response curves were unrealistically complex and did not make ecological sense when the default regularization penalty of 1 was used. All other parameter settings were assigned default values.

3.2.6. Correcting for sample bias

Bias in sampling effort, wherein environmental covariates are assigned importance because they are typical of intensely surveyed areas, not because they represent a real biological relationship (Phillips et al., 2009; Baldwin, 2009), can greatly reduce model accuracy if not accounted for. Sample bias is particularly problematic for presence-only models such as Maxent, as presence-only datasets almost invariably comprise a collection of undesigned, opportunistic, or purposive observations obtained from multiple sources of varying integrity (Franklin, 2009b). Therefore, to compensate for sample bias in bird datasets, in addition to spatially-filtering presence points, we also created 'bias grids', which modify the location and frequency of background data collection. The goal of applying a bias grid is to characterize the 10,000 point background sample with similar spatial bias as that exhibited by presence points, thereby factoring out the sample bias in occurrence data (Phillips & Dudik, 2008).

In this study, bias masks were created by generating a kernel density map of presence points for each bird using the 'Kernel Density with barriers' tool included in the Hawth's tools extension for ArcMap (Beyer, 2004). In creating bias grids, we adopted a kernel radius of 10 km and normalized output kernel density values between 1 and 20 (following Elith et al., 2010b and Fourcade et al., 2014). Normalized kernel density maps were used as sampling probability surfaces for the selection of background points in all subsequent Maxent model runs (Figure 3.1).

3.2.7. Reverse stepwise elimination

The initial list of candidate covariates used in this study was established after performing extensive tuning experiments (data not shown). This list included 10 candidate covariates for the Rusty Blackbird and the Olive-sided Flycatcher and 11 candidate covariates for the Canada Warbler (Table 3.1). Candidate covariates were the same for each bird with the exception of covariates representing forest cover type. Specifically, we did not include ‘distance to deciduous stand’ in reverse stepwise elimination for the Rusty Blackbird and Olive-sided Flycatcher in order to match known habitat requirements of these species. Conversely, both ‘distance to deciduous stand’ and ‘distance to coniferous stand’ were considered for the Canada Warbler, as this species is associated with mixedwood forests.

We applied a reverse stepwise elimination technique to identify the most parsimonious subsets of covariates from the initial list and thereby establish final ‘best’ models. Specifically, for each bird, we first ran a Maxent model that included the complete list of candidate covariates shown in Table 3.1. The covariate that contributed the least to predictive power (according to permutation importance score; Yost, 2008; Baldwin, 2009) was identified, and a new model was run without this covariate. This procedure was repeated until a single covariate remained, yielding a set of ‘n’ candidate models, where n = the number of covariates included in the initial run. Of these, the most parsimonious model was identified using Akaike’s Information Criterion (AIC_c) (corrected for small sample sizes), which was calculated using a Perl-script developed for Maxent by Warren and Seifert (2010).

3.2.8. Model evaluation

Upon identifying the most parsimonious model according to AIC_c score, we evaluated model fit using Area under the Receiver Operating Curve (AUC) statistics and by comparing expected versus observed omission rates. AUC is a ranked approach that provides a measure of the likelihood that a randomly selected presence point has a higher suitability score than a randomly selected absence or, in a Maxent context, background point (Elith et al., 2006; Fourcade et al., 2014). AUC scores range from 0 (no power to discriminate between presence and absence/background) to 1 (perfect discriminatory power). A score of 0.5 indicates that model predictions are no better than random.

After final models for each bird were identified via AIC_c, mean AUC values were determined over 10 cross-validated runs. For each of these runs, 90% of occurrence data were used to train the model and 10% of data were set aside for testing. Therefore, 2 AUC values were generated for each final model, 1 based on training data (AUC_{train}) and 1 based on test data (AUC_{test}). However, although AUC is the most widely used evaluation measure in SDM studies, this metric has been widely criticized for tending to reward models that have been over-fit (Lobo et al., 2008). Therefore, in evaluating the reliability of final models, we placed special emphasis on the difference between AUC_{train} and AUC_{test} scores (AUC_{diff} hereafter), as over-fit models tend to predict training data well and test data poorly (Warren & Seifert, 2011).

In comparing expected and observed omission rates, we adopted 2 thresholds: the lowest presence threshold (i.e. LPT) and the 10% presence threshold (10PT). LPT refers to the maximum suitability score for which no presence locations were incorrectly classified as 'background', and 10PT refers to the suitability score at which 10% of presence locations were incorrectly classified as background. For each bird, we calculated the LPT and 10PT of training data (i.e. expected omission rates) and determined how many points were excluded when these thresholds were applied on test data (i.e. observed omission rates). Observed omission rates that are close to 0% (for LPT) and 10% (for 10PT) indicate that the model is well calibrated.

3.3. Results

Final habitat models included 4 or 6 covariates, which comprised both topo- and micro-level features, although specific subsets differed among birds. For example, 'D2W' was identified as having the most important influence on relative habitat suitability for the Canada Warbler and the Rusty Blackbird, but this covariate was not selected in the Olive-sided Flycatcher model. Additionally, while forest canopy and forest patch characteristics were important determinants of relative habitat suitability for all birds, no model included the same subset of forest covariates. (However, '1^{st} story height STD' was selected in all models.)

For all birds, while AUC_{train} and AUC_{test} values were fairly low (0.6850 to 0.7246 for AUC_{train} and 0.6541 to 0.692 for AUC_{test}), AUC_{diff} values were also low (between 0.0176 and 0.0428) (Table 3.2), and observed omission rates were 0.29% to 3.2% higher than expected for LPT and 1.39% to 4.23% higher than expected for 10PT (Table 3.2). Both of these metrics indicate that over-fitting did not significantly confound our SDM results.

For all birds, maps of relative habitat suitability indicated that, at the landscape-scale, suitable habitat remains fairly abundant and well distributed across the province of Nova Scotia (Figure 3.2). Furthermore, when the maximum training sensitivity plus specificity (MaxSS) threshold was applied to create a binary surface delineating suitable and unsuitable habitat (Figure 3.3), the models predicted that 43% of the Nova Scotia landmass is suitable for the Rusty Blackbird, 49% is suitable for the Olive-sided Flycatcher, and 35% is suitable for the Canada Warbler. (The MaxSS value is determined by optimizing sensitivity and specificity values and was identified as the most robust threshold by Liu et al. [2013]).

Response curves, percent contribution (i.e. to training gain), and permutation importance (calculated according to the drop in AUC that occurs if the variable is excluded from the model; Phillips, 2006) scores for each covariate included in final models for each bird are shown in Table 3.3. Species-specific final model results are described over subsequent sections.

3.3.1. Rusty Blackbird

Across 10 cross-validated runs, the most parsimonious model (i.e. the model which yielded the lowest AIC_c score during reverse stepwise selection) for the Rusty Blackbird showed mean AUC_{train} and AUC_{test} scores of 0.6969 and 0.6541, respectively, and an AUC_{diff} score of 0.0428. Over these same runs, observed omission rates were 3.2%

higher than expected for LPT and 4.23% higher than expected for 10PT (Table 3.2); however, the model predicted that 43% of Nova Scotia nonetheless contains suitable Rusty Blackbird habitat. Note that both AUC and omission rate-based metrics showed lower scores for the Rusty Blackbird than for the other birds considered in this study.

The final Rusty Blackbird model contained 4 covariates (listed from greatest to least importance), as follows: 'D2W', '1st story height MEAN', '1st story height STD', and 'distance to coniferous stand' (Table 3.3a). Model results indicate that, at the landscape scale, 'D2W' had a greater influence on relative habitat suitability for this bird than any other covariate. Specifically, this covariate had a permutation importance score of 43% and a response curve that showed relative habitat suitability steeply declining as the distance between the water-table and the soil surface increased. Conversely, the next 2 covariates included in the Rusty Blackbird model, '1st story height MEAN' and '1st story STD' (with importance scores of 30% and 18.2%, respectively), describe forest structure. Response curves for these covariates were linear and indicate that areas characterized by lower mean canopy height but greater canopy heterogeneity tended to be more suitable for this bird. The final covariate in the Rusty Blackbird model was 'distance to coniferous stand' (importance score of 8.7%), and its response curve showed that habitat became less suitable away from conifer-dominated areas (Table 3.3a).

3.3.2. Olive-sided Flycatcher

The most parsimonious model for the Olive-sided Flycatcher showed mean AUC_{train} and AUC_{test} scores of 0.6850 and 0.6674, respectively, and an AUC_{diff} score of 0.0176 across 10 cross-validated runs. Observed omission rates were 0.39% higher than expected for LPT and 1.98% higher than expected for 10PT (Table 3.2). This model showed the best fit and also indicated that more suitable breeding habitat remains in Nova Scotia (49% of the provincial landmass) for the Olive-sided Flycatcher than for the other bird species considered by this study (Figure 3.3). These results are consistent with those of Westwood et al. (2015), who found that provincial parks in Nova Scotia and New

Brunswick retained a greater proportion of suitable habitat for the Olive-sided Flycatcher than for the Rusty Blackbird and Canada Warbler.

Five covariates were included in the Olive-sided Flycatcher model, as follows (listed from greatest to least importance): '1st story height MEAN', '1st story height STD', 'distance to coniferous stand', 'TPI', and 'distance to stand with dead material' (Table 3.3b). Covariates related to forest structure showed the highest importance scores (28.7% and 25.9% for '1st story height MEAN' and '1st story height STD', respectively) and, similar to the Rusty Blackbird, relative habitat suitability improved as heterogeneity in canopy height increased but mean canopy height decreased. 'Distance to coniferous stand' showed moderate importance (21.3%), with relative habitat suitability rapidly decreasing away from conifer-dominated areas (Table 3.3b). Results for 'TPI', which also received a moderate importance score (19.3%), indicate that the Olive-sided Flycatcher was more likely to occur in valleys and low-slope areas. Finally, relative habitat suitability also decreased away from stands that contained dead material, although this covariate had the lowest importance score (4.8%) in the model.

3.3.3. Canada Warbler

The most parsimonious Canada Warbler model showed mean AUC_{train} and AUC_{test} scores of 0.7246 and 0.6920, respectively, and an AUC_{diff} score of 0.0326 across 10 cross-validated runs (Table 3.2). Observed omission rates were 0.64% higher than expected for LPT and 1.39% higher than expected for 10PT (Table 3.2). Our results indicate that, in Nova Scotia, the amount of potentially suitable breeding habitat available for the Canada Warbler is 35% (when the MaxSS threshold is applied) (Figure 3.3).

The Canada Warbler model contained 6 covariates (listed from greatest to least importance), as follows: 'D2W', 'distance to coniferous stand', '1st story height STD', 'distance to deciduous stand', 'distance to stand with dead material', and 'landscape complexity' (Table 3.3c). As with the Rusty Blackbird, 'D2W' (importance score of 36.8%) had a greater influence on the relative suitability of Canada Warbler habitat than any other covariate, wherein suitability scores decreased as ‘D2W’ values increased. Indeed, the permutation importance score for ‘D2W’ in the Canada Warbler model was more than twice as high as that of the 2nd most important covariate. However, the decrease in habitat suitability as distance between the water table and the soil surface increased was slightly less striking for the Canada Warbler than for the Rusty Blackbird.

The 2nd most important covariate in the Canada Warbler model was ‘distance to coniferous stand’ (importance score of 17.1%). The Canada Warbler showed a similar response to this covariate as did the Rusty Blackbird and the Olive-sided Flycatcher, wherein relative habitat suitability decreased away from conifer-dominated areas. ‘1st story height STD’, ‘distance to deciduous stand’, and ‘distance to stand with dead material’ all showed moderate importance (~10-15%) in the Canada Warbler model, and response curves for these covariates indicate that relative habitat suitability increased in areas characterized by greater variation in canopy height but decreased away from areas dominated by deciduous trees and woody detritus. The response curve for ‘landscape complexity’, which was the last covariate in the Canada Warbler model (importance score of 8.7%), indicates that areas of complex topography provided superior Canada Warbler habitat than did areas without complex topography (Table 3.3c).

3.4. Discussion

This is the first study to develop province-wide models for the Olive-sided Flycatcher, Canada Warbler, and Rusty Blackbird in Nova Scotia. At first glance, the AUC_{train} (0.6850 to 0.7246) and AUC_{test} (0.6541 to 0.6920) scores associated with our SDMs appear to suggest that their predictive power was only marginally better than random. However, although AUC is among the most widely used model evaluation metrics, many previous researchers have reported that it is a poor evaluator of SDMs (Lobo et al., 2007, Gonzales et al., 2011), and this is especially true for presence-only models (Van Proosdij et al., 2015). For example, using background points to calculate AUC scores inevitably increases the number of false absences, confounding the accuracy of this metric (Lobo et al., 2007). Furthermore, while AUC helps evaluate a model’s discriminatory power, it provides no indication of goodness-of-fit and tends to reward overly complex models. Finally, multiple factors are known to artificially inflate AUC scores, including species prevalence across the study landscape, the number of observation points in occurrence datasets, and sample bias (Lobo et al., 2007, Van Proosdij et al., 2015). Indeed, in chapter 2 of this thesis, we found that the models which yielded the highest AUC scores were those that employed species datasets that were most severely affected by sample bias. In the current study, presence points were well distributed across the study area, and we took extra care to account for sample bias. Therefore, we suspect that the AUC scores associated with our models likely underestimate their overall quality, at least for 2 of the 3 study species.

Conversely, AUC_{diff} and a comparison of expected versus observed omission rates indicate that Olive-sided Flycatcher and Canada Warbler models are reasonably well fit. The Rusty Blackbird model had the highest AUC_{diff} score, and the observed omission rates showed the largest deviation from expected omission rates for this bird. Therefore, among the 3 study species, the Rusty Blackbird model had the poorest fit, which was also the case in modeling work conducted by Westwood et al. (2015). (Note that in both that study and the current one, the number of observation points available to model Rusty Blackbird habitat was considerably lower than the number of observation points available to model Olive-sided Flycatcher and Canada Warbler habitat.)

We therefore suspect that our model overestimated the amount of suitable Rusty Blackbird habitat in Nova Scotia, likely due to its generality (4 covariates versus 5 for the Olive-sided Flycatcher and 6 for the Canada Warbler). Specifically, this SDM predicted that 43% of the province contains suitable Rusty Blackbird habitat. In contrast, recent MBBA surveys (conducted between 2006 and 2010) only found evidence of Rusty Blackbird breeding activity in 19% of atlas squares (each of which measured $10km^2$) (Bird Studies Canada, 2012). Nonetheless, given the low detectability of Rusty Blackbirds (Powell et al., 2014; McNulty et al., 2016), the overestimation of suitable habitat may not be as severe as a comparison with the MBBA data suggests. (Note that results were more comparable between this study and MBBA data for the Olive-sided

Flycatcher and the Canada Warbler. Specifically, our model predicted that 49% of Nova Scotia contains suitable Olive-sided Flycatcher habitat, and breeding evidence was found in 57% of atlas squares for this bird. For the Canada Warbler, our model predicted that 35% of the province is suitable, and breeding evidence was found in 40% of atlas squares.)

Nonetheless, for all bird models, covariates selected through reverse stepwise elimination generally correspond well with known habitat preferences of assessed species; therefore, all SDMs show good ecological realism. The covariates that reverse stepwise elimination identified as important for each bird are discussed over subsequent sections.

3.4.1. Rusty Blackbird

The Rusty Blackbird is a wetland obligate that is dependent on shallow-water habitat to meet its foraging needs (Powell et al., 2010, 2014). This well-recognized habitat requirement likely explains why 'D2W' was assigned the highest permutation importance score in the model, and why relative habitat suitability was found to rapidly decrease as 'D2W' values increased. Rusty Blackbird nesting preferences (i.e. dense patches of stunted conifers surrounded by sparse canopy closure; Matsuoka et al., 2010) were also reflected in model results. Specifically, the patchy nature of Rusty Blackbird habitat was illustrated through the response curves for '1st story height MEAN' and '1st story height STD', which showed increases in habitat suitability as (1) mean canopy height increased and (2) variation in canopy height decreased, respectively. The importance of coniferous trees to this species was confirmed by the response curve for 'distance to coniferous stand', in which relative habitat suitability decreased away from conifer-dominated areas.

3.4.2. Olive-sided Flycatcher

The Olive-sided Flycatcher is known to defend large territories (10-45 ha; COSEWIC, 2007), and our model suggests that, in Nova Scotia, these territories contain both open and treed areas. We also found that the most suitable Olive-sided Flycatcher habitat is characterized by patchy vegetation dominated by coniferous trees, which has been noted in other parts of this species' range as well (e.g. in Oregon, McGarigal & McComb, 1995; in California, Brandy, 2001). In the current study, the importance of conifers was demonstrated by the response curve for 'Distance to coniferous stand' (the third most important covariate), in which habitat suitability rapidly decreases away from these areas. The importance of patchy vegetation was emphasized by response curves for the 2 covariates with the highest permutation importance scores in the Olive-sided Flycatcher model (i.e. '1st story height MEAN' and '1st story height STD'), which showed that the most suitable habitat was located in areas where (1) average canopy height was low but (2) overall, canopy height was highly variable, similar to the Rusty Blackbird. The Olive-sided Flycatcher is well-recognized as an edge specialist (McGarigal and McComb, 1995), commonly nesting in emergent trees along forest edges, which improves visibility for foraging (Meehan & George, 2003). Therefore, areas of high quality habitat are also likely to be characterized by a high proportion of forest edges; however, this can only be inferred indirectly from the canopy covariates in our model.

'D2W' was not selected in the Olive-sided Flycatcher model; however, moisture regime is less important to nest-site selection for this bird than for the Canada Warbler and Rusty Blackbird. Therefore, we suspect that the influence of this covariate, which describes access to water, was masked by covariates describing forest canopy conditions. Nonetheless, the fourth most important covariate in the Olive-sided Flycatcher model was 'TPI', which revealed that, in Nova Scotia, habitat quality tends to be superior in valleys and on low-slopes. These areas favor the formation of hydrological landforms, such as wetlands and watercourses (Mackay & Lindenmayer, 2001), that are often associated with the natural edge habitat that the bird prefers. The final covariate included in the Olive-sided Flycatcher model was 'distance to stand with dead material', which may also reflect the bird's status as an edge specialist and its preference for post-disturbance, early-seral habitat with higher snag densities (Robertson & Hutto, 2007).

3.4.3. Canada Warbler

Previous studies on Canada Warbler habitat have identified the presence of vegetated wetlands and moist forests as being critical to bird occurrence (e.g., Lambert and Faccio, 2005; Goodnow and Reitsma, 2011; Westwood, 2015). Our findings are consistent with these earlier works, wherein 'D2W' was identified as the most important covariate in the Canada Warbler model, and the response curve for this covariate showed a decrease in relative habitat suitability as the distance between the water-table and the soil surface increased. The inclusion of 'landscape complexity' in the Canada Warbler model was also likely due to the bird's facultative preference for wet habitat. Specifically, the algorithm used to create the landscape complexity index assigns higher complexity scores to areas with greater wetland density (Anderson et al., 2012), and complex landscapes were found to improve habitat suitability for the Canada Warbler.

Other key features of Canada Warbler habitat that have been noted in previous research include a vertically complex forest structure (Reitsma et al., 2008) with a dense understory layer. Indeed, the Canada warbler is a ground nester, and numerous studies have identified dense understory growth as the single most important determinant of Canada Warbler habitat (Goodnow & Reitsma, 2011; Becker et al., 2012). In our Canada Warbler model, this habitat preference was captured by 'distance to stand with dead material', which had a response curve that showed a linear decrease in relative habitat suitability as distance to stands with woody debris increased. Conversely, the Canada Warbler preference for forest patches characterized by high vertical complexity was evident from the response curve for '1st story height STD'. Specifically, areas with high variation in canopy height were associated with the best relative habitat suitability scores, a trend that was also observed for the Rusty Blackbird and Olive-sided Flycatcher.

Previous studies have noted that the Canada Warbler will nest in a wide range of deciduous and coniferous forests but is slightly more common in mixed stands (Becker et al., 2012; Reitsma et al., 2008). Our model results correspond with those earlier findings, wherein relative habitat suitability for the Canada Warbler decreased away from both coniferous and deciduous stands. However, that 'distance to coniferous stand' showed a higher permutation importance score than 'distance to deciduous stand' may reflect the predominance of this cover type in the province of Nova Scotia, rather than a real ecological preference for cover type.

3.4.4. Benefits of using topographic covariates in landscape-scale SDM research

While micro-level environmental features (e.g. covariates related to forest cover) are typically considered to have a more direct influence over species distributions, our models, all of which included topo-level covariates, demonstrate that topographic features can have predictive value in landscape-scale SDM research as well. Topography may also offer practical advantages to this type of work, as characteristics of forest vegetation often change (e.g., through silviculture practices or the natural processes of disturbance and succession) more quickly than GIS layers representing them can be updated, which can put the reliability of forest data in question. Conversely, changes in topography occur at geologic timescales, and topographic GIS layers can therefore be expected to remain relatively accurate over the long-term, as long as the underlying mapping methods are sound.

The stability of topography is especially important in an era of climate change, as shifts in temperature and precipitation regimes are expected to significantly alter North American forest ecosystems (Stralberg et al., 2015). As noted, topographic processes help regulate micro-level forest characteristics, and topography should not be affected by a changing climate, unlike micro-scale forest features (Holling, 1986; Mackay & Lindenmayer, 2001). In developing forest landbird SDMs, we adopted the assumption that complementing the use of micro-level features with suitable topo-level features can help SDMs identify more climate-resilient habitat (i.e. habitat patches which are more likely to retain similar structures, processes, and feedbacks over the long-term as climate changes).

In this study, not only did reverse stepwise elimination identify both topo-level and micro-level covariates as being important to relative habitat suitability for all 3 birds, at the landscape-scale that we considered, topographic covariates showed stronger explanatory power than did covariates describing characteristics of forest stands in many cases. In both the Rusty Blackbird and Canada Warbler model, the covariate with the highest permutation importance score was ‘D2W’ (43% and 36.8%, respectively), and in the Canada Warbler model, this covariate was more than twice as important than the covariate with the 2nd highest permutation importance score (‘distance to coniferous stand: 17.1%). ‘Landscape complexity’ increased predictive power for the Canada Warbler model as well, although the importance score of this covariate was comparatively low (8.7%). For the Olive-sided Flycatcher, 3 covariates with the highest permutation scores were related to micro-level forest characteristics; however, ‘TPI’ (a topo-level covariate) nonetheless received a permutation importance score of 19.3%. That topo-level covariates showed stronger predictive power in Rusty Blackbird and Canada Warbler models than in the Olive-sided Flycatcher is not surprising, as the importance of topography to habitat suitability for our study species is very likely related to its control over local moisture regimes, and the Rusty Blackbird and Canada Warbler have much stronger associations with wet habitat than does the Olive-sided Flycatcher.

Indeed, the utility of individual topographic features to landscape-scale SDM research is likely to vary across both study species and study regions. We also note that, although there is theoretical and modeled evidence to suggest abiotic topography can be used to help identify climate-resilient habitat, the utility of our resilience-based approach to species distribution modeling in an era of climate change must be confirmed through field testing and long-term empirical studies.

3.4.5. Implications for conservation and forest management

Currently, 80% of Nova Scotia is covered by forest (NSDNR, 2008). Results from this research suggest that (1) Nova Scotian forests retain a high proportion of breeding habitat for the bird species considered in this study and that (2) this habitat is well distributed throughout the province, providing opportunities for conservation (Figures 3.2 and 3.3). Our results further suggest that the Rusty Blackbird, Olive-sided Flycatcher, and Canada

Warbler prefer the same moisture-rich ecosites, and thus have the potential to be managed as a suite, which corroborates findings from previous work by Westwood et al. (2015). When binary habitat suitability surfaces were compared in an overlay, we found that approximately 22% of the Nova Scotia land-base was characterized as suitable for all 3 birds (Figure 3.4). We suggest that these areas could be prioritized in a conservation plan as a means to help attenuate their declines, both now and in the future as climate changes.

Unlike forest vegetation, topography will remain largely unaffected by changing climatic regimes. We therefore posit that conservation plans which target topographic features can reduce the uncertainty associated with other approaches to species distribution modeling and conservation planning in an era of climate change. Topographic control over hydrological conditions causes moisture to accumulate in low-slope and low-elevation areas in response to gravitational potential energy gradients (Mackay and Lindenmayer, 2001; Murphy et al., 2009). The critical importance of a wet moisture regime to the Canada Warbler and the Rusty Blackbird was demonstrated in this study through response curves for 'D2W' (the most important variable in both models), which was itself developed using topographic data (i.e. slope and distance to nearest hydrographic feature) (Murphy et al., 2007). While 'D2W' was not included in our Olive-sided Flycatcher model, 'TPI' was, and lowland topographic positions showed better suitability than upland ones. Furthermore, previous modeling conducted by Westwood et al. (2015) found higher Olive-sided Flycatcher densities in territories that included a greater proportion of wet areas. Earlier studies have observed greater productivity and passerine richness in lowlands as well, and hypothesized that this correlation can be explained by (1) increased moisture and nutrient accumulation (Neave et al., 1996) and (2) increased vertical complexity due to the juxtaposition of multiple habitats in riparian forest ecotones (LaRue et al., 1995). Indeed, work by LaRue et al. (1995) demonstrated that many birds which typically prefer drier environments can also be found in lowland riparian sites, but the same could not be said for birds that prefer wetter habitat (LaRue et al., 1995). Given the critical importance of wetness to these birds (especially the Rusty Blackbird and Canada Warbler), habitat conservation sites established for their benefit should include wet habitat under both current and future climate regimes. Our results show that the topo-level covariates of 'D2W' and 'TPI' are effective at identifying currently suitable habitat, and theoretical evidence suggests that these topo-level features can promote the persistence of wet moisture regimes over time (see Table 3.4).

Nonetheless, preserving suitable topography alone is insufficient to promote the conservation of these species in Nova Scotia; favorable forest conditions are critical as well. Habitat alteration and loss due to silviculture practices on breeding grounds are believed to have significantly contributed to the decline of the forest landbirds considered in this study (COSEWIC, 2007, 2008). Given the crucial importance of wet forest habitat to these species in Nova Scotia, like Westwood et al. (2015), we recommend that the maintenance or restoration of these areas be a key priority of forest management. We further posit that, to mitigate the effects of silviculture harvesting on the species of interest in Nova Scotia, maintaining buffers of a sufficient width around wetlands and watercourses is likely more important than preserving residual forest patches (Westwood et al., 2015) Currently, provincial regulations require that silviculture activities maintain a buffer measuring between 20 m and 60 m around wetlands and watercourses (Province of Nova Scotia, 2002). However, this size is unlikely to be sufficient for the species of interest. From a wildlife conservation perspective, larger buffers are widely understood to be more effective than smaller ones (e.g. The Nature Conservancy 2015, Ives et al. 2005). Similar to Westwood et al. (2015), we recommend that, ideally, the width of wetland and watercourse buffers should be increased to 225 m in order to be large enough to minimize edge effects, offer protection from upland predators, and contain at least 1 complete territory for each of the species of interest. In addition, when harvesting timber outside buffer areas, practices that promote increased vertical complexity such as 'structural complexity enhancement' (Gottesman & Keeton, 2017) could benefit the Canada Warbler. Conversely, the Olive-sided Flycatcher should benefit from residual snags left in harvest areas.

Nonetheless, the large amount of suitable habitat that was identified in this study suggests that, in Nova Scotia, decreases in bird populations may not be primarily related to the loss of landscape-scale breeding habitat (even if the amount of suitable habitat was over-estimated in the Rusty Blackbird model). Indeed, factors affecting other geographic areas or scales that have been cited as potential causes of Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler declines include the loss of wintering habitat (Greenberg et al., 2011), mercury contamination (Edmonds et al., 2010), predation (Savard et al., 2011), and parasite infections (Bernard et al., 2010). It is important to note that the effectiveness of landscape-scale conservation measures applied to protect breeding habitat may be limited if bird declines are being primarily driven by phenomena that occur at a different scale or location along the Atlantic flyway.

3.5. Limitations

It is possible that the reliability of our results were affected by classification errors in underlying datasets, which may be considerable in some parts of the FID at the landscape-scale (Westwood, 2015). To minimize the confounding effects of these classification errors, we defined cover-types generally (i.e. coniferous or deciduous, rather than by dominant tree species). While we did not make similar adjustments for '1st story height' and '% canopy closure', response curves for these variables make ecological sense, and we therefore consider them to be reasonably reliable. Nonetheless, as with all SDMs, results should be treated with caution until adequate ground-truthing is conducted.

Secondly, while we represented 1st story canopy height according to mean and standard deviation, in-line with other bird modeling studies (e.g. Lesak et al. 2011, Eldegard et al 2014, Westwood et al. 2015), it is possible that, given the nature of FID data in Nova Scotia, a different representation of canopy height (e.g. defined according to the majority rule) could have stronger predictive power and/or increase model accuracy. Nonetheless, as noted above, we consider the bird responses that were modeled for canopy height covariates to be reasonable in this study.

Thirdly, it is possible that the temporal disconnect between FID data and species occurrence points may also have affected our results. However, the ACCDC dataset contained observations of target species which were made between 2005-2013 (Olive-sided Flycatcher), 2006-2013 (Canada Warbler), and 2006-2012 (as well as single sightings made in 1998 and 2001; Rusty Blackbird). The FID is partially updated every year, and though some data came from aerial photos taken in 1988, most of the data is from 2003-2012. Therefore, the temporal disconnect is not expected to be overly severe in the current study.

3.6. Conclusions

As human demands upon a limited land and water base continue to increase, identifying, prioritizing, and protecting key habitats will become ever more important to biodiversity conservation goals. In a context of climate change, the ability to identify suitable habitat that is also resilient to changing temperature and moisture regimes is especially critical. In this study, we used Maxent modeling techniques and an intersection of topo-level (covariates describing regional topography) and micro-level (i.e. covariates describing forest characteristics) features to develop predictive, spatially explicit habitat models for the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler. In so doing, our goal was to identify areas of habitat that are not only suitable currently, but may be more resilient against the effects of climate change as well. The migratory landbird habitat identified herein can directly support conservation, land acquisition, and biodiversity conservation initiatives in Nova Scotia. Moreover, if confirmed through longer-term monitoring and field studies, our resilience-based approach to species distribution modeling could potentially be applied to benefit the conservation of other terrestrial vertebrate species as well. While we acknowledge that it is impossible to guarantee the persistence of any specific species in an era of climate change, protecting key areas of climate-resilient habitat is a strong first step towards attenuating species loss

3.7 Tables and figures

Table 3.1 List of covariates included in reverse stepwise elimination for the 3 study species. DEM = Digital elevation model; RUBL = Rusty Blackbird; OSFL = Olive-sided Flycatcher; CAWA = Canada Warbler. All base datasets were obtained from the Nova Scotia Department of Natural Resources.

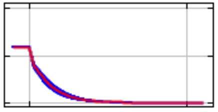
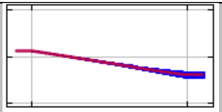
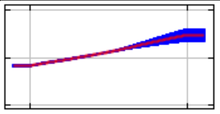
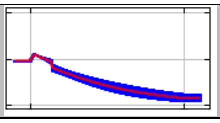
Covariate name	Base dataset(s)	Considered for birds
Topographic position index (TPI)	DEM	RUBL, OSFL, CAWA
Landscape complexity index	DEM; wetland inventory	RUBL, OSFL, CAWA
Depth to water-table (D2W)	D2W	RUBL, CAWA
1st story height MEAN	FID	RUBL, OSFL, CAWA
1st story height STD	FID	RUBL, OSFL, CAWA
% crown closure MEAN	FID	RUBL, OSFL, CAWA
% crown closure STD	FID	RUBL, OSFL, CAWA
Distance to coniferous stand	FID	RUBL, OSFL, CAWA
Distance to deciduous stand	FID	CAWA
Distance to all-height stand	FID	RUBL, OSFL, CAWA
Distance to stand with dead material	FID	RUBL, OSFL, CAWA

Table 3.2: Evaluation metrics for Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler models. Note that, for the lowest presence threshold (LPT) omission rate, values closer to 0% indicate a better calibrated model and, for the 10% presence threshold (10PT) omission rate, values closer to 10% indicate a better calibrated model. AUC = Area under the curve.

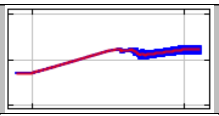
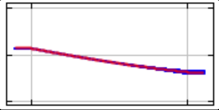
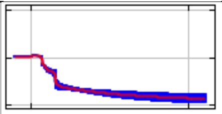
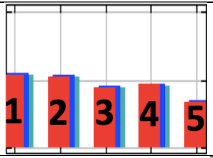
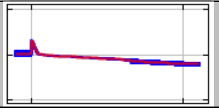
Bird	AUC_{train}	AUC_{test}	AUC_{diff}	Observed LPT omission rate	Observed 10PT omission rate
Rusty blackbird	0.6969	0.6541	0.0428	3.2%	14.23%
Olive-sided Flycatcher	0.6850	0.6674	0.0176	0.39%	11.98%
Canada Warbler	0.7246	0.6920	0.0326	0.64%	11.39%

Table 3.3: Covariates included in final "best" models as well as associated percent (%) contribution scores, permutation importance scores, and response curves for (A) the Rusty Blackbird, (B) the Olive-sided Flycatcher, and (C) the Canada Warbler. Note that, the y axis of all response all curves represents relative habitat suitability, wherein suitability increases from the bottom to the top of the axis. The x axis of all response curves except TPI begins at 0 (left side of figure), and values (e.g. height, distance) increase towards the right. For TPI 1 = valley, 2 = low-slope, 3 = mid-slope, 4 = upper-slope, and 5 = ridgetop.

A. Rusty Blackbird

Covariate	**% Contribution**	**Permutation Importance**	**Response Curve**
D2W	62.4%	43%	
1st story height MEAN	19.2%	30%	
1st story height STD	12.5%	18.2%	
Distance to coniferous stand	7.1%	8.7%	

B. Olive-sided Flycatcher

Covariate	**% Contribution**	**Permutation Importance**	**Response Curve**
1st story height MEAN	24.2%	28.7%	
1st story height STD	29.5%	25.9%	
Distance to coniferous stand	19.5%	21.3%	
TPI	20.9%	19.3%	
Distance to stand with dead material	6%	4.8%	

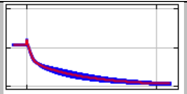
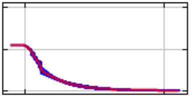
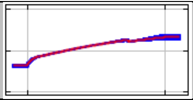
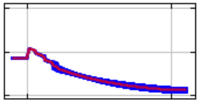
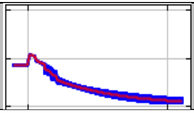
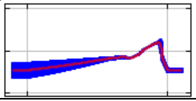
C. Canada Warbler			
Covariate	**% Contribution**	**Permutation Importance**	**Response Curve**
D2W	36.5%	36.8%	
Distance to coniferous stand	18.7%	17.1%	
1st story height STD	18.2%	14.6%	
Distance to deciduous stand	8%	12.2%	
Distance to stand with dead material	11.2%	10.6%	
Landscape complexity	7.3%	8.7%	

Table 3.4 Percentages of (1) habitat that was identified as being suitable for all birds and (2) the entire province of Nova Scotia that were classified as valley or valley/lowslope by the 'TPI' and as wet by the 'D2W'.

	% classified as valley by 'TPI'	**% classified as valley or low-slope by 'TPI'**	**% classified as wet area by 'D2W'**
Habitat identified as suitable for all birds	43%	66%	49%
All of NS	7%	34%	8%

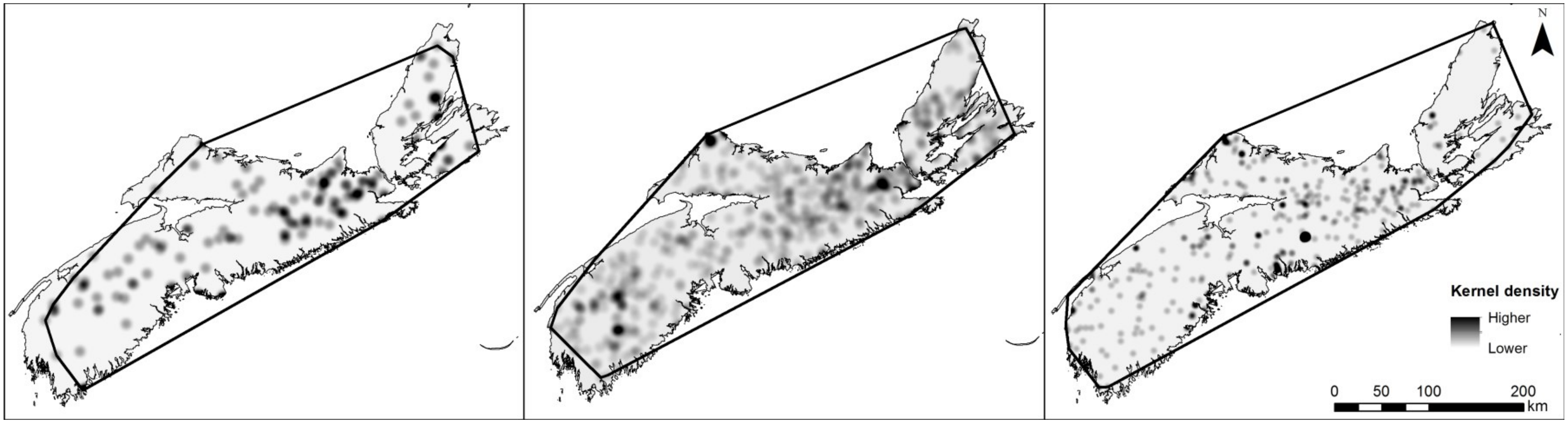


Figure 3.1: Kernel density maps illustrating the relative density of presence points in the (left) Rusty Blackbird, (center) Olive-sided Flycatcher, and (right) Canada Warbler datasets used in this study, where darker areas denote higher point densities. The minimum convex polygons that enclose all points are also shown (black outlines on maps). In training Maxent models, kernel density maps were used as bias grids to help account for spatial autocorrelation in species occurrence data. Actual occurrence locations are not displayed due to the sensitive nature of species at-risk data.

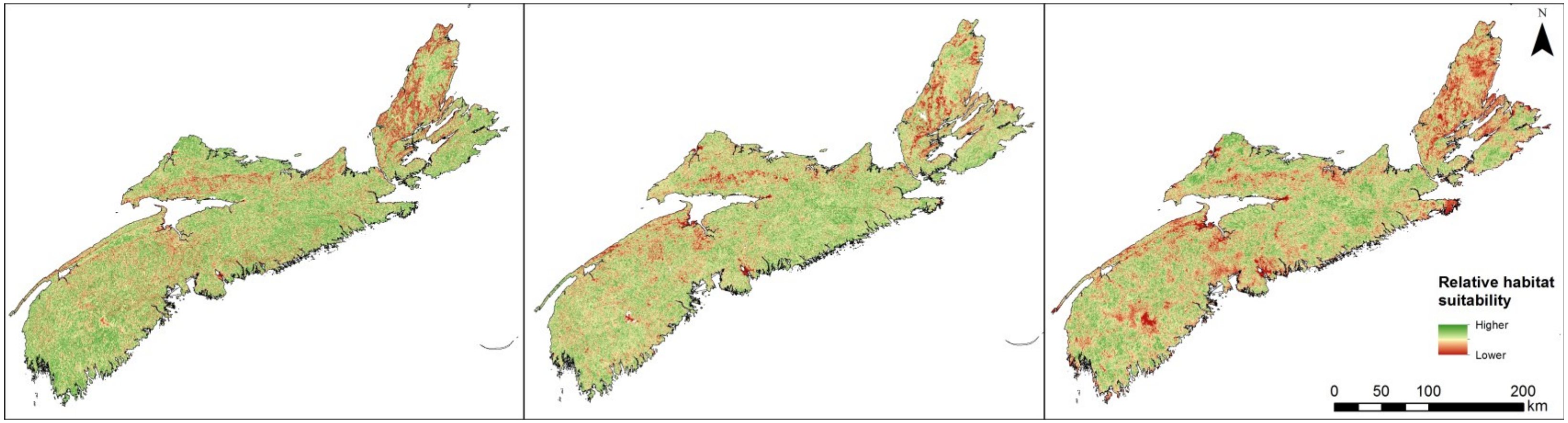


Figure 3.2: Heat maps (output by Maxent software) delineating relative habitat suitability for (left) the Rusty Blackbird, (center) the Olive-sided Flycatcher, and (right) the Canada Warbler.

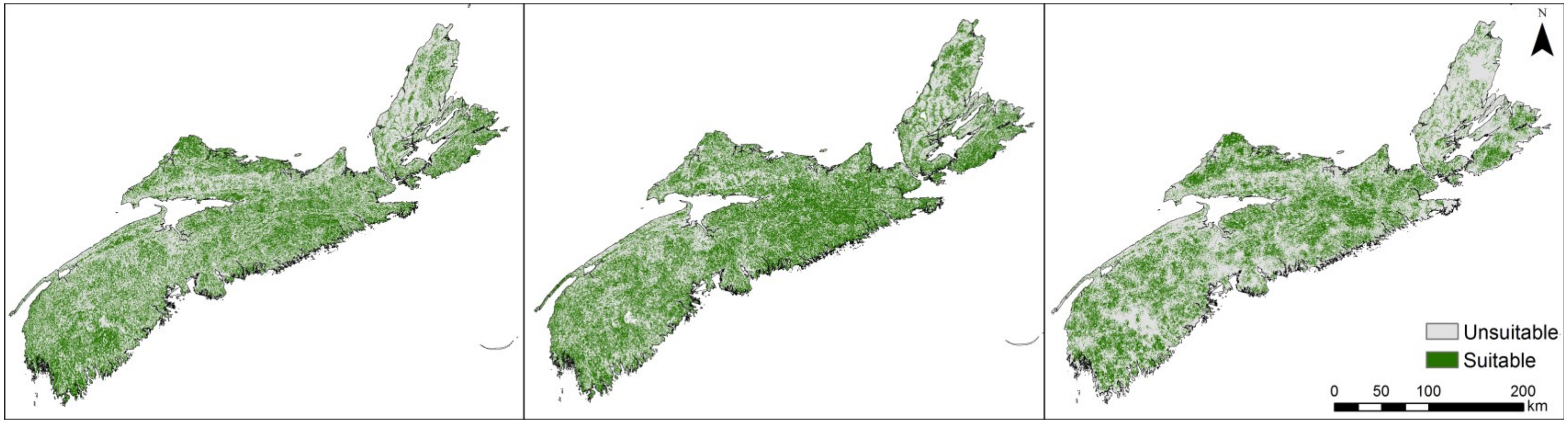


Figure 3.3: Binary habitat suitability maps created by applying the MaxSS threshold for (left) the Rusty Blackbird, (center) the Olive-sided Flycatcher, and (right) the Canada Warbler, where green denotes areas of suitable habitat and grey denotes areas of unsuitable habitat.

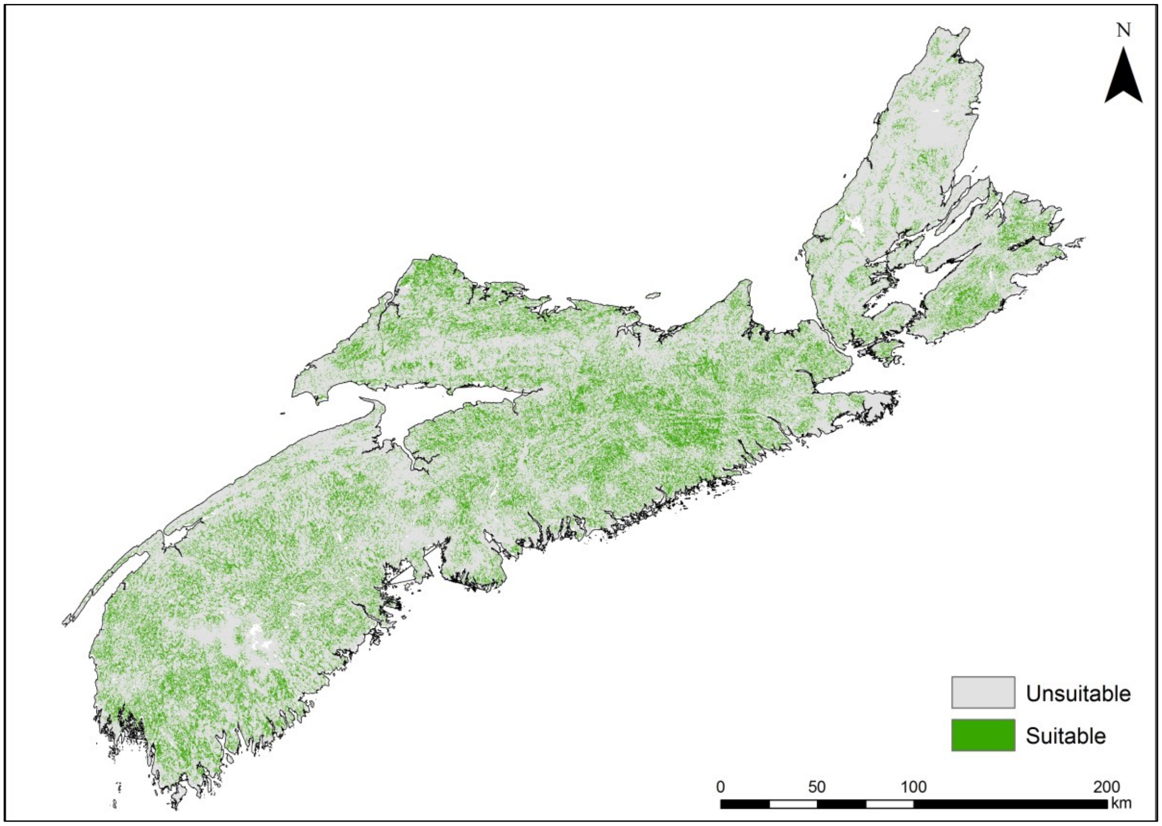


Figure 3.4: Map showing areas in Nova Scotia that contain suitable habitat for all 3 birds considered in this study. These areas were delineated by overlaying the binary suitability surfaces created for each individual bird and identifying the intersecting areas of suitable habitat.

CHAPTER 4: BUILDING AN ARC IN THE ANTHROPOCENE[1] -- APPLYING PRINCIPLES OF ECOLOGICAL RESILIENCE TO DELINEATE CLIMATE RESILIENT HABITAT FOR THE OLIVE-SIDED FLYCATCHER IN NOVA SCOTIA

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Abstract

Climate change is causing the ranges of many species to shift or contract in geographic space, which challenges landscape-scale conservation planning efforts (e.g. protected area delineation and reserve design), as areas which are set aside for their unique biodiversity values may not retain those values in the future. To account for the effects of climate change, conservation planning that targets specific at-risk species often prioritizes areas that have been predicted to fall within *future* range shift boundaries. Conversely, a conservation planning strategy known as the "Conserving Nature's Stage (CNS)" approach does not target any single species, but aims to maintain overall levels of biodiversity by prioritizing areas according to their resilience against the effects of climate change. However, both of these methods have limitations, as predictions of future range shifts can be highly uncertain, and the CNS approach alone is unlikely to be sufficient to protect all individual vulnerable species. To address these gaps, we present a novel, resilience-based approach to single-species conservation planning that (1) targets individual species which may be missed by more general conservation planning strategies and (2) also contributes towards the maintenance of overall biodiversity in an era of climate change. Specifically, our proposed approach combines the results of predictive modeling with elements of CNS to delineate climate resilient refugia and reduce uncertainty in conservation plans. The application of the proposed approach was illustrated through an analysis of Olive-sided Flycatcher (*Contopus cooperi*) habitat in the province of Nova Scotia, Canada, and involves 3 stages. First, patches of habitat that are currently suitable for the target species are identified using a species distribution model that has been trained using a suite of topographic (topo-scale) and forest (micro-scale) covariates. Second, the identified habitat patches are prioritized according to their landscape resilience score (calculated using methods adapted from the CNS approach). Finally, these results are overlain onto a range shift model in order to identify resilient habitat patches that also coincide with future range shift boundaries. Due to their high resilience scores, protecting prioritized patches should not only increase the likelihood

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[1] The title for this chapter was taken from a September 27th, 2014 *New York Times* column, entitled "Building an Arc for the Anthropocene". Permission to use this title was kindly granted by author Jim Robbins.

that the target species persists over the longer-term, but should support the maintenance of general biodiversity as well. Nonetheless, the approach presented here cannot efficiently meet biodiversity conservation goals on its own; therefore, it is intended to complement, not replace, existing conservation planning strategies that seek to protect representative arrays of species, natural land cover types, and enduring topographic and landscape features.

Keywords: Resilience, climate change, climate refugia, resilient habitat, Olive-sided Flycatcher

4.1. Introduction

Three and a half billion years of natural selection generated an enormous diversity of life on planet Earth (Taylor et al., 2009), but today, the synergistic effects of human activities are driving a mass extinction, whereby species are being lost between 1,000 and 10,000 times faster than the natural background extinction rate (Chivian & Bernstein, 2008). Vertebrate species declined 52% between 1970 and 2010 (World Wildlife Federation [WWF], 2014), and it has been predicted that up to 50% of all species could be extinct or near extinct by mid-century if climate-change-induced warming is severe (Thomas et al., 2004).

Although multiple causes are contributing to species' plummeting populations, the most significant threat to biodiversity is habitat modification, fragmentation, and destruction (Wagler, 2011; WWF, 2014). Maintaining a functionally connected network of high quality habitat sites has thus been cited as one of the most effective responses to species loss (Rubio & Saura, 2012). Traditionally, systematic conservation planning efforts have prioritized areas with high endemic species richness or sets of areas with broad species representation. However, these strategies assume that ecosystems are stationary and that habitat which is suitable today will remain so in the future (Lawler et al., 2015). In an era of climate change, altered temperature and precipitation regimes are predicted to cause species' distributional ranges to shift and/or contract in geographic space (Beier & Brost, 2009; Anderson & Ferree, 2010). Indeed, for some species, significant range shifts have already been observed, and more extensive shifts are predicted over the next century (Schloss et al., 2011; McClure et al., 2012; Lawler et al., 2015).

In recent years, ecologists have recognized that a more robust strategy for conservation planning is needed, and new approaches to address climate change have begun to emerge. One example is a species-by-species (i.e. “fine-filter”) approach which involves projecting habitat models created using current climatic conditions onto predictions of future climatic conditions (e.g. based on global circulation models and potential emissions scenarios) to improve understanding of how habitat location and extent will change over time (Stralberg et al., 2015). Habitat models are in-turn derived from species distribution models (SDMs), which use a correlative approach to quantify the niche of a species and map spatial predictions of species’ distributions under a given set of environmental conditions. However, both SDMs and climate models suffer from uncertainty, which can be severe in many cases, leading some to question whether the noise exceeds the signal when this strategy is used (Stralberg et al., 2015).

Conversely, the “conserving nature’s stage” (CNS) strategy is a coarse-filter approach that seeks to protect a diverse set of enduring abiotic conditions (e.g. geology, topography), which are considered the “stage” upon which ecological processes take place. This approach posits that, as abiotic conditions shape not only ecological processes but the biological responses of organisms as well, areas of high abiotic diversity should support high biotic diversity, even if the specific species and communities inhabiting these areas vary over time (Hunter et al., 1988; Lawler et al., 2015). The CNS approach is increasingly seen as particularly useful in an era of climate change, as many of the abiotic features targeted by CNS will not be affected by altered temperature and precipitation regimes (Gill et al., 2015). Furthermore, topographically diverse areas offer more options for species to adapt to climate change, such as the opportunity to move up or down slope or to different aspects (Anderson et al., 2012). Conservation plans that leverage this approach may therefore be less uncertain than plans derived from SDMs and future climate projections alone. However, the ability of CNS to conserve specific species and ecosystems is likely to be limited, as the strength of the relationship between abiotic features and species’ distributions varies greatly between taxa (Beier et al., 2015) and, for mobile vertebrate species especially, biotic (i.e. floristic) factors tend to be more proximate predictors of habitat suitability (Franklin, 2009). Indeed, findings from Schloss et al. (2011) indicated that conservation sites selected solely to conserve abiotic features protected specific types of rare taxa poorly. Therefore, even proponents of CNS suggest that this approach should be complemented by strategies that focus on species themselves (Lawler et al., 2015).

In this chapter, we propose a novel approach to single-species conservation planning for an era of climate change. The proposed approach combines predictive-modeling with elements of CNS to delineate climate resilient refugia habitat for vulnerable species that may be missed by coarse-filter strategies. Refugia are defined as areas that enjoy some degree of buffering against climate change; thus, in such areas, the *in situ* climate state experienced on the ground deviates from regional trends (Dobrowski, 2010; Keppel et al, 2015; Morelli et al, 2017). Habitat that occurs within these resilient refugia sites can be expected to remain suitable over longer time periods than habitat which occurs in non-resilient areas. Consequently, resilient habitat sites represent good candidates for new protected core protected areas or mixed-use forest management strategies. We illustrate the application of our approach through an analysis to identify the most resilient Olive-sided Flycatcher (*Contopus cooperi*) habitat in the province of Nova Scotia, Canada.

In brief, our approach involves 3 stages: (1) modeling patches of currently suitable habitat for the target species using an SDM that has been trained using a suite of topographic and forest covariates (this was done for the Olive-sided Flycatcher in chapter 3 of this thesis); (2) prioritizing suitable habitat patches according to landscape resilience scores (calculated using methods adapted from Anderson et al., 2012); and (3) overlaying these results onto a range shift model in order to identify resilient habitat that also coincides with current future range boundaries. Patches which meet all 3 criteria are considered to be areas of high priority "core" habitat, as greater confidence can be placed in the accuracy and stability of areas that are predicted to be suitable by multiple models using multiple definitions of resilience. Patches that meet the first 2 criteria may be considered patches of 'stepping stone' habitat, which can be important in maintaining functional connectivity in the shorter term and can facilitate northward migrations as ranges begin to shift. These areas may also be considered as potential cores in cases where the area and/or configuration of patches that meet all 3 criteria are insufficient to satisfy conservation goals (e.g. protecting a sufficient amount of habitat to support population viability), or when sociopolitical and/or economic factors make it impossible to protect patches that meet all 3 criteria.

The first 2 stages of our strategy each focus on a separate (but related) aspect of ‘resilience’. The first stage considers the cross-scale organization of ecological systems, which was originally theorized by Holling (1986). The phenomenon of cross-scale organization relates to resilience in that it regulates the ability of an ecosystem to support the same ecological structures and functions following disturbance. The second stage considers aspects of resilience which are a cornerstone of the CNS approach: i.e., topographic complexity and permeability. For the sake of clarity, in this chapter, we refer to resilience *sensu* Holling as “disturbance resilience” and to resilience *sensu* CNS as “landscape resilience”. However, note that we are both of these concepts relate to the ability of an area to provide a buffer against the effects of climate change.

While we acknowledge that it is not possible to guarantee the indefinite persistence of any specific, individual taxa, there is theoretical and historical evidence to suggest that securing the most resilient habitat patches on a landscape can increase both the likelihood and duration that a species persists in a region (e.g. Keppel et al., 2012; Gill et al., 2015). Nonetheless, our proposed strategy is not intended to replace existing conservation planning techniques that focus on protecting representative arrays of species and natural land cover types. Rather, the methods presented here aim to complement existing approaches by identifying critical refugia that can benefit key species by helping them persist in the midst of large-scale, long-term climate change (Keppel et al (2015) while simultaneously advancing broader (i.e. coarse-filter) conservation goals that benefit multiple species and ecosystems. Moreover, such resilient sites, or refugia, can also help maintain critical spatial and temporal connectivity as species undergo northward migrations in the face of changing temperature and precipitation regimes. We hope that the work presented here will help further the discussion about which conservation planning strategies will be the most effective in an era of climate change.

4.1.1 Scientific underpinnings of the proposed approach to refugia delineation

The scientific underpinnings of the current chapter are rooted in the works of C. S. Holling (1986), MacKay & Lindenmayer (2001), Hunter et al. (1988), and Anderson et al. (2012). The conceptual relationship between these earlier publications and our proposed approach to refugia delineation is discussed in greater detail over subsequent paragraphs.

Applying the concept of cross-scale ecosystem organization to species distribution modeling. According to Holling (1986) and Mackay & Lindenmayer (2001), the structure and function of ecosystems are regulated by a limited number of critical organizational scales, which correspond to natural breaks in the distribution and availability of primary environmental resources that control biological productivity: heat, light, water, and mineral nutrients. These scales are defined at the global-, meso-, topo-, micro-, and nano-levels, and they represent ever-finer spatial and temporal variation in the delivery of water and energy (Holling, 1986; Mackay & Lindenmayer, 2001).

In brief, at the global-level, latitude, cloud cover, and levels of atmospheric CO_2 control solar energy inputs to climate and weather patterns. At the meso-level, interactions between prevailing weather systems and coarse-grain topographic elevation in-turn control long-term precipitation and radiation regimes, and geological substrates influence soil chemistry (Mackay & Lindenmayer, 2001). At the topo-level, slope, aspect, and topographic shading regulate the availability of meso-level precipitation, temperature, light, and nutrient inputs. In addition, the influence of surface morphology over catchment hydrology occurs at the topo-level, and this interaction has important consequences over where moisture and nutrients accumulate on the landscape. In a micro-level forest context, vegetation canopy has a critical influence over light, heat, water, and mineral nutrient availability for understory plants and animals. Finally, the nano-level describes sub-canopy conditions and processes, such as the composition (i.e.

living vs. dead) of woody biomass or nutrient cycling performed by soil microorganisms (Mackay & Lindenmayer, 2001).

Although Mackay & Lindenmayer (2001) did not address the implications of their theories on resilience, a key concept to emerge from Holling's framework is that the hierarchical structuring of environmental processes can be used to identify the most resilient ecosystems in a landscape (i.e. those least likely to be irreversibly impacted by disturbance; Holling, 1986). This is possible because large-scale conservative structures maintained at higher levels of the environmental hierarchy stabilize and conserve successful ecosystem configurations, and thus, following disturbance, they encourage a natural system to reorganize with the same key structures, processes, and feedbacks (Holling & Gunderson, 2002).

In the previous chapter, we delineated disturbance-resilient (sensu Holling, 1986), landscape-scale breeding habitat for the Olive-sided Flycatcher in Nova Scotia, Canada, by developing a maximum entropy (Maxent) model using both topo- and micro-level covariates. (Note that, from a CNS perspective, topo- and micro-level covariates can be considered abiotic and biotic features of the environment, respectively.) Global-, meso-, and nano-level covariates were not considered as they affect scales that are not relevant to provincial SDMs.

Prioritizing habitat patches according to landscape resilience scores. The CNS approach was first proposed by Hunter et al. (1988) (then named the coarse-filter approach), who summarized paleoecological evidence to show that communities are not internally-regulated natural systems resulting from millions of years of co-evolution. Rather, they are relatively ephemeral entities that comprise transitory assemblages of species whose abundances, distributions, and associations change in response to large-scale climatic shifts. Like Holling et al. (1986), those researchers cited the influence of geophysical factors over species' distributions and further noted that, during previous periods of global climate change, diverse geophysical environments were able to support diverse arrays of species. Hunter et al. (1988) therefore proposed that a coarse-filter approach which protects a comprehensive representation of geophysical environments (e.g. as defined by topography, soils, and climate) should be more effective at maximizing the long-term persistence of biodiversity than a coarse-filter approach which seeks to protect a comprehensive representation of ecological communities (the dominant conservation planning strategy of that time).

The potential utility of the CNS approach was corroborated by Anderson & Ferree (2010), who provided empirical evidence to confirm that geophysical diversity was highly correlated with species diversity, and by Gill et al. (2015), who used 2.6 million years of paleoecological data to demonstrate how, although previous periods of large-scale climate change caused many local extirpations, global extinctions were relatively rare. This was likely because (1) geophysical settings were diverse enough that refugial populations of species were able to persist in place (Keppel et al., 2012), and (2) a lack of dispersal barriers allowed species range shifts' to keep pace with shifting climate envelopes (Prentice et al., 1991).

In 2012, Anderson et al., working for The Nature Conservancy, applied the CNS approach in a conservation planning exercise across the northeast coast of the US and the Maritime provinces of Canada. For that, researchers first classified 1000-acre (404.7-ha) sites according to geophysical setting (which was in-turn defined by elevation zone, geology class, and landform type). Then, sites that (1) belonged to the same geophysical setting and (2) fell within the same ecoregion were prioritized using landscape resilience scores. Landscape resilience scores were themselves defined according to landscape complexity (i.e. the number of micro-climates present in a single site; a function of landform variety, elevation range, and wetland density) and landscape permeability (i.e. the degree to which a landscape supports species' movement and sustains ecological processes).

In this current study, we used methods modified from Anderson et al. (2012) to calculate landscape resilience across the province of Nova Scotia. We then used these scores to prioritize the patches of disturbance resilient Olive-sided Flycatcher habitat that had been identified in chapter 3.

4.2. Methods

4.2.1 Study area and study species

Our study area was Nova Scotia (45° N, 63° W, Figure 2.1), a Maritime province of southeastern Canada that lies on the Atlantic migratory flyway and contains the easternmost breeding habitat of the Olive-sided Flycatcher. A description of the demographics, topography, and land-use/land-cover that characterize the province is provided in chapters 2 and 3 of this thesis.

The Olive-sided Flycatcher (*Contopus cooperi*) is a neotropical migrant with widespread breeding habitat in Acadian and Boreal forests. Although both Nova Scotia and Canada appear to contain an abundance of suitable breeding habitat at first glance, this bird has shown widespread and persistent population declines across the breeding range, 54% of which is found in Canada (i.e. the bird declined by 79% between 1968 and 2006, and by 29% between 1996 and 2006; COSEWIC, 2007.) These losses have resulted in the Olive-sided Flycatcher being designated as "threatened" in the Canadian federal species at risk registry (COSEWIC, 2007). A more detailed description of habitat preferences exhibited by the Olive-sided Flycatcher is available in chapter 3 of this thesis.

4.2.2 Delineation of disturbance resilient patches of Olive-sided Flycatcher habitat in Nova Scotia

Suitable patches of disturbance-resilience Olive-sided Flycatcher habitat were delineated using the provincial Maxent model that was developed in chapter 3. In brief, that model was created using a reverse stepwise elimination process, whereby Akaike's Information Criterion (corrected for small sample sizes; AIC_c) was used to identify the forest (micro-level) and topographic (topo-level) covariates (out of 10 possible candidates) that most strongly influence the distribution of Olive-sided Flycatcher habitat in Nova Scotia at the landscape-scale. The final Olive-sided Flycatcher model contained 5 covariates, including (listed in order of importance): mean canopy height in a 2.25 ha area, standard deviation of canopy height (which describes variability in canopy height) in a 2.25 ha area; distance to coniferous stand; topographic position; and distance to stand with dead material.

In the current chapter, we converted the continuous habitat suitability surface predicted by the aforementioned Maxent model into a binary surface delineating the presence and absence of suitable Olive-sided Flycatcher habitat using the 'Equal Sensitivity and Specificity' threshold, which was the most conservative threshold among those suggested by Maxent software. Then, as the Olive-sided Flycatcher is known to have a fairly large territory size (i.e., between 10 – 20 ha; Altman and Sallabanks, 2012), and as larger patches tend to be more resilient than smaller ones, we rejected patches that measured less than 20 ha as unsuitable, even if these areas had a suitability score that was above the Equal Sensitivity and Specificity threshold.

4.2.3. Creation of a landscape resilience index for Nova Scotia

We generated a landscape resilience index for Nova Scotia using methods adapted from Anderson et al. (2012). The generation of this index involved 2 phases: (1) creating a layer to delineate landscape complexity; and, (2) creating a layer to delineate landscape permeability. (Note that, while the original work by Anderson et al. also included Nova Scotia, our analysis was performed at a finer-resolution.) These layers were then combined to determine overall landscape resilience scores. All analyses were performed using ArcMap 10.2.2 software and tools contained therein (Environmental Systems Research Institute (ESRI), 2014). All datasets used in the creation of these layers were provided by the Nova Scotia Department of Natural Resources (NSDNR).

Our study area (55,284 km^2) was much smaller than the 13 state and 3 province region considered by Anderson et al. (2012). Therefore, to address landscape resilience at a finer-resolution than those researchers, we employed smaller cell (analytical unit) and neighbourhood sizes. Down-scaling had practical advantages as well. Specifically, the digital elevation model (DEM) produced by NSDNR (2006), which is the base layer we used in the determination of landscape complexity, had a smaller cell size than that of the smallest analytical unit used by Anderson et al. (2012) (i.e. 20 m versus 30 m).

4.2.3.1 Delineating landscape complexity

We derived landscape complexity scores from 3 indices: (1) landform variety, (2) elevation range, and (3) wetland density. Landforms describe natural surface features that are created by the topographic shape of the landscape (e.g. cliffs, valleys, slopes, coves, etc.) (Anderson et al., 2012). These features express local solar radiation and, even when climate is not considered, regulate species distributions edaphically through their control over erosion and deposition rates, soil texture and depth, and nutrient and moisture availability. A greater variety of landforms not only increases the likelihood of species' persistence by providing a larger number of micro-climates in an area, but also serves as a buffer against the effects of climate change (Anderson et al., 2012; Dobrowski, 2010).

Landform variety. To delineate landform variety, we used a 20 m topographic position index (TPI). This layer had been created for our previous SDM study (in chapter 3) and was derived from the 20 m Nova Scotia DEM (NSDNR, 2006). Originally, this index distinguished among 5 topographic positions: valleys, low-slopes, mid-slopes, up-slopes, and ridgetops. However, the TPI employed by Anderson et al. (2012) (called a land position class index by those researchers) only distinguished among 4 topographic positions. Therefore, for the current research, we combined the up-slopes and ridgetops from our original index into a single class. We opted to combine the top 2 topographic positions (i.e. as opposed to valleys and low-slopes) because Nova Scotia is mostly flat and because a visual examination of the modified TPI overlaid on a hillshade DEM revealed that combining the higher topographic positions generally yielded a more accurate index than did combining the lower ones.

We then used the DEM to create a 20 m slope map over Nova Scotia and combined this with the TPI to delineate 10 landform types, in accordance with Anderson et al. (2012). Specifically, these were: cliff or steep slope (any area with a slope between 24-90°), slope crest (ridgetop/up-slope with a slope between 6-24°), flat ridgetop (ridgetop/up-slope with a slope between 0-6°), rounded ridge (mid-slope with a slope between 6-24°), gentle hill (mid-slope with a slope between 2-6°), hilltop (mid-slope with a slope between 0-2°), lower sideslope (low-slope with a slope between 6-24°), toe slope (low-slope with a slope of 2-6°), flats (low-slope with a slope of 0-2°), and cove or slope-bottom (valley with a slope between 0-35°). Slopes were then further sub-divided according to aspect (i.e. northeast or southwest), and flats were further subdivided by flow accumulation (i.e. wet or dry), for a total of 12 landforms (Figure 4.1). We subsequently performed a focal variety analysis to determine the number of landforms within a 27 ha circular neighbourhood. (This number was selected so that the ratio of cell size to neighbourhood size matched that used by Anderson et al. (2012)).

Elevation range. As climate changes, species ranges may shift, increase, or decrease in concert with elevation. This is particularly true in mountainous or hilly landscapes, where slopes can magnify the effects of a changing climate (Anderson et al., 2012). To determine local elevation ranges within Nova Scotia, we performed a focal range analysis on the same 27 ha circular neighbourhood as that used in the aforementioned landform variety analysis. As elevation range values were highly skewed towards zero, we log transformed this data prior to further analysis.

Wetland density. A large portion of Nova Scotia is wet and flat as a result of past glaciations. In flat areas, Anderson et al. (2012) suggest that using landform variety and elevation range alone is insufficient to delineate landscape complexity. They therefore recommend that wetland density be used to infer micro-scale topographic diversity and freshwater accumulation patterns, positing that areas of high wetland density should have higher levels of topographic variation, and that small, isolated wetlands are at greater risk of shrinkage or disappearance. To create a wetland density index, we calculated the density of wetlands within 27 ha and 270 ha neighbourhoods (with this size again selected to match the ratios used by Anderson et al., 2012) using the provincial wetland inventory (NSDNR, n.d.). We then combined these fine- and coarse-scale wetland density values to obtain a single wetland density index, whereby the fine-scale values were given twice the weight of the coarse-scale values.

Finally, the landform variety, elevation range, and wetland density indices were normalized by Z-score and combined (using the equation shown below) to obtain a final landscape complexity index (Anderson et al., 2012). However, in creating this index, note that wetland density values were only applied to relatively flat landforms (i.e. landforms with a slope between 0-6°: flats, flat hilltops, and flat ridgetops), where wetlands could reasonably be expected to occur.

Landscape complexity:
Flat areas = (2*Landform variety + 1*elevation range + 1*wetland density)/4
Incline areas = (2*Landform variety + 1*elevation range)/3

4.2.3.2 Delineating landscape permeability

In this study, landscape permeability was defined as the degree to which the landscape is able to support species movement and sustain ecological processes (Meiklejohn et al., 2010; Anderson et al., 2012). Landscape permeability is a measure of landscape structure, and describes the hardness of barriers and the connectedness of natural cover. Due to time and data constraints we performed a relatively simple landscape permeability analysis in this study. Specifically, we calculated road density in the same 27 ha neighbourhood used in the calculation of landform variety and elevation range. Road density values were then normalized by Z-score. A visual overlay revealed that our road density layer had good similarity with the landscape permeability layer that Anderson et al. (2012) produced using a more complex analysis (Figure 4.2).

4.2.4. Delineating overall landscape resilience

To delineate overall landscape resilience in the province of Nova Scotia, we combined scores from the landscape complexity and road density (i.e. landscape permeability) indices. As high landscape complexity scores were considered ‘good’ and high road density scores were considered ‘bad’, the overall landscape resilience index was calculated by subtracting road density scores from landscape complexity scores. Finally, the overall landscape resilience index was again normalized according to Z-Score.

4.2.5. Prioritization of Olive-sided Flycatcher patches and delineation of climate refugia

To prioritize suitable patches of Olive-sided Flycatcher habitat in Nova Scotia, we first determined the extent to which each patch contributes to the resilience of the overall landscape. This was achieved by calculating mean landscape resilience scores; i.e., by averaging the landscape resilience scores of all cells in a given patch. Following this, patches were binned into 7 categories by comparing the landscape resilience score of each patch to that of the overall landscape (using standard deviation; STD): far below average (<-2 STD), below average (-1 to -2 STD), slightly below average (-0.5 to -1 STD), average (-0.5 to 0.5 STD), slightly above average (0.5 to 1 STD), above average (1 to 2 STD), and far above average (>2 STD).

The categorized patches were then overlain onto range-shift models that predicted Olive-sided Flycatcher range boundaries for the years 2020, 2050, and 2080 under 3 IPCC emissions scenarios (i.e., A1B, A2, and B2; Table 4.1). These range shift models were generated by the National Audubon Society (2014) at a 10 km resolution (i.e. the analytical unit size) using boosted regression trees, bird data (collected between 1999 and 2008) from the Audubon Christmas Bird Count and the North American Breeding Bird Survey, and temporally matched data for 17 biologically relevant climate variables (for a complete description of modeling processes used in that work, see National Audubon Society 2013, 2014). To ensure the highest confidence in modeled range boundary predictions, for the years 2020 and 2050, we only considered areas that were predicted to remain within the bird’s climatically suitable range under all emissions scenarios. By the year 2080, only scenario B2 predicted that climatically suitable areas would remain in Nova Scotia, and so we did not consider the other 2 emissions scenarios.

Upon completing this overlay, we identified habitat patches that could be considered potential core areas and highest priority climate refugia for the Olive-sided Flycatcher. Specifically, these were patches that (1) had landscape resilience scores that were in the 'above average' or 'far above average' categories, and (2) fell within the range boundaries agreed upon by all Audubon models (i.e. models produced for the A1B, A2, and B2 scenarios) through at least 2050 or by the Audubon model for scenario B2 through 2080.

4.3. Results

4.3.1. Resilient landscapes in Nova Scotia

The landscape resilience index that we produced for this study showed a normal distribution and was qualitatively similar to the coarser-scale index produced by Anderson et al. (2012) (Figure 4.3). Both resilience indices reveal that large contiguous areas with high landscape resilience scores (i.e. in the 'far above average' or 'very far above average' categories) occur in the northern part of Cape Breton Island, which is itself the northernmost part of Nova Scotia (Figures 4.4a and 4.4b). Indeed, according to our index, of the 10 largest contiguous highly resilient areas, 5 occur in northern Cape Breton, including the 3 largest such areas (Figure 4.4b). In addition, 9 of the 10 largest contiguous highly resilient areas occur within and adjacent to existing protected conservation lands. The only large, highly-resilient area that is completely isolated from existing protected land is an irregularly shaped patch in Port Bickerton (the 4th largest resilient area), located in the northeastern Nova Scotia mainland (Figure 4.4a).

Like Anderson et al. (2012), we also found that the areas with the lowest landscape resilience scores occurred around (1) major urban centers (Halifax - the provincial capital, Dartmouth, and Sydney) and (2) major highways (highways 101, 102, and 103), which run through the center of the province and the Annapolis valley (Figure 4.3).

4.3.2. Resilient Olive-sided Flycatcher habitat patches

According to the Maxent model developed in chapter 3 of this thesis, Olive-sided Flycatcher habitat is well distributed in Nova Scotia, covering approximately 49% of the provincial landmass (Figure 4.5a). However, only around 1% of the provincial landmass contains Olive-sided Flycatcher patches with landscape resilience scores that are far above or very far above average (highly resilient patches, hereafter) (Figures 4.5b and 4.6a). Unsurprisingly, large, highly resilient Olive-sided Flycatcher patches tend to occur in and adjacent to existing conservation lands in northern Cape Breton Island (Figure 4.6b). Indeed, of the top 10 largest resilient patches, 7 are found in Cape Breton, with the 3 largest patches occurring within the federally protected crown land of Cape Breton Highlands National Park and the 4th largest patch occurring in the provincially protected Polletts Cove—Aspy Fault Wilderness Area directly to the north. The 5th largest patch is located on unprotected land that connects Cape Breton Highlands National Park with the Jim Campbell Barrens Wilderness Area and the Margaree River Wilderness Area. The 7th largest patch is located next to the French River Wilderness Area, also in Cape Breton (Figure 4.6b).

The 3 large, highly resilient Olive-sided Flycatcher patches that occur on the Nova Scotia mainland are also found on existing protected conservation land, located near the northeastern coastline. In the interior of the province, Olive-sided Flycatcher habitat tends to be characterized by lower landscape resilience scores; however, small isolated patches with landscape resilience scores that are far above or very far above average do exist (Figure 4.6a). The number and average size of resilient Olive-sided Flycatcher patches in various parts of the province are summarized in Table 4.2.

4.3.3. Overlay of highly resilient habitat with range shift models

Range shift models produced by the National Audubon Society (2014) under all 3 emissions scenarios (A1B, A2, and B2) predict that, through 2020, fairly large areas will remain climatically suitable for the Olive-sided Flycatcher in the southernmost and northernmost parts of Nova Scotia, including Cape Breton Island (Figure 4.7a), and that a smaller area will persist in the Terence Bay Provincial Wilderness Area (located around the eastern coastline). By 2050, all 3 of the Audubon range shift models predict that Olive-sided Flycatcher habitat will have contracted to Cape Breton in northern Nova Scotia and completely disappeared in both southern Nova Scotia and in the Terence Bay Provincial Wilderness Area (Figure 4.7b). Only 1 range shift model (i.e. that created for emissions scenario B2) predicts that areas which are climatically suitable for the Olive-sided Flycatcher will persist in Nova Scotia through the year 2080, specifically: 2 areas measuring 100 km^2 in Cape Breton (i.e. the analytical unit size of the Audubon study) (Figure 4.7c).

Areas that were predicted by Audubon models to be climatically suitable for the Olive-sided Flycatcher through 2020 and 2050 under all 3 emissions scenarios intersect the 7 large, contiguous, highly resilient habitat patches in Cape Breton that were identified in the previous section (i.e. Figure 4.8). None of these habitat patches intersect the range areas predicted for the Olive-sided Flycatcher in 2080 under emissions scenario B2. However, 8 smaller resilient patches occur in 1 of those range areas, and 3 of these occur within Cape Breton Highlands National Park (Figure 4.8).

4.4. Discussion

In this study, we developed a novel resilience-based approach to single-species conservation planning that can be used to identify critical climate refugia for a target species while also benefitting coarse-filter conservation goals. We applied our approach in a conservation planning exercise that focused on identifying highly resilient habitat for the Olive-sided Flycatcher in the province of Nova Scotia. Over the following, we discuss (1) the spatial distribution of resilient areas and habitat patches, (2) implications for Olive-sided Flycatcher conservation and core area prioritization, and (3) the potential importance of resilient areas outside predicted range boundaries, and (4) the strengths and limitations of our proposed approach.

4.4.1. Spatial distribution of resilient areas and habitat patches in Nova Scotia

As noted in the Results section, nearly all large, contiguous resilient areas in Nova Scotia occur on land that has already been granted some form of protection status (Table 4.2, Figure 4.4). The coarser-scaled analysis by Anderson et al. (2012) reported similar findings, both in Nova Scotia and throughout their entire study area. An examination of the underlying layers that were used to derive our finer-scale resilience index (i.e. landform variety, elevation range, wetland density, and road density) revealed that the far-above and very-far-above average scores which occur on existing protected lands largely result from the low road densities that characterize these areas. This is not surprising, as securing land from development tends to maintain or even improve landscape permeability (Anderson et al., 2012). Protected lands also tend to be characterized by above average wetland density scores due to the recognized ecological importance of these areas as well as the difficulties and expenses associated with infrastructure development and silviculture harvesting on water-logged soils (Beazley, personal comm.).

According to our analysis and that of Anderson et al. (2012), the highest landscape resilience scores in Nova Scotia are found within and adjacent to protected conservation land in the northern part of Cape Breton Island: Cape Breton Highlands National Park, Polletts Cove—Aspy Fault Wilderness Area, and the French River Wilderness Area (Figure 4.4b). Indeed, of the 1% of Nova Scotia land that contains highly resilient Olive-sided Flycatcher habitat, approximately 63% is found in northern Cape Breton Island (Figures 4.5b, 4.6a, and 4.6b). The fact that these areas received higher resilience scores than protected land in other parts of Nova Scotia can primarily be explained by the larger elevation ranges that distinguish Cape Breton Island from the rest of the province. Mountains, such as those found in the Cape Breton highlands, support over 25% of terrestrial biodiversity worldwide and often contain patchy habitat and steep climatic gradients. Indeed, the high topographic and elevation diversity that characterizes Cape Breton (and regions like it) serves to parse regional climate patterns into variable local-scale microclimates, providing species with numerous opportunities to move as climate changes (Dobrowski et al., 2012). Protecting areas with large elevation ranges makes strong pragmatic sense as well, as such areas are more expensive to develop and are not conducive to road construction, silviculture harvesting, and other resource extraction applications (Beazley, pers. comm.).

Furthermore, in complex, mountainous landscapes, the phenomenon of cold air pooling is common and widespread (Dobrowski et al., 2012), whereby cold air pools in low topographic positions. (Note that the Maxent model presented in chapter 3 indicated that Olive-sided Flycatchers tend to occur in valleys or along slope bottoms). Cold air pooling can shelter affected areas from regional advective influences and lower minimum temperatures (which have increased almost twice as fast as maximum temperatures over the past century; IPCC, 2007). These effects act to decouple the local *in situ* climate from the regional climate, thereby providing a buffer against climate change and making low topographic positions in complex landscapes particularly probable candidates for the persistence of refugia (Dobrowski et al., 2012).

4.4.2. Implications for Olive-sided Flycatcher conservation planning

Areas of Olive-sided Flycatcher habitat that are currently suitable, highly resilient, and also predicted to overlap future range boundaries comprise key conservation areas for this species in a context of climate change. These climate refugia should help support refugial populations that have the potential to expand and colonize newly formed habitat patches should climatic conditions once again become suitable (Keppel et al., 2015). Indeed, this process is predicted to have occurred at the end of the last ice age, and has been proposed as a partial explanation as to why so few extinctions occurred during the most recent historical period of rapid climate change (Keppel et al., 2012; Gill et al., 2015). Such areas can also enhance functional connectivity by providing ‘stepping-stone habitat’ at the continental scale, which should facilitate spatial movements.

Based on this rationale, we recommend that the areas of Nova Scotia which were found to meet all conservation criteria (i.e. suitable, resilient, and part of both the current and future Olive-sided Flycatcher range) be targeted as conservation priorities. Specifically, we recommend targeting the following areas as core Olive-sided Flycatcher habitat: (i) the highly resilient Olive-sided Flycatcher patch that connects Cape Breton Highlands National Park with the Jim Campbells Barren Wilderness Area, (ii) the highly resilient Olive-sided Flycatcher patch that occurs to the southeast of the French River Wilderness Area, and (iii) the land that lies south of the central-southern border of Cape Breton Highlands National Park and includes the 2 small, highly resilient Olive-sided Flycatcher patches (Figure 4.9). All priority areas occur within the 2000, 2020 & 2050 Olive-sided Flycatcher range boundaries predicted under all emission scenarios, and the area to the south of the central-southern border of Cape Breton Highlands National Park is also spatially coincident with the 2080 Olive-sided Flycatcher range boundary predicted under emissions scenario B2 (National Audubon Society, 2014). Note that, because these areas were characterized by high landscape resilience scores, protecting them should benefit not just Olive-sided Flycatchers but other endemic species as well.

4.4.3 Potential importance of resilient areas outside of predicted future range boundaries

The stability (i.e. buffering capacity) of a refugial site is dependent on a variety of factors, including local climate (Keppel et al., 2015). While resilient habitat that exists outside of future range boundaries are not likely to persist as long as resilient habitat within future range boundaries, such areas are nonetheless likely to serve as refugia over the shorter term. Shorter-term refugia are important to conservation. Firstly, such areas enhance functional connectivity by providing ‘stepping-stone habitat’ at the continental scale, which can help facilitate spatial movements from southern to northern latitudes and help provide connectivity across time as climate conditions change.

Note that, for our specific species in our specific study area, additional “stepping-stone” habitat may not be required, as species with long dispersal distances do not typically depend on intermediate stepping stones to reach other core areas (Saura and Rubio, 2010; Gil-Tena et al., 2012). Although the maximum dispersal distance travelled by Olive-sided Flycatchers is not known (Altman and Sallabanks, 2012), the bird’s status as a neotropical migrant with a large territory size suggests that it is likely to be substantial (Paradis et al., 1998). Therefore, we suspect that preserving stepping-stone patches is less critical to Olive-sided Flycatcher conservation in a study area the size of Nova Scotia. Furthermore, given that most of the existing protected areas on the Nova Scotia mainland already contain resilient Olive-sided Flycatcher habitat (Figure 4.6), investing funds to maintain additional “stepping-stone” patches may not represent the most efficient use of limited financial resources.

Nonetheless, landscape connectivity is a species specific phenomenon, wherein the same landscape can be perceived as connected or disconnected by different species with different life history traits (Rubio & Saura, 2012). Even within future range boundaries, the effectiveness of refugial habitat largely depends on accessibility (Keppel et al., 2015). Therefore, while functional connectivity for the Olive-sided Flycatcher may not require that smaller patches of evenly distributed residual habitat remain well distributed along the entire north-south plane of the province, other species do undoubtedly need such areas to successfully reach and colonize more northerly habitat. For example, in a study by Saura et al. (2014), stepping-stone habitat greatly increased the maximum distance that an endangered bird species in Spain was able to traverse in colonizing a new area, provided that the patches of stepping-stone habitat were of sufficient quality and size. Indeed, for species with poorer dispersal abilities, resilient stepping-stone patches (or continuous corridors) are likely to be essential in facilitating migration across highly fragmented landscapes (Saura et al., 2014) and therefore in promoting their long-term persistence.

Secondly, while numerous large areas of resilient Olive-sided Flycatcher habitat fell within both current and future range boundaries in Nova Scotia, this will not be the case for all species in all study areas. In instances where (1) the amount and/or spatial configuration of habitat patches which meet all 4 conservation criteria are insufficient to meet species' survival and movement requirements or (2) if other stakeholder concerns make the conservation of highest priority areas impossible, resilient patches outside of predicted range shift boundaries should also be considered as potential core habitat areas.

4.4.4. Advantages of proposed approach

A key advantage of the refugia delineation method introduced in this chapter is that it reduces the uncertainty associated with single-species conservation planning in an era of climate-change. By prioritizing patches that have been identified as suitable by multiple models under multiple definitions of resilience, the likelihood that protected core areas will retain suitable habitat for the target species amidst long-term climate change increases. For example, Austin & Van Niel (2011) found that SDMs which had been generated using climate covariates alone were often unable to identify potential refugia and tended to under-predict the amount of suitable future habitat. Moreover, in both that study and another by Luoto & Heikkinen (2008), models generated using both climate and topographic covariates were found to be more reliable and have greater explanatory power than models generated using climatic covariates alone. Furthermore, due to inevitable deficiencies in GIS data and the increasing complexity of modeling methods, both SDMs and range shift models tend to suffer from uncertainty and error, and these issues can be severe in some cases (Hunter & Goodchild, 1997; Yackulic et al., 2013; Stralberg et al., 2015). Indeed, there are often discrepancies in habitat areas predicted by models that have been conceptualized or parameterized differently.

In the current study, most of the highly resilient Olive-sided Flycatcher patches that we delineated on the Nova Scotia mainland fell outside the range boundaries predicted by the National Audubon Society (for all years); however, many (349 out of 581) Olive-sided Flycatcher observation points contained in the ACCDC dataset also fell outside predicted range boundaries for all years (including the years 2000 and 2020, the interval in which bird observations were made). We suspect that these errors are related to the coarse resolution of the Audubon models and the fact that these models only included climatic covariates; they did not consider covariates related to habitat and resource availability. It is therefore plausible to expect that, due to their high landscape resilience scores, some patches which were identified by our model but fell outside range boundaries predicted by Audubon could nonetheless remain suitable over the long-term. However, due to their smaller size, these highly resilient patches are likely only relevant when a finer resolution is considered than the 10 km cells employed by Audubon. Nonetheless, by combining results from multiple models that employed different definitions of future habitat suitability (i.e. based on range shift modeling and climate resilience, respectively), different scales, and different parameters, we were able to identify resilient Olive-sided Flycatcher habitat common to both current and future climate contexts, thereby reducing uncertainty and representing a more reliable conservation bet than habitat patches highlighted by a single model.

A second key advantage of our proposed method is that, by integrating fine-filter approaches to single-species conservation planning with the coarse-filter CNS approach of Anderson et al. (2012), the prioritized areas should help create opportunities for not only the target species, but for other taxa as well. Therefore, our approach allows conservationists to target individual at-risk species while hedging conservation bets in an uncertain future characterized by climate change. For example, even if the areas of Cape Breton that we proposed for protection (Figure 4.9) do not end up being suitable for the Olive-sided Flycatcher in 2050 and/or 2080, the high landscape resilience scores these areas received suggest that they can still contribute to the maintenance of overall biodiversity in Nova Scotia.

Thirdly, most of the resilient areas identified in this study and in that of Anderson et al. (2012) occur within or adjacent to existing protected areas (Figure 4.4). As land that has been secured against development tends to be characterized by good permeability and high complexity (Anderson et al. 2012), we expect that this trend will be present in other parts of the world as well. Moreover, several of the characteristics which confer good climate resilience (i.e. large elevation range, high wetland density) naturally discourage development and resource extraction, as logging, mining, and erecting human infrastructure tends to be more challenging on steep slopes and in waterlogged areas. Therefore, our proposed strategy should provide a relatively low-cost way to complement or justify existing conservation plans and can also help inform regional-scale connectivity planning by identifying important areas which (1) expand the spatial extent of currently protected land or (2) link multiple protected lands.

4.5. Limitations

As noted in chapter 3, some of the environmental data layers used to train our Olive-sided Flycatcher SDM contained errors. Although we took steps to minimize these errors, they could not be completely eliminated, which may have reduced the spatial accuracy of the Olive-sided Flycatcher patches that were delineated in the current work. Furthermore, the landscape resilience layer that was created for this study may have been similarly affected by errors in the Nova Scotia wetland inventory (Westwood et al., 2015). Nonetheless, nearly all spatial datasets suffer from some level of uncertainty or error (Chrisman, 1991), and by combining results of multiple modeling techniques, our refugia delineation strategy seeks to hedge against these inaccuracies.

In addition, while theoretical and historical evidence exists to support the utility of our proposed approach to conservation planning in an era of climate change, currently, empirical evidence does not. As noted by Beier et al. (2015), rigorously testing climate change adaptation strategies such as ours could require 50 to 100 years of repeated field observations, which is too slow and risky to be considered feasible. However, this research gap is not limited to the work presented here. Indeed, studies on climate change and biodiversity have thus far tended to be strongly focused around impact and vulnerability assessments, while investigations pertaining to the utility and feasibility of adaptation strategies have been minimal. Like Beier et al. (2015), we suggest that climate change research which compares and evaluates alternative adaptation strategies (e.g. in terms of cost, practicality, theoretical underpinnings, and likely outcomes) should greatly benefit the field of conservation planning.

4.6. Conclusions

Habitat loss and climate driven range shifts have precipitated a mass-extinction on a global scale. As human population growth and infrastructure development continues to exert pressure on remaining natural landscapes, more effective approaches to conservation planning and the delineation of conservation areas will be needed. Our proposed strategy leverages strengths of both fine- and coarse-filter techniques to identify climate refugia and promote connectivity over space and time while minimizing uncertainty and meeting multiple conservation goals. We posit that the areas identified through our strategy should support the maintenance of biodiversity in general while also promoting the persistence of species, in this case Olive-sided Flycatcher, that may not be adequately protected when a coarse-filter approach alone is used. However, we also recognize that, given the complex nature of both climate change and ecological systems, diverse and flexible conservation planning strategies are needed. Therefore, our proposed strategy is intended to reduce risk and uncertainty, and to complement, not replace, existing conservation planning techniques in a context of climate change.

4.7 Tables and figures

Table 4.1 Description of emissions scenarios (created by the Intergovernmental Panel on Climate Change; IPCC) that were adopted by the National Audubon Society in generating range shift predictions for North American birds. Descriptions were obtained from IPCC (2001).

IPCC Climate Change Scenario	Description
A1B	World characterized by rapid economic growth, increasingly efficient technologies that include both fossil and non-fossil based-energy sources, and a global population that peaks around 2050.
A2	Heterogenous world characterized by increased self-reliance, the preservation of local identities, regionally oriented economic development, slower technological change, and a continually increasing global population.
B2	World that emphasizes local solutions to economic, social, and environmental sustainability and is characterized by intermediate economic development, technological change that is less rapid but more diverse than that of scenario A1, and a global population that is continually increasing, albeit at a slower rate than that of scenario A2

Table 4.2 Number and average size of resilient Olive-sided Flycatcher patches in various parts of Nova Scotia.

Categorization of resilient Olive-sided Flycatcher patch	Number of resilient patches	Average patch size (ha) +/- STD
All resilient patches	586	92.0 +/- 368.5
Resilient patches, Cape Breton only	253	134.2 +/- 546.7
Resilient patches, mainland only	332	60.0 +/- 97.7
Resilient patches within all protected areas of Nova Scotia	211	166.0 +/- 601.4
Resilient patches outside all protected areas of Nova Scotia	375	50.3 +/- 62.1
Resilient patches in protected areas of Cape Breton only	126	212.3 +/- 762.0
Resilient patches outside protected areas of Cape Breton only	127	56.6 +/- 85.5
Resilient patches in protected areas of the mainland	85	97.4 +/- 171.4
Resilient patches outside protected areas of the mainland	247	47.1 +/- 45.5

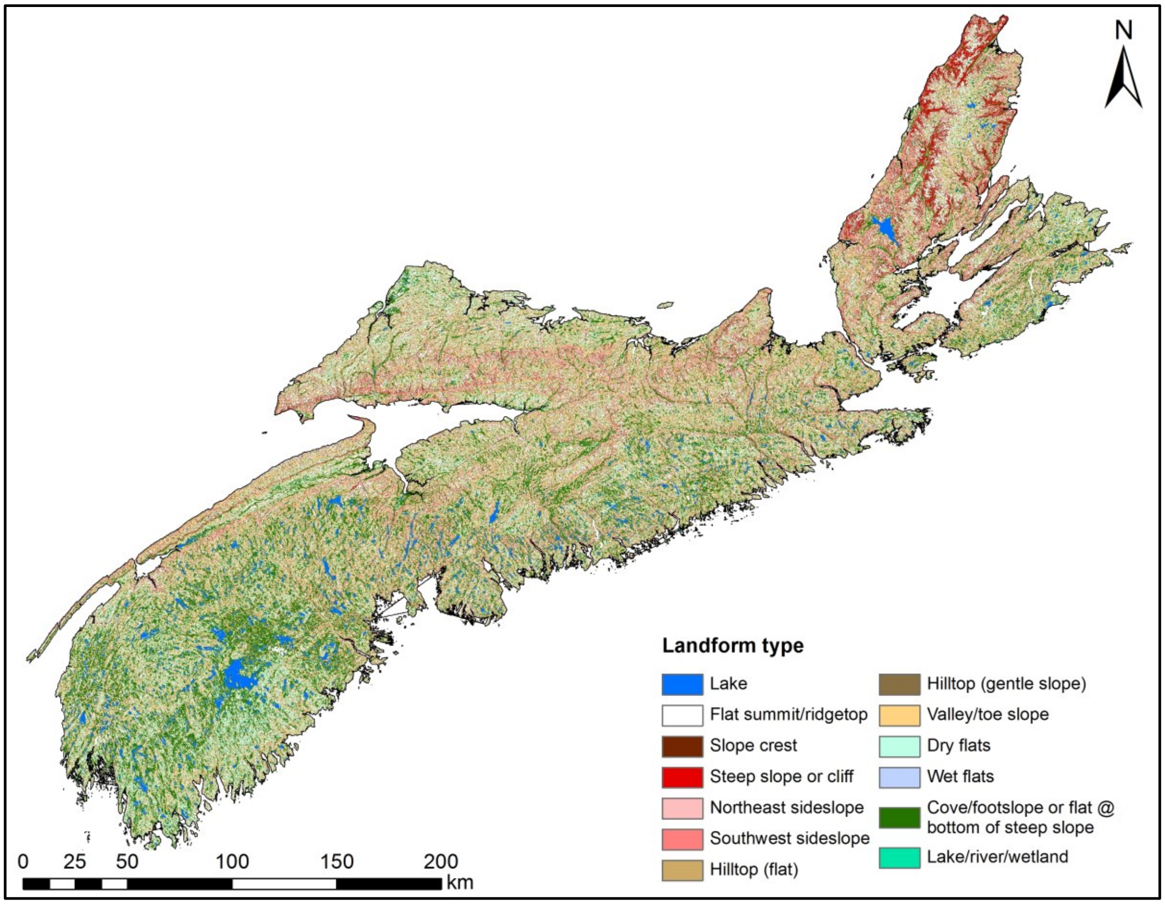


Figure 4.1 Landforms in Nova Scotia, delineated using methods from Anderson et al. (2012). Note that lakes are shown on this map for illustrative purposes only; they were not included in the landscape complexity analysis.

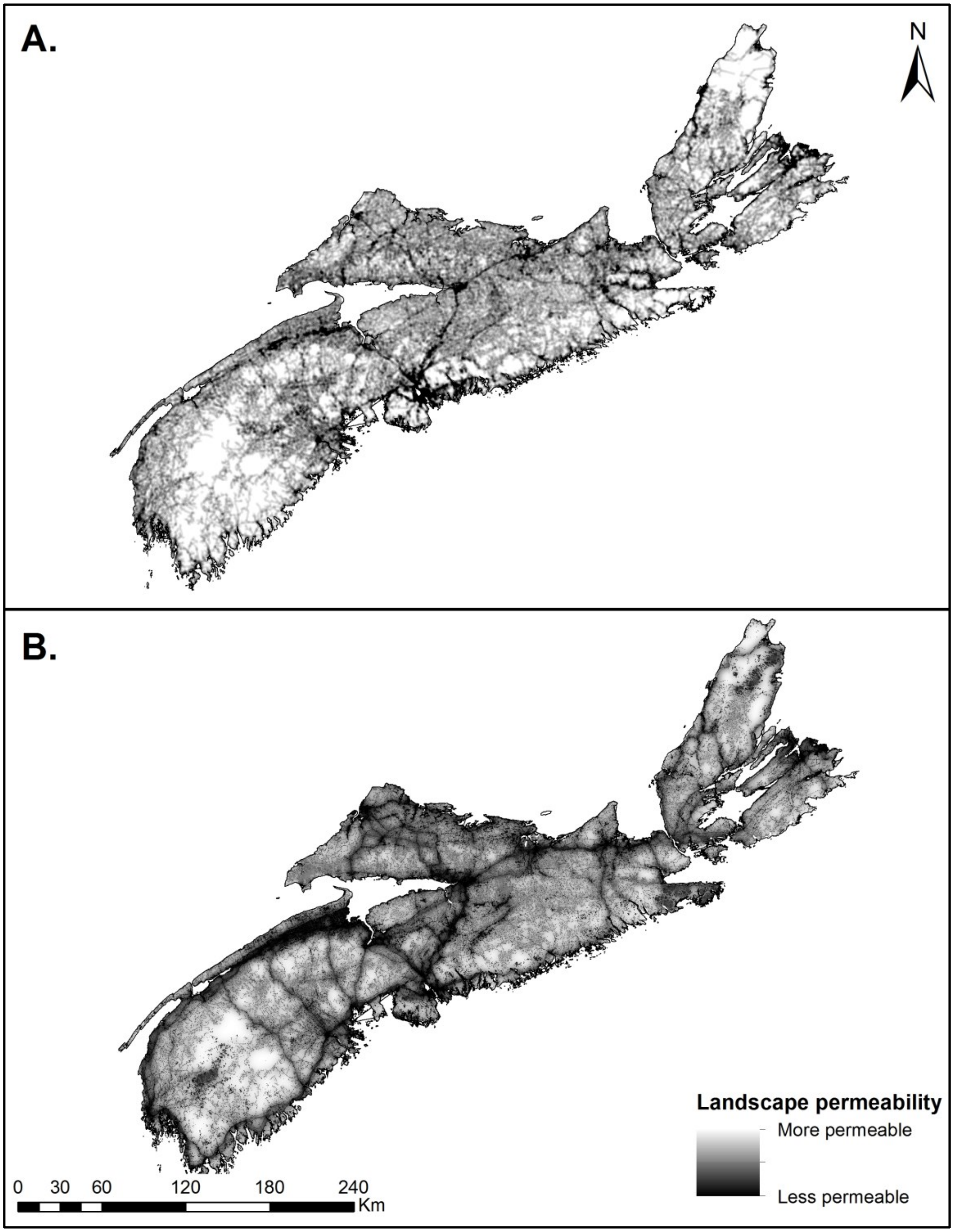


Figure 4.2: Landscape permeability defined according to (A) provincial road density and (B) an analysis of local connectedness by Anderson et al. (2012).

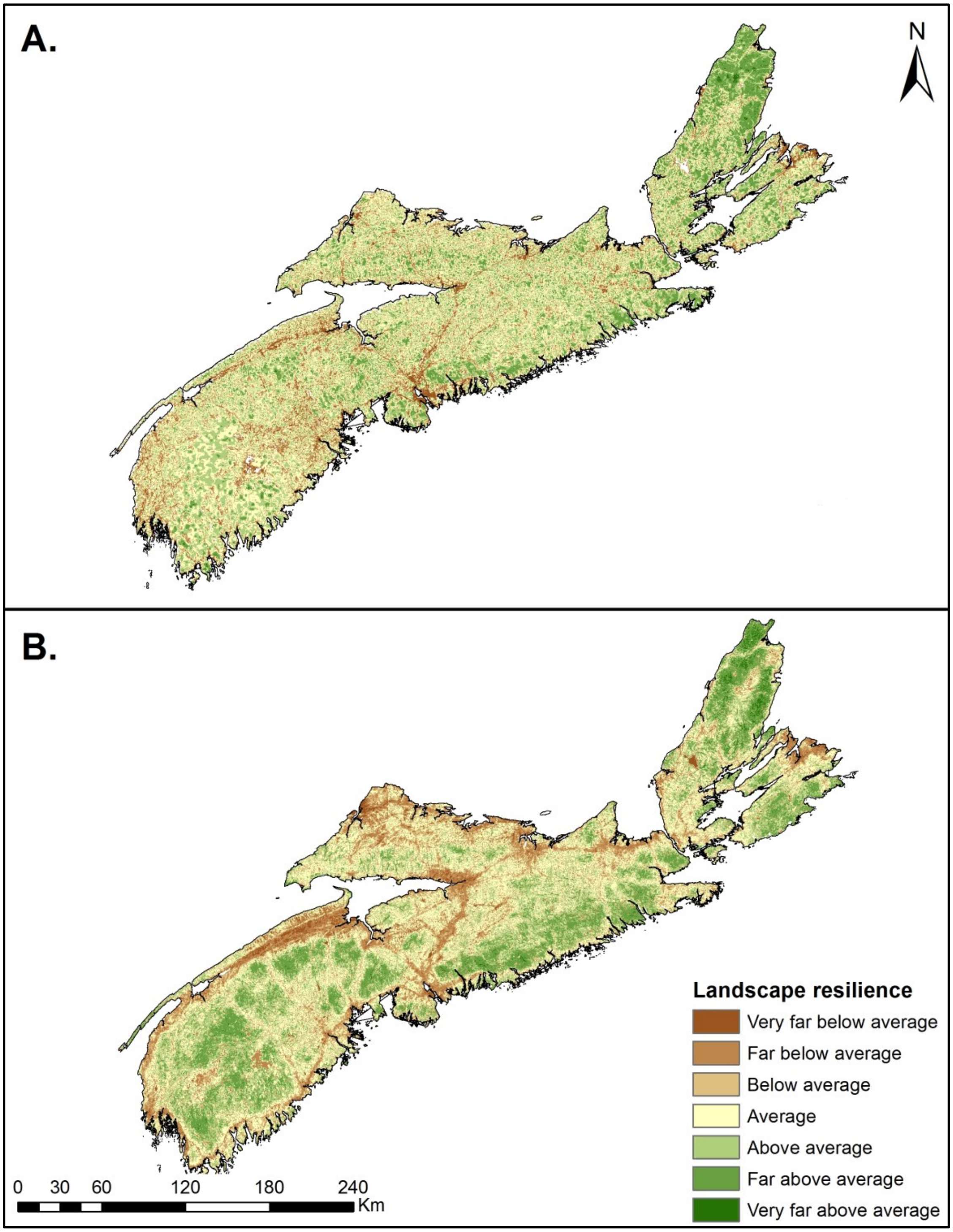


Figure 4.3: Landscape resilience analyses (A) conducted for the current study at a provincial (finer) scale and (B) conducted by Anderson et al. (2012) at a regional (coarser) scale.

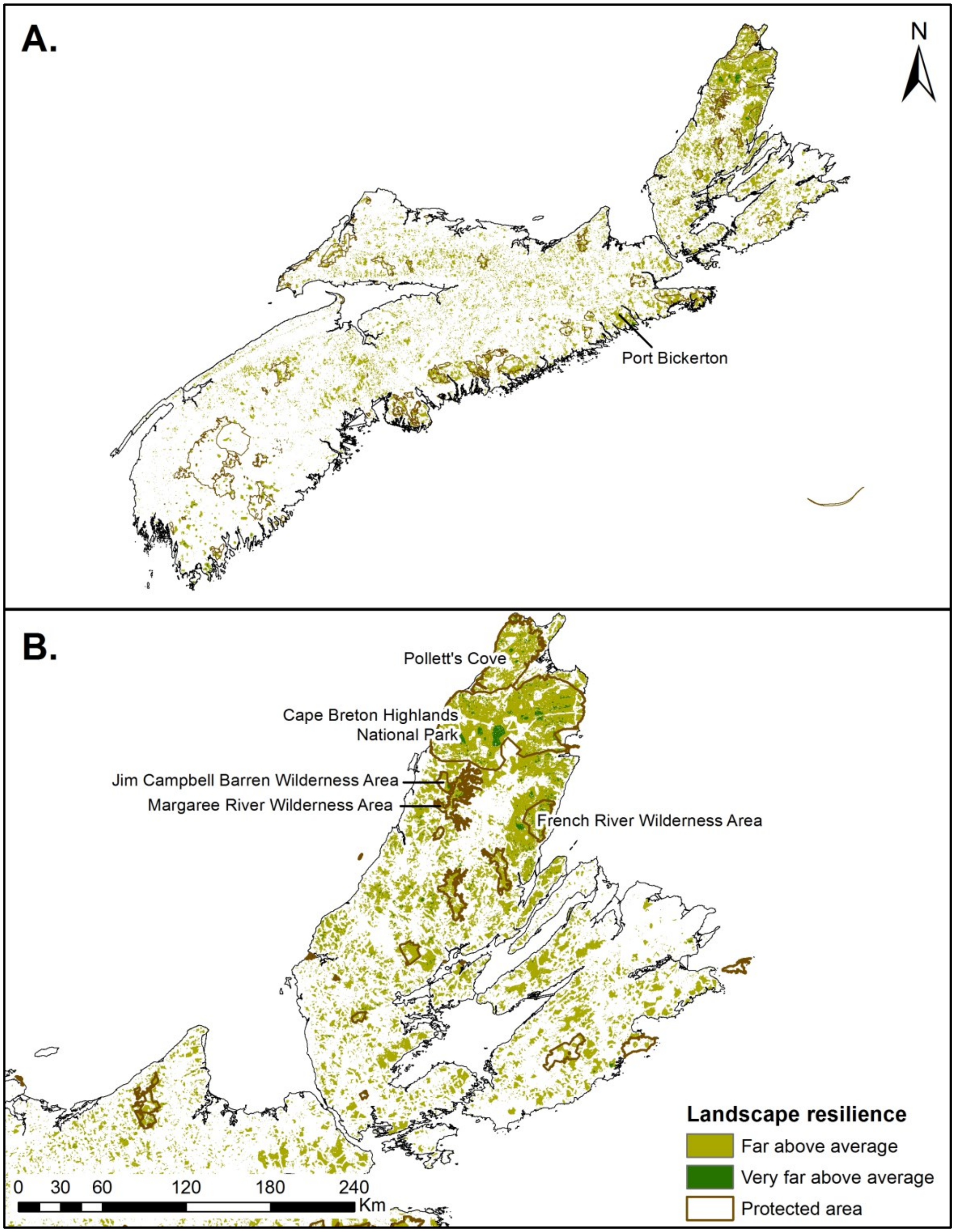


Figure 4.4: Areas in (A) Nova Scotia and (B) Cape Breton that received landscape resilience scores which were far above average (1-2 STD) or very far above average (>2 STD) in the provincial-scale resilience analysis.

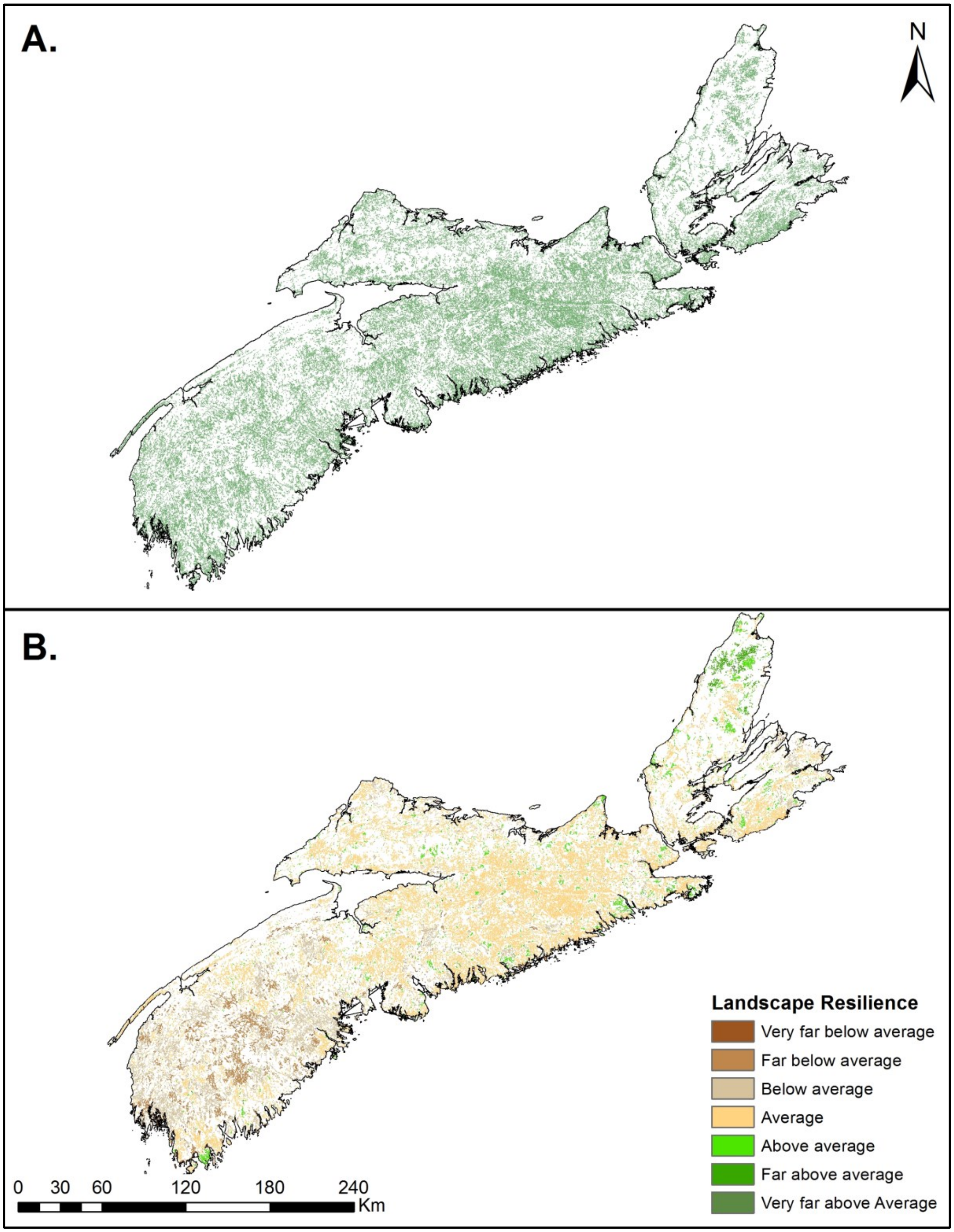


Figure 4.5: (A) Olive-sided Flycatcher patches delineated using a Maxent model (see chapter 3) and the equal sensitivity and specificity threshold; (B) Olive-sided Flycatcher patches by mean landscape resilience class.

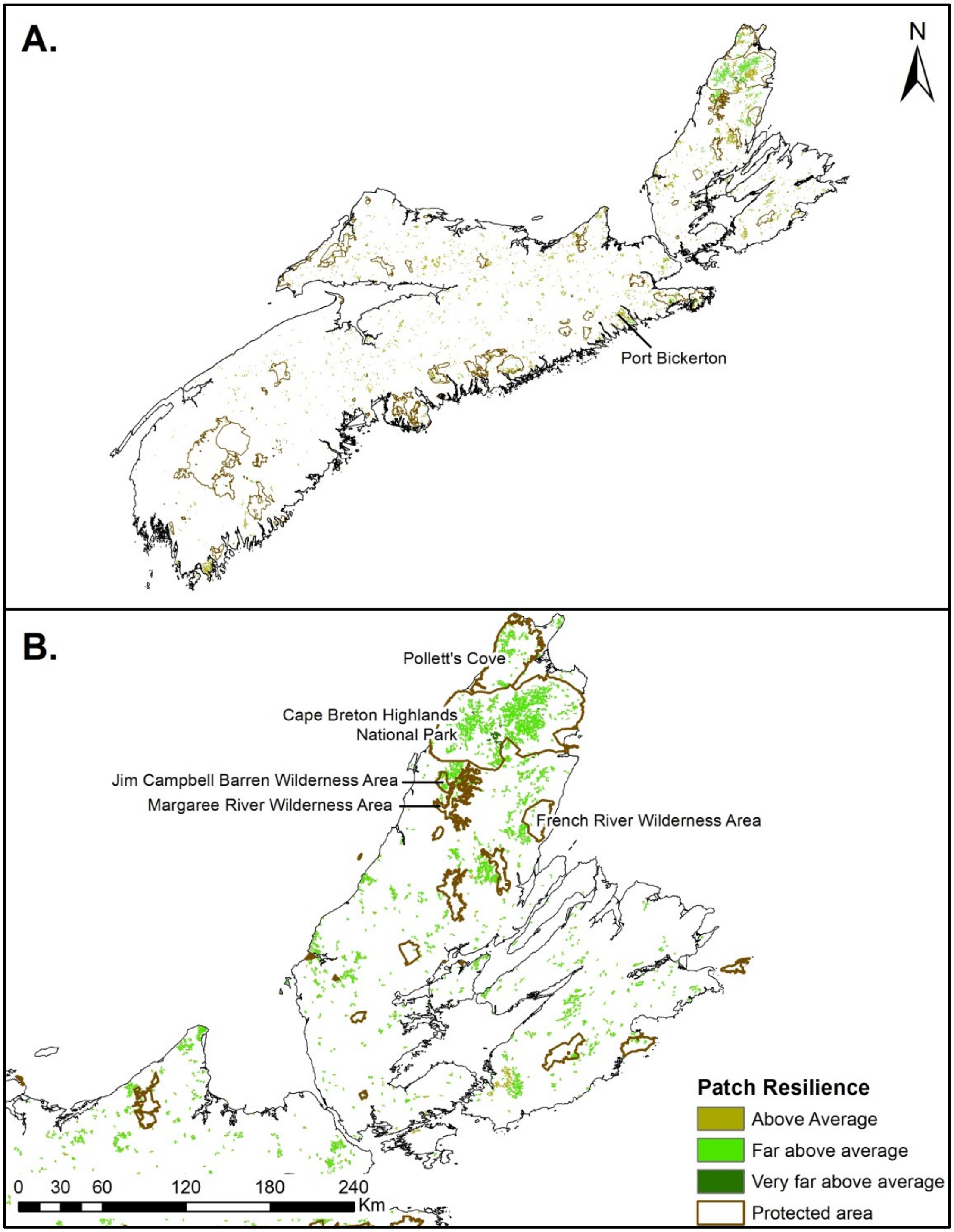


Figure 4.6: Olive-sided Flycatcher patches with landscape resilience scores that are above average (0.5-1STD), far above average (1-2 STD) or very far above average (>2 STD) in (A) Nova Scotia and (B) Cape Breton, in relation to boundaries of existing protected areas. Note that only those patches which with far above or very far above average resilience scores were considered in the delineation of high priority core Olive-sided Flycatcher habitat

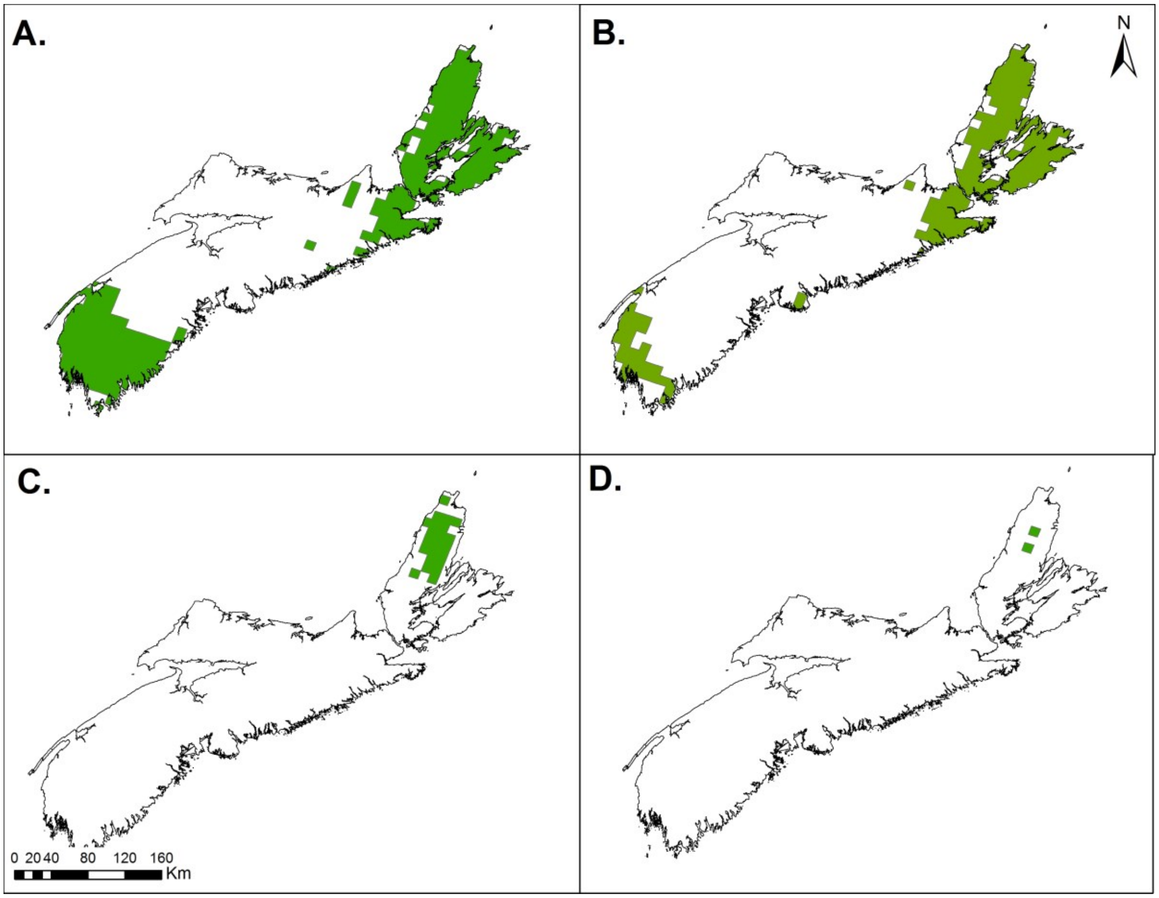


Figure 4.7: Olive-sided Flycatcher range boundaries predicted by National Audubon Society models (2014) for (A) 2000 (created using climate data for the years 1999-2008); (B) 2020 under all emissions scenarios (i.e. common to all emissions scenarios); (C) 2050 under all emissions scenarios; and (D) 2080 under emissions scenario B2. (The other 2 scenarios indicate that there will be no climatically suitable areas remaining for the Olive-sided Flycatcher in Nova Scotia.)

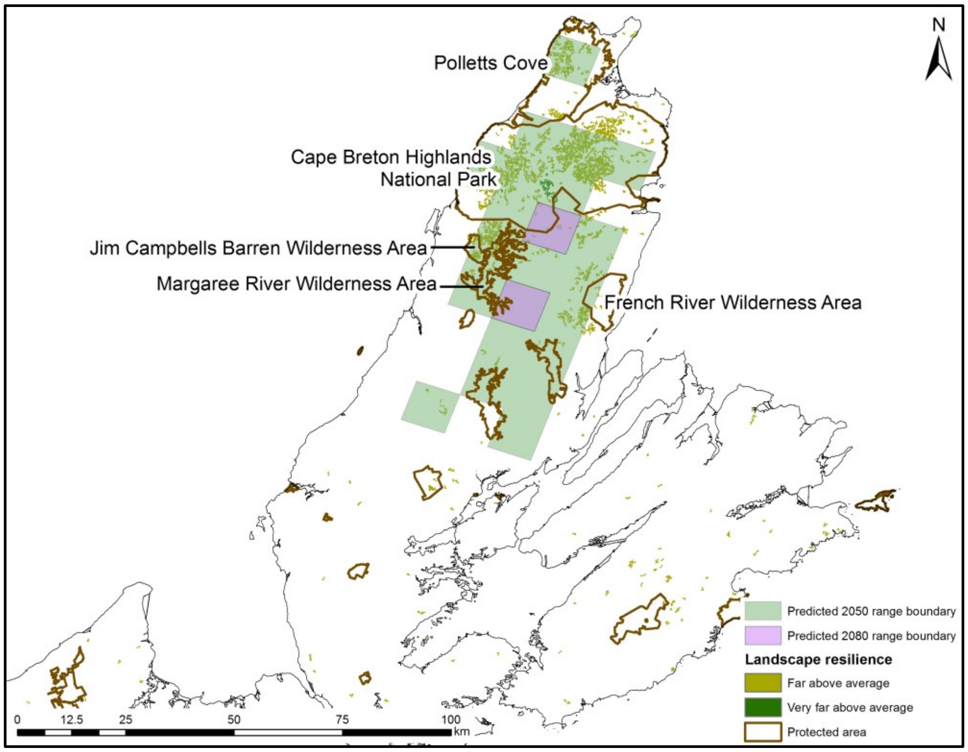


Figure 4.8: Highly resilient Olive-sided Flycatcher patches overlain onto predicted range shift boundaries for 2050 (under all emissions scenarios) and 2080 (under emissions scenario B2) (National Audubon Society, 2014).

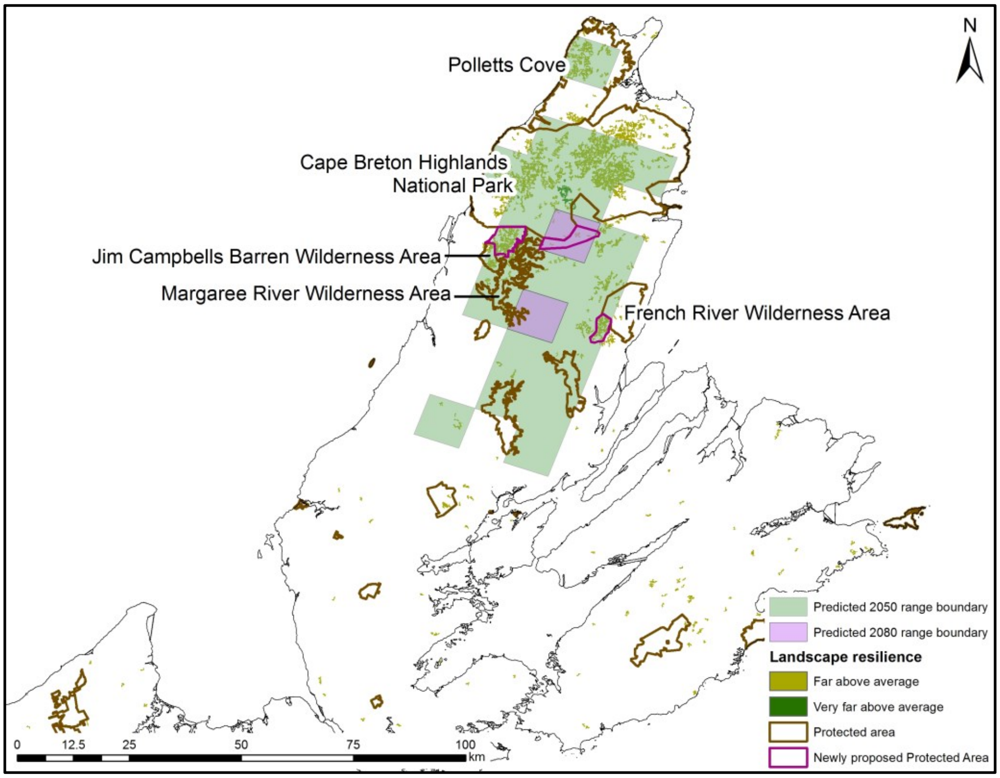


Figure 4.9: Priority conservation areas of core Olive-side Flycatcher habitat in Cape Breton.

CHAPTER 5: CONCLUSION

Habitat is being lost and fragmented at higher rates than ever before, which is driving mass extinction on a global scale. Indeed, since the dawn of the agricultural era, more than one third of the world's natural forest cover has been lost, and only 23% of what remains can be considered intact (i.e. minimum area of 500 km^2 and not near human activity) (Potapov et al., 2008; Haddad et al., 2015). Rates of fragmentation are expected to further accelerate as human population growth places increasingly greater demands on land-use and natural systems (Crooks et al., 2011). The United Nations predicts that the global human population will reach 9.7 billion in the year 2050 and 11.2 billion in the year 2100 (United Nations Department of Economic and Social Affairs, 2015).

The challenges of maintaining biodiversity in the face of habitat fragmentation and loss are further compounded by climate change. Changes in temperature and precipitation regimes cause concomitant changes in the structure and function of ecosystems, thereby placing many species at greater risk of extinction (IPCC, 2007a). Over the past few decades, unequivocal warming has been observed (IPCC, 2007b), and the Intergovernmental Panel on Climate Change (IPCC) predicts that the average global temperature will increase by an additional 1.4 – 5.8°C between 2000 and 2100 (2007a). In Nova Scotia, temperature is predicted to increase by 3.5°C between 1980 and 2080 (Province of Nova Scotia, 2014).

Although the earth experienced rapid warming in the past, such as at the start of the Holocene period (11,700 years ago), the number of extinctions associated with those events is believed to have been minimal (Gill et al., 2015), partly because the pre-human landscape exhibited high connectivity, which made it possible for species to track shifting climate envelopes (Prentice et al., 1991). This is in stark contrast with the modern landscape; therefore, identifying, protecting, and connecting the areas which confer the greatest benefits to biodiversity is critically important to attenuating species loss. However, what constitutes optimal conservation land is not always obvious and can vary according to conservation goals, target species, stakeholder priorities, and planning strategies (Beier et al., 2011). Furthermore, when predictive modeling is used to inform conservation planning (i.e. by elucidating future range shifts of species), applying different parameter settings can affect model results, increasing uncertainty and causing competing areas to be identified as top conservation priorities (Elith et al., 2011).

5.1. Revisiting research goals and objectives

In this thesis, I sought to improve and refine single species approaches to core area delineation and landscape-scale conservation planning in an era of climate change. To achieve this objective, I performed numerous modeling and conservation planning studies with the specific goals of (1) reducing the uncertainty associated with presence-only species distribution modeling, both in terms of parameterization choices (chapter 2) and predictions of future habitat (chapter 3), thereby improving the reliability of model results; and (2) reducing the risk and uncertainty associated with the implementation of species distribution model (SDM) results (i.e. habitat maps) in real-world conservation plans (chapter 4).

The 3 research studies each investigated specific research questions. Chapter 2 addressed the uncertainty associated with sample bias and choice of training covariates in maximum entropy (Maxent) modeling, the most popular presence-only species distribution modeling algorithm. Chapter 3 investigated whether resilient topographic features that have been applied in coarse-filter conservation can also be useful in predicting individual species habitat. In chapter 4, a novel single-species conservation strategy was developed that can also benefit coarse-filter conservation goals given the challenges of climate change.

The modeling and conservation planning studies presented in chapters 2 through 4 targeted 3 vulnerable migratory forest landbirds: the Rusty Blackbird (*Euphagus carolinus*), the Olive-sided Flycatcher (*Contopus cooperi*), and the Canada Warbler (*Wilsonia canadensis*). Therefore, a secondary thesis objective was to contribute information for conservation planning for these birds in Nova Scotia.

5.2. Practical and theoretical contributions in support of research goals

In working towards thesis goals and objectives, the research performed herein made contributions with both practical and theoretical relevance to multiple disciplines. The nature and relevance of these contributions are described in relation to (1) methodological practices in presence-only species distribution modeling, (2) species distribution modeling strategies in an era of uncertain climate change, (3) Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler core area delineation and conservation in Nova Scotia, and (4) conservation planning in an era of climate change.

5.2.1. Methodological contributions towards the refinement of best practices in presence-only species distribution modeling

Species distribution modeling has become increasingly important in supporting a wide range of conservation applications, including reserve design, protected area delineation, and range shift prediction under varying climate change scenarios (Franklin, 2009). However, when absence data (i.e. geographic coordinates delineating locations where the species has been observed *not* to be found) are lacking, as is the case for many rare and cryptic species, "presence-only" modeling algorithms must be used (Elith et al., 2011). Unfortunately, the credibility of results generated by presence-only models has often been called into question, partly because the application of these models has rapidly outpaced requisite methodological refinements to guide their use (Merow et al., 2013; Yackulic et al., 2013). In this thesis, I joined the ongoing discussion about what constitutes "best practices" for Maxent, the most popular presence-only SDM, by investigating one of the most commonly cited methodological concerns in presence-only modeling: how to best address sample bias in species occurrence datasets (e.g. Kramer-Schadt et al., 2013; Yackulic et al., 2013; Boria et al., 2014).

By conducting comparative analyses using both real and virtual species data, I demonstrated that spatially filtering presence points prior to reverse stepwise elimination consistently resulted in the production of Maxent models with greater parsimony and ecological realism. (In other words, spatially filtering presence points resulted in the selection of fewer covariates compared to when unfiltered datasets were used.) I also determined that (1) none of the bias correction strategies considered (i.e. spatial filtering, background manipulation based on the distribution of the species of interest alone, background manipulation based on the distribution of a target group of species, and a combination of spatial filtering and background manipulation) was particularly or universally superior at correcting prediction errors or improving quantitative metrics; and (2) mapped predictions were much more sensitive to changes in the subset of environmental covariates used to train the model than to bias correction strategy.

There is no reason to expect that the use of presence-only SDMs in conservation will decline any time soon. Therefore, developing a set of more standardized methodologies that can reliably generate trustworthy results has become an active and critical area of study (Rodasavlijevic & Anderson, 2013; Crist et al., 2014; Morales et al., 2017). Findings of the comparative analysis performed in chapter 2 of this thesis help fill important research gaps by providing practical and easily applicable suggestions to researchers and conservation practitioners who employ Maxent in their work.

5.2.2. Conceptual contributions towards species distribution modeling in an era of uncertain climate change

In developing landbird SDMs, a reverse stepwise elimination process revealed that abiotic, topo-level, topographic features (which have shown utility in coarse-filter conservation plans) can be used alongside biotic, micro-level, floristic features to produce credible fine-filter SDMs. The predictive power of topography can likely be explained by its role in helping to regulate local micro-climates and in controlling nutrient and moisture accumulation (Mackay and Lindenmayer, 2001; Anderson et al., 2012). Previous researchers have tended to frown upon the inclusion of abiotic features in models, only using them as surrogates when mapped data delineating the spatial distribution of biotic features were unavailable (Beier et al., 2015). However, I found that, not only were both biotic micro-level features and abiotic topo-level features important to the landscape-scale distribution of breeding habitat for the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler, most of the selected topographic covariates showed strong predictive power as well. Indeed, in many cases, topographic covariates were better predictors than biotic ones. While specific habitat preferences can vary greatly among different species and even geographic regions (Laurent et al., 2010), the theoretical rationale underlying my inclusion of abiotic topography should be broadly applicable. Namely, in considering topographic features, I assumed they: (1) have the ability to promote ‘ecological memory’ (Holling, 1992), whereby ecosystems retain similar structures and functions following disturbance (Holling, 1992; Larkin et al., 2006) and (2) will generally not be affected by changing temperature and precipitation regimes (Anderson et al., 2012). Therefore, topographic features should comprise more reliable targets for conservation planning in an era of climate change compared to other commonly used targets (i.e. areas predicted to be suitable according to future climate models, which can be notoriously uncertain; Murphy et al., 2004; Stralberg et al., 2015). Topographic features offer pragmatic benefits to modelers as well, as topographic data tends to be more readily mapped and thus more readily available than biotic data (Barry & Elith, 2006). Moreover, as topography tends to change much more slowly than biotic data, such as forest characteristics, topographic data tends to remain more accurate and reliable over a longer period.

The theoretical (e.g., Holling, 1986; Hunter et al., 1988) and modeled evidence cited in chapters 3 and 4 also leads me to posit that, when developing an SDM, complementing biotic micro-level covariates with abiotic topo-level ones may help in the delineation of habitat patches that are not only suitable currently, but are more likely to remain suitable over the long-term as climate changes and other disturbances occur. Although the validity of including topographic features in SDMs will need to be further confirmed through field investigations and research involving other species, findings presented both here and in previous research (e.g. Holling, 1992; Dobrowski, 2010; Gill et al., 2015) suggest that the ability of a properly chosen combination of topo-level (abiotic) and micro-level (biotic) covariates to predict more climatically resilient habitat is at least worthy of further investigation.

5.2.3. Practical contributions towards Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler core area delineation and conservation in Nova Scotia

The Rusty blackbird, Olive-sided Flycatcher, and Canada warbler have all suffered steep population declines in recent decades and are designated as at-risk by both federal and provincial governments (Environment Canada, 2014). For this thesis, I used covariates (selected through a reverse stepwise elimination process) representing (1) biotic, micro-level features related to forest characteristics and (2) abiotic, topo-level features related to regional topography to develop landscape-scale SDMs which predict the distribution of suitable bird breeding habitat in the province of Nova Scotia, Canada. By including topo-level covariates in model development, I sought to produce mapped outputs which delineate key areas of climate-resilient habitat that can be targeted for protection, restoration or compatible mixed-use forest management, thereby contributing to the provincial conservation of these birds. For the Olive-sided Flycatcher, I took this analysis a step further, prioritizing suitable habitat according to landscape resilience score (using methods adapted from Anderson et al. (2012)).

The SDMs developed in chapter 3 also revealed landscape-scale ecological associations that exist between the landbirds of interest and key topographic and forest features at the eastern-most extent of current breeding habitat. These findings should contribute to a more comprehensive understanding of landscape-scale habitat selection strategies exhibited by the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler across the full extent of their range, knowledge of which has previously been lacking (but see Westwood, 2015). In particular, the SDM results presented in this thesis highlight the importance of topographic features that help regulate local hydrologic conditions to bird distributions.

5.2.4. Conceptual contributions towards conservation planning in an era of climate change

Although SDMs are important fine-filter conservation tools, conserving biodiversity one species at a time is not practical or even possible. Conversely, coarse-filter strategies that target a wider range of taxa are likely to miss certain unique, rare, or sensitive species that need conservation attention the most (Noss, 1987; Darwall et al. 2011; Jenkins et al. 2015; Runge et al. 2015). Therefore, the final contribution of this thesis was to propose a novel approach to conservation planning that (1) targets specific at-risk species, (2) simultaneously benefits coarse-filter conservation goals, and (3) increases the likelihood that the expenditure of limited conservation resources will be a worthwhile long-term investment. My proposed approach delineates high-value conservation habitat by combining elements of multiple modeling strategies (i.e. species distribution modeling, range shift modeling, and landscape resilience modeling) in a series of stages. The first stage is to overlay the results of multiple SDMs generated using different techniques and at different resolutions and different scales (e.g. a continental-scale range shift model trained using climatic covariates and a landscape-scale model trained using covariates that represent regional topography (topo-level covariates) and characteristics of forest habitat (micro-level covariates). Habitat patches identified as suitable by multiple models yield greater confidence that they are good choices for conservation areas. In this way, risks are minimized that limited conservation resources could be wasted protecting habitat that is (1) unsuitable for the target species (e.g. that was delineated using a poorly specified model) or (2) will only be suitable over the short term (e.g. due to climate-driven changes to ecosystems). In the second stage, high priority areas of core habitat are identified according to landscape resilience score (determined using methods adapted from Anderson et al. (2012)), as theoretical evidence suggests that areas with high resilience are more likely to remain suitable in the face of a changing climate are selected for conservation attention.

Highly resilient areas are expected to serve as climate refugia and/or improve connectivity between lower and higher latitudes, thereby facilitating range shifts as climate changes (Dobrowski, 2010; Morelli et al., 2016). Therefore, although the prioritized areas should be especially valuable to the species of interest, they should also increase the overall resilience of the entire landscape, thereby benefitting a broader range of species as well.

5.3. Limitations and directions for future research

The SDM results presented in chapter 3 suggest that certain topographic features have a strong ability to predict the occurrence of certain migratory forest landbirds at the landscape-scale. As landscape-scale topography helps to regulate local micro-climates, nutrient accumulation, and moisture accumulation (Mackay and Lindenmayer, 2001; Anderson et al., 2012), and as species-specific physiological constraints are often related to temperature, moisture, and nutrient regimes (Diez and Pulliam, 2007), I suspect that topography should prove useful in predicting the occurrence of at-least some other taxa as well. However, species with different habitat preferences and life histories will likely exhibit different relationships with different topographic features and, for some species, no topo-level feature may prove overly useful. For example, in this thesis, topographic features that help regulate local hydrologic conditions were found to be important to Olive-sided Flycatcher occurrence and very important to Rusty blackbird and Canada Warbler occurrence. However, these species have all shown strong associations with wet habitat in the eastern part of their range. For taxa that do not prefer wet habitat, features that represent topographic control over hydrology may be less useful. In addition, for species that show different habitat preferences across their range, as do the forest landbirds considered in this thesis, the importance of specific topo-level features may even vary across study areas.

Future research could nonetheless benefit conservation by working to better elucidate general correlations between various types of topographic features and specific species groups (e.g. classified according to habitat preferences or evolutionary relationships). Nonetheless, as shown in chapter 2 of this thesis and elsewhere (e.g. Synes and Osborne, 2011), mapped results of SDMs are highly sensitive to the environmental covariates used to train them, wherein including inappropriate covariates can lead to a poorly specified model. Furthermore, when data limitations require that presence-only datasets be used, modelers should be aware that sample bias in occurrence data can cause spurious correlations to be erroneously identified. Therefore, I caution that modelers should take extra care to ensure that the topographic covariates used to train SDMs are at the very least grounded in ecological theory, and ideally field tested. If possible, confirming the utility of covariates through statistical testing can further increase the robustness and reliability of model results.

While there is considerable theoretical, paleoecological, and modeled evidence to support the use of abiotic, topo-level features in the delineation of climate resilient habitat, empirical data that confirms the ability of abiotic features to delineate climate-resilient habitat is severely lacking. Indeed, as noted by Beier et al. (2015), thus far, most research that has investigated associations between biodiversity and climate change has focused on impact and vulnerability assessments. Indeed, in research published in both academic literature and technical reports by governments and environmental NGOs, very little attention has been paid to developing and evaluating adaptation strategies. This is at least partly due to practical reasons, as rigorous empirical studies would require that species responses to adaptive measures be monitored for 50-100 years (Beier et al., 2015). Nonetheless, as climate change adaptation strategies cannot be implemented without the expenditure of limited conservation resources, greater justification is needed when selecting the most appropriate strategy to use. Shorter-term empirical studies may not be conclusive on their own, but can none-the-less provide useful data that can inform the discussion about which mitigation strategies are potentially effective and which are not.

Similar to Beier et al. (2015), I posit that comparative studies which analyze the theoretical foundations, costs, risks, practicality, and likely benefits of competing adaptation strategies, including those based on the conservation of resilient topographic features, should not require a large commitment of time or financial resources and can therefore help to bridge an important research gap. If the approach to refugia delineation presented in chapter 4 were to be considered in such a comparative analysis, I suspect that the following characteristics would allow it to perform well relative to other strategies. First, it is a low-risk approach to fine-filter conservation. Even if priority areas fail to retain suitable habitat for the target species (i.e. due to erroneous SDM and/or range shift predictions), these areas should still benefit coarse-filter conservation goals because of the high landscape resilience scores that characterize them. Second, it is relatively low cost. In both my research and that of Anderson et al. (2012), the largest areas of contiguous and highly resilient habitat occurred within or adjacent to existing protected areas. Therefore, my proposed approach can also be used to help justify and extend existing conservation plans. Third, the approach is flexible and can be adapted according to data availability. For example, habitat patches can be delineated using many or few range shift models and/or landscape-scale SDMs. Alternatively, if researchers and/or managers are uncomfortable with the high degree of uncertainty that tends to characterize range shift predictions, range shift models can be foregone completely, and habitat patches can be delineated and prioritized according to landscape-based measures of climate-resilience alone.

5.4. Concluding thoughts

Climate change poses unique challenges to reserve delineation and conservation system design, as altered temperature and precipitation regimes cause areas of suitable habitat to shift in geographic space over time (Beier and Brost, 2009; Anderson & Ferree, 2010; Lawler et al., 2015). Thus far, most single-species (“fine-filter”) conservation planning strategies which have sought to account for these challenges have tended to rely on predictions of range shift models and global emissions scenarios, both of which are typically characterized by a high degree of uncertainty (Murphy et al., 2004; Stralberg et al., 2015). Landscape-scale strategies which seek to circumvent the use of uncertain model predictions (e.g. by relying on topographic-based measures of climate resilience) have thus far been coarse-filter in nature.

Together, the findings derived from each of the research studies performed for this thesis achieve the primary thesis objective: to improve and refine approaches used in single species ("fine-filter") conservation planning so that they are better able to meet the challenges posed by climate change. In addition to providing parameterization guidance that can increase the reliability of Maxent model results (which are often used to help delineate conservation areas) and demonstrating the predictive power of topography in SDMs, I also attempted to improve the utility of conservation planning strategies that target specific at-risk species by combining uncertainty-reducing elements of the "Conserving Nature's Stage" (CNS) (Anderson et al., 2012) strategy with results of multiple predictive models to delineate core areas of highly resilient habitat. While it is impossible to empirically gauge the effectiveness of my proposed approach (i.e. presented in chapter 4) in the absence of repeated, long-term field studies, theoretical and modelled evidence suggests that it has strong potential to identify those habitat patches which are likely to remain suitable for the longest periods of time. Indeed, an increasing number of research studies are recognizing both (1) the potential role of resilient refugial habitat in helping to maintain biodiversity in an era of climate change and (2) the ability of topographic features to promote resiliency (e.g. Luoto & Heikkinen, 2008; Austin & Van Neil, 2010; Keppel et al., 2015).

When applied in tandem, the SDM and conservation planning strategies presented in this thesis constitute an integrated approach that can be used to increase the likelihood that individual at-risk species (which are likely to be missed by conservation planning strategies that target biodiversity more generally; e.g. Schloss et al., 2011) persist over the long-term as climate changes. Nonetheless, even as conservation planning techniques continue to advance, it is impossible to guarantee the indefinite persistence of all species. Despite this, with comprehensive scientific understanding about the challenges of habitat loss and climate change and sufficient political will to address them, the most severe biodiversity losses can be avoided. It is my hope that the findings of this thesis research will be of tangible use to conservation researchers and planners as they attempt to stave off a worsening mass extinction and promote species recoveries in the Age of the Anthropocene.

BIBLIOGRAPHY

Agriculture and Agri-Food Canada. (2015). Land Use 2010 [Raster GIS dataset]. Available from Agriculture and Agri-Food Canada: http://open.canada.ca/data/en/dataset/9e1efe92-e5a3-4f70-b313-68fb1283eadf

Ahola, M. P., Laaksonen, T., Eeva, T. & Lehikoinen, E. (2007). Climate change can alter competitive relationships between resident and migratory birds. *Journal of Animal Ecology, 76*(6), 1045-1052. doi: 10.1111/j.1365 2656.2007.01294.x

Altman B & Sallabanks, R. (2010). Olive-sided Flycatcher (*Contopus cooperi*). In A. Poole (Ed.), *The Birds of North America Online*. Retrieved from Cornell Lab of Ornithology: https://birdsna.org/SpeciesAccount/bna/species/olsfly.

Altman, B. & Sallabanks, R. (2012). Olive-sided Flycatcher (*Contopus cooperi*). In P.C. Rodewald (Ed.), *The Birds of North America* (P. G. Rodewald, Ed). doi: 10.2173/bna.502.

Anderson, M. G., Clark, M. & Sheldon, A. O. (2012). *Resilient sites for terrestrial conservation in the Northeast and Mid-Atlantic region*. Available from The Nature Conservancy, Eastern Conservation Science: https://www.conservationgateway.org/ConservationByGeography/NorthAmeric UnitedStates/edc/Documents/TerrestrialResilience020112.pdf

Anderson M. & Ferree, C. (2010). Conserving the Stage: climate change and the geophysical underpinnings of species diversity. *PLoS ONE*, *5*(7):E11554. doi:10.1371/journal.pone.0011554

Anderson, M., Ray, D., Prince, J., Sutton, M., & Watland, A. (2012). *Southern Blue Ridge: An Analysis of Matrix Forests.* Available from The Nature Conservancy: https://www.conservationgateway.org/Files/Documents/FINAL_SBR_Forest_Bl ck_Report_May2013.pdf

Anderson, R. P. & Gonzalez Jr., I. (2011). Species-specific tuning increases robustness to sampling bias in models of species distributions: An implementation with Maxent. *Ecological Modelling, 222*, 2796-2811. doi: 10.1016/j.ecolmodel.2011.02.011.

Andrew, M. E., Wulder, M. A., & Coops, N. C. (2011). Patterns of protection and threats along productivity gradients in Canada. *Biological Conservation, 144,* 2891-2901. doi: 10.1016/j.biocon.2011.08.006

Araujo, M. B. and Guisan, A. (2006). Five (or so) challenges for species distribution modeling. *Journal of Biogeography, 33,* 1677-1688.

Atlantic Canada Conservation Data Center. (2014). About the ACCDC. Retrieved from: http://accdc.com/en/about-us.html

Atlantic Canada Conservation Data Center. (2015). Occurrence points for the Rusty Blackbird, Olive-sided Flycatcher, and Canada Warbler [Vector GIS dataset]. Sackville, NB: Alantic Canada Conservation Data Center.

Austin, M. (2007). Species distribution models and ecological theory: A critical assessment and some possible new approaches. *Ecological Modelling 200*, 1–19. doi: 10.1016/j.ecolmodel.2006.07.005

Austin, M. & Van Niel, K. P. (2011). Improving species distribution models for climate change studies: variable selection and scale. *Journal of Biogeogrphy, 38*(1). doi: 10.1111/j.1365-2699.2010.02416.x

Baldwin, R. A. (2009). Use of Maximum Entropy Modeling in Wildlife Research. *Entropy*, *11,* pp 854-866.

Barry, S. & Elith, J. (2006). Error and uncertainty in habitat models. *Journal of Applied Ecology*, *43*(3), 413-423. doi: 10.1111/j.1365-2664.2006.01136.x

Becker, D. A., Wood, P. B., & Keyser, P. D. (2012). Canada warbler use of harvested stands following timber management in the southern portion of their range. *Forest Ecology and Management*, *276*, 1-9. doi: 10.1016/j.foreco.2012.03.018

Beese, W. J. & Bryant, A. A. (1999). Effect of alternative silvicultural systems on vegetation and bird communities in coastal montane forests of British Columbia, Canada. *Forest Ecology and Management, 115*(2), 231-242.

Beier, P. & Brost, P. (2009). Use of Land Facets to Plan for Climate Change: Conserving the Arenas, Not the Actors. *Conservation Biology 24*(3), 701-710.

Beier, P., Hunter, M. L., & Anderson, M. (2015). Introduction. *Conservation Biology*, *29*(3). doi: 10.1111/cobi.12511

Beier, P., Spencer, W., Baldwin, R. F., & McRae, B. H. (2011). Toward Best Practices for Developing Regional Connectivity Maps. *Conservation Biology*, *25*(5), 879 892. doi: 10.1111/j.1523.1739.2011.01716.x

Beier, P. Sutcliffe, P., Hjort, J. Faith, D. P., Pressey, R. L., & Albuquerque, R. (2015). A review of selection-based tests of abiotic surrogates for species representation. *Conservation Biology, 29*(3), 668-679. doi: 10.1111/cobi.12509.

Bird Studies Canada. (n.d.). *Canada's Birds: An Overview of National Status*. Retrieved 20 November 2013, from The State of Canada's Birds 2012: http://www.stateofcanadasbirds.org/overview.jsp

Bird Studies Canada, Environment Canada – Canadian Wildlife Service, New Brunswick Department of Natural Resources, Nova Scotia Department of Natural Resources, Prince Edward Island Department of Agriculture and Forestry. (2012). Maritime Breeding Bird Atlas Database. Data accessed from the Maritimes Breeding Bird Atlas Website and/or NatureCounts, a node of the Avian Knowledge Network, Bird Studies Canada. Available: http://www.naturecounts.ca. Accessed October 2017.

Becker, D. A., Wood, P. B., & Keyser, P. D. (2012). Canada Warbler use of harvested stands following timber management in the southern portion of their range. *Forest Ecology and Management*, *276*, 1-9. doi: 10.1016/j.foreco.2012.03.018

Beier, P. & Brost, P. (2009). Use of Land Facets to Plan for Climate Change: Conserving the Arenas, Not the Actors. *Conservation Biology 24*, 701-710.

Bevan, K. J. & Kirkby, M. J. (1979). A physically based, variable contributing model of Basin Hydrology. *Hydrological Sciences 24*, 43-69.

Beyer, H. L. (2004). Hawth's Analysis Tools for ArcGIS [software]. Retrieved from http://www.spatialecology.com/htools

Bird Studies Canada. (2012). *The State of Canada's Birds 2012.* Retrieved from Canada's Birds: An Overview of National Status. http://www.stateofcanadasbirds.org/overview.jsp

Bird Studies Canada. (2015). *Second Atlas of Breeding Birds of the Maritime Provinces* (In: Stewart, R. L. M., K. A. Bredin, A. R. Couturier, A. G. Horn, D. Lepage, S. Makepeace, P. D. Taylor, M.-A. Villard, and R. M. Whittam, Eds.) Sackville, NB: Bird Studies Canada; Gatineau, QC: Environment Canada; Charlottetown, PEI: Natural History Society of Prince Edward Island, Prince Edward Island Department of Agriculture and Forestry; Fredericton, NB: Nature New Brunswick, New Brunswick Department of Natural Resources; Halifax, NS: Nova Scotia Bird Society, Nova Scotia Department of Natural Resources.

Blancher, P. (2003). *Importance of Canada's boreal forest to landbirds* (Report commissioned by the Boreal Songbird Initiative and Bird Studies Canada). Ottawa, Ont: Canadian Boreal Initiative.

Boreal Leadership Council. (2003). *Canadian Boreal Forest Conservation Framework.* Retrieved from the Boreal Leadership Council: http://www.borealbirds.org/sites/default/files/publications/Framework-ENG.pdf

Boria, R. A., Olson, L. E., Goodman, S. M., & Anerson, R. P. (2014). Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecological Modelling*, *275,* 73-77.

Brandy, P. M. 2001. *A hierarchical analysis of olive-sided flycatcher habitat use in a managed landscape* (*Unpublished master's thesis*). Humboldt State University, Arcata, CA.

Cameron, R., Goudie, I., & Richardson, D. (2013). Habitat loss exceeds habitat regeneration for an IUCN flagship lichen epiphyte: *Erioderma pedicellatum*. *Canadian Journal of Forest Research, 43*(11), 1075-1080. doi: 10.1139/cjfr-\ 2013-0024.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., Garcia, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Environmental Sciences, 1.* doi: 10.1126/sciadv.1400253

Chambers, C. L., McComb, W. C., & Tappeiner, J. C. (1999). Breeding bird responses to three silvicultural treatments in the Oregon Coast Range. *Ecological Applications, 9*(1), 171-185.

Chivian, E. & Bernstein, A. (Eds.) (2008). *Sustaining life: How human health depends on biodiversity.* New York, NY: Oxford University Press.

Chrisman, N. R. (1991) The error component in spatial data. In D. J. Maguire, M. F. Goodchild, & D. W. Rhind, Eds.) *Geographical Information Systems: principles and applications* (Vol. 1). New York, NY: John Wiley and Sons, Inc

Cooley, S. (2014). *Terrain roughness – 13 ways*. Retrieved from GIS 4 Geomorphology: http://gis4geomorphology.com/roughnesstopographic-position

COSEWIC. (2007). *COSEWIC assessment and status report for the Olive-sided Flycatcher Contopus cooperi in Canada*. Ottawa, Ontario: Committee on the status of endangered wildlife in Canada.

COSEWIC. (2008). *COSEWIC assessment and status report on the Canada Warbler Wilsonia canadensis.* Ottawa, Ontario: Committee on the status of endangered wildlife in Canada.

Crist, P., Maybury, K., Carr, S., & Hak, J. (2014). Tools for Landscape-Level Assessment and Planning. A guide for the North Pacific Landscape Conservation Cooperative. Available from NatureServe: http://www.natureserve.org/biodiversity-science/publications/tools landscape level-assessment-and-planning

Crooks, K. R., Burdett, C. L., Theobald, D. M., Rondinini, C., & Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B*, *366*(1578). 2642 2651. doi: 10.1098/rstb.2011.0120.

Crutzen, P. J. (2002). Geology of mankind. *Nature, 415*, 23.

Daly, C. (2006). Guidelines for assessing the suitability of spatial climate data sets. *International Journal of Climatology, 26*(6), 707-721. doi: 10.1002/joc.1322.

Darwall, W. R. T., Holland, K. G., Smith, D., Allen, E. G. E., Brooks, V., Katarya, C. M., Pollock, C. M., Yichuan, S., Clausinitzer, V. Cumberlidge, N., Cuttelod, A., Klaas-Douwe, B., Dijkstra, K-D B., Diop, M. D., Garcia, N., Seddon, M. B., Skelton, P. H., Snoeks, J., Tweddle, D., Vie, J-C. (2011). Implications of bias in conservation research and investment for freshwater species. *Conservation Letters, 4,* 474-482. doi: 10.1111/j.1755-263X.2011.00202.x

Diez, J. M. & Pulliam, H. R. (2007). Hierarchical Analysis of Species Distributions and Abundance Across Environmental Gradients. *Ecology*, *88*(12), 3144-3152, doi: 10.1890/07-0047.1

Dixon, J. (1920). Nesting of the Olive-Sided Flycatcher in Berkeley, California. *The Condor, 22*, 200–202.

Dobrowski, S. Z. (2010). A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology, 17*(2), 1022-1035. DOI: 10.1111/j.1365 2486.2010.02263.x

Elith, J., Graham, C. H., Anderson, R. P., Dudik, M. Ferrier, S., Guisan, A. Hijmans, R. J., Huettmann, F., Leathwick, Lehmann, A. Li, J., Lohmann, L. G., Loiselle, B. A., Manion, G., Moritz, C. Nakamura, M., Nakazawa, Y., McC, J., Overton, M., Townsend Peterson, A., Phillips, S. J., Richardson, K., Scachetti-Pereira, R., Schapire, R. E., Soberon, J., Williams, S., Wisz, M. S., & Zimmermann, N. E. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography, 29*, 129-151. doi: 10.1111/j.2006.0906.7590.04596.x

Elith, J., Kearney, M., & Phillips, S. J. (2010b). The art of modeling range-shifting species. *Methods in Ecology and Evolution*, *1*, 330-342. doi: 10.1111/j.2041 201x.2010.00036

Elith, J. & Leathwick, J. R. (2009). Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics, 40,* 677-697. doi: 10.1146/annurev.ecolsys.110308.120159

Elith, J., Phillips, S. J., Hastie, T., Dudik, M., En Chee, Y., & Yates, C. J. (2010a). A statistical explanation of Maxent for ecologists. *Biodiversity Research*, *17*, 43-57. doi: 10.1111/j.1472.4642.2010.00725.x

Endangered Species Act, [1998, c. 11, §. 1]. Retrieved from the Nova Scotia Legislature: http://nslegislature.ca/legc/statutes/endspec.htm

Environment and Climate Change Canada. (2016). *Canadian Environmental Sustainability Indicators: Canada's Protected Areas*. Retrieved from Environment and Climate Change Canada: http://www.ec.gc.ca/indicateurs indicators/A1570B00-E7C5-4A6A-9485-98435F041A33/CanadasProtectedAreas_EN.pdf.

Environment Canada. (2014). *North American Breeding Bird Survey - Canadian Trends Website: Data version 2012*. Available from the Government of Canada: http://www.ec.gc.ca/ron-bbs/.

Environmental Systems Research Institute. (2014). ArcGIS for Desktop (10.2.2) [Computer software]. Redlands, CA: EnvironmentalSystems Research Institute.

Erskine, A. J. (1992). *Atlas of Breeding Birds of the Maritime Provinces*. Halifax, N. S.: Nimbus Publishing Ltd.

Fourcade, Y., Engler, J. O., Rodder, D., & Secondi, J. (2014). Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessments of Methods for Correcting Sampling Bias. *PlosOne*, *9*(5). doi: 10.1371/journal.pone.0097122

Franklin, J. (2009a). Ecological understanding of species distributions. In M. Usher, D. Saunders, R. Peet, & A. Dobson (Eds.), *Mapping Species Distributions: Spatial Inference and Predictions* (pp. 34-54). Cambridge, UK: Cambridge University Press.

Franklin, J. (2009b). Data for species distribution models: the biological data. In M. Usher, D., Saunders, R. Peet, & A. Dobson (Eds.), *Mapping Species Distributions: Spatial Inference and Predictions* (pp. 55-75). Cambridge, UK: Cambridge University Press.

Franklin, J. & Miller, J. (2009). Statistical Models – Modern Regression. In M. Usher, D. Saunders, R. Peet, & A. Dobson (Eds.), *Mapping Species Distributions: Spatial Inference and Predictions* (pp 113-153). Cambridge, UK: Cambridge University Press.

Gill, J. L., Blois, J. L., Benito, B., Dobrowski, S., Hunter, M. L. Jr., & McGuire, J. L. (2015). A 2.5-million year perspective on coarse-filter strategies for conserving nature's stage. *Conservation Biology, 29*(3), 640-648. doi: 10.1111/cobi.12504

Gil-Tena, A., Brotons, L., Fortin, M-J., Burel, F., & Saura, S. (2013). Assessing the role of landscape connectivity in recent woodpecker range expansion in Mediterranean Europe: forest management implications. *European Journal of Forest Research, 132*(1), 181-194. doi: 10.1007/s10342-012-0666-x.

Goodnow, M. L. & Reitsma, L. R. (2011). Nest-site selection in the Canada warbler (*Wilsonia canadensis*) in central New Hampshire. *Canadian Journal of Zoology*, *89*, 1172-1177.

Gottesman, A. J. & Keeton, W. S. (2017). Regeneration Responses to Management for Old-Growth Characteristics in Northern Hardwood-Conifer Forests. *Forests, 8*(45). doi: 10.3390/f8020045

Haché, S., Solymos, P., Fontaine, T., Bayne, E., Cumming, S., Schmiegelow F., & Stralberg, D. (2014). *Critical habitat of Olive sided Flycatcher, Canada Warbler, and Common Nighthawk in Canada* (Technical Report for Project K4B20-13 0367). Edmonton, AB: Boreal Avian Modelling Project.

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., Melbourne, B. A., Nicholls, A. O., Orrock, J. L., Song, D-K., & Townsend, J. R. (2015). Habitat Fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2). doi: 10.1126/sciadv.1500052

Hansen, A. J., Garman, S. L., Marks, B., & Urban, D. L. (1993). An approach for Managing Vertebrate Diversity Across Multiple-Use Landscapes. *Ecological Applications, 3,* pp. 481-496.

Hirzel, A. H., Helfer, V., & Metral F. (2001). Assessing habitat-suitability models with a virtual species. *Ecological Modelling*, 145, 111-121.

Holling, C. S. (1986). The Resilience of Terrestrial Ecosystems. In L. H. Gunderson, C. R. Allen, & C. S. Holling (Eds.), *Foundations of Ecological Resilience* (2010 ed.) (pp. 67-118). Washington, D.C.: Island Press, Washington, D. C.

Holling, C. S. (1992). Cross-Scale Morphology, Geometry, and Dynamics of Ecosystems. *Ecological Monographs*, *62*(4), 447-502.

Holling, C. S. & Gunderson, L. H. (2002). Resilience and adaptive cycles. In L. H. Gunderson & C. S. Holling (Eds.), *Panarchy: understanding transformations in human and natural systems* (pp. 25-62). Washington, D.C.: Island Press.

Hooke, R. LeB. & Martin-Duque, J. F. (2012). Land transformation by humans: A review. *The Geological Society of America, 22*(12). doi: 10.1130/GSAT151A.1

Hunter, G. J. & Goodchild, M. F. (1997). Modeling the Uncertainty of Slope and Aspect Estimates Derived from Spatial Databases. *Geographical Analysis, 29*(1).

Hunter, M. L. Jr., Jacobson, G. L Jr., & Webb III, T. (1988). Paleoecology and the Coarse-Filter Approach to Maintaining Biological Diversity. *Conservation Biology, 2*(4), 375-385.

IBM Corp. (2013). IBM SPSS Statistics for Windows (22) [Computer software]. Armonk, NY: IBM Corporation.

IPCC. (2001). The IPCC Special Report on Emissions Scnearios In *Working Group I: The Scientific Basis.* Retrieved from https://www.ipcc.ch/ipccreports/tar/wg1/029.htm

IPCC. (2007a). *Climate Change 2007: Impacts, Adaptation and Vulnerability*. Cambridge, UK: Cambridge University Press. Available from the IPCC: https://www.ipcc.ch/publications_and_data/publications_and_data_reports.shtml

IPCC. (2007b). *Climate Change 2007 – The Physical Science Basis*. Cambridge University Press, Cambridge, UK. Available from the IPCC: https://www.ipcc.ch/publications_and_data/publications_and_data_reports.shtml

Ives, C., Taylor, M., Davies, P., & Wilks, D. (2005). How wide is wide enough? The relationship between riparian buffer width, condition and biodiversity: An assessment of urban creek systems in the Ku-ring-gai Local Government Area, North Sydney, NSW. In N. Khanna, D. Barton, D. Beale, R. Cornforth, A. Elmahdi, M. McRae, N. Seelsaen, & A. Shalav (Eds), *Environmental Change: making it happen: 9th Annual Environmental Research Conference, 29th November to 2nd December 2005.* Hobart, Tasmania: Annual Environmental Postgrad Conference.

Jenkins, C. N., Van Houtan, K. S., Pimm, S. L., & Sexton, J. O. (2015). US protected lands mismatch biodiversity priorities. *PNAS, 112*(16), 5081-5086. doi: 10.1073/pnas.1418034112

Jimenez-Valverde, A. (2012). Insights into the area under the receiver operating characteristic curve (AUC) as a discrimination measure in species distribution modelling. *Global Ecology and Biogeography 21*(4), 498-507. doi: 10.1111/j.1466-8238.2011.00683.x

Kadmon, R., Farber, O., & Danin, A. (2004). Effect of roadside bias on the accuracy of predictive maps produced by bioclimatic models. *Ecological Applications 14*(2), 401-413. doi: 10.1980/02-5364.

Keppel, G., Mokany, K. Wardell-Johnson, G. W., Phillips, B. L., Welbergen, J. A., Reside, A. E. (2015). The capacity of refugia for conservation planning under climate change. *Frontiers in Ecology and the Environment, 13*(2). doi: 10.1890/140055.

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Schut, A. G. T., Hopper, S. D., & Franklin, S E. (2012). Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography, 21*(4), 393-404. doi: 10.1111/j.1466 8238.2011.00686.x

Kerr, J. T. & Cihlar, J. (2004). Patterns and Causes of Species Endangerment in Canada. *Ecological Applications, 14*(3), 743-753.

Kirby, J. S., Stattersfield, A. J., Butchart, S. H. M., Evans, M. I., Grimmett, R. F. A., Jones, V. R., O'Sullivan, J., Tucker, G. M., & Newton, I. (2008). Key conservation issues for migratory land- and waterbird species on the world's major flyways. *Bird Conservation International, 18.* doi: 10.1017/S0959270908000439.

Kramer-Schadt, S., Niedballa, J., Pilgrim, J. D., Scroder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A. K., Augeri, D. M., Cheyne, S. M., Hearn, A. J., Ross, J., Macdonald, D. W., Mathai, J., Eaton, J., Marshall, A. J., Semiadi, G., Rustam, R., Bernard, J., Alfred, R., Samejima, H., Duckworth, J. W., Breitenmoser-Wuersten, C., Beland, J. L., Hofer, J., & Wilting, A. (2013). The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions, 19,* 1366 – 1379. doi: 10.1111/ddi.12096.

Lambert, J. D. & Faccio, S. D. (2005). *Canada Warbler: Population Status, Habitat Use, and Stewardship Guidelines for Northeastern Forests* [Technical Report 05-4]. Woodstock, VT: Vermont Institute of Natural Science.

Larkin, D. J., Vivian-Smith, G., & Zedler, J. B. (2006). Topographic heterogeneity: Theory and ecological restoration. In D. A. Falk, M. A. Palmer, & J. Zedler (Eds.), *Foundations of Restoration Ecology* (pp. 142-164). Washington, DC: Island Press.

LaRue, P., Belanger, L., & Huot, J. (1995). Riparian edge effects on boreal balsam fir bird communities. *Canadian Journal of Forest Research*, *25*, 555-566.

LaSorte, F. A. & Jetz, W. (2012) Tracking of climatic niche boundaries under recent climate change. *Journal of Animal Ecology, 81*(4), 914-925. doi: 10.1111/j.1365.2656.2012.01958.x

Laurent, E. J., Drew, C. A., & Thogmartin, W. E. (2010). The Role of Assumptions in Predictions of Habitat Availability and Quality. In C. A. Drew, Y. Wiersma, & F. Huettmann (Eds.), *Predictive Species and Habitat Modeling in Landscape Ecology*. New York, NY: Springer-Verlag.

Lawler, J. J., Ackerly, D. D., Albano, C. M., Anderson, M. G., Dobrowski, S.Z., Gill, J. L., Pressey, R. L., Sanderson, E. W., & Weiss, S. B. (2015). The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. *Conservation Biology, 29*(3). doi: 10.1111/cobi.12505.

Lee, P., Aksenov, D., Laestadius, L., Nogueron, R. & Smith, W. (2003). *Canada's Large Intact Forest Landscapes*. Retrieved from Global Forest Watch Canada: http://globalforestwatch.ca/sites/gfwc/files/publications/20030915A_Can_Lg_Intct_Forest_Landscapes.pdf

Lewis, S. L. (2006). Tropical forests and the changing earth system. *Philosophical Transactions of the Royal Society B, 361,* 195-210.

Liu, C., White, M., & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*, *40*, 778 789. doi: 10.1111/jbi.12058

Lobo, J. M., Jimenez-Valverde, A., & Real, R. (2008). AUC: a misleading measure of the performance of predictive distribution models. *Global Ecology and Biogeography 17,* 145-151. doi: 10.1111/j.1466-8238.2007.00358.x

Locke, H. (2014). Nature Needs Half: A Necessary and Hopeful New Agenda for Protected Areas in North America and around the World. *The George Wright Forum, 31*(3), 359-371.

Luoto, M. & Heikkinen, R. K. (2007). Disregarding topographical heterogeneity biases species turnover assessments based on bioclimatic models. *Global Change Biology, 14*(3). doi: 10.1111/j.1365.2486.2007.01527.x

Mackay, B. G. & Lindenmayer, D. B. (2001). Towards a hierarchical framework for modeling the spatial distribution of animals. *Journal of Biogeography*, *28*, 1147 1166. doi: 10.1046/j.1365-2699.2001.00626.x

Mahon, C.L., Bayne, E. M., Sólymos, P., Matsuoka, S. M., Carlson, M., Dzus, E., Schmiegelow, F. K. &, Song, S. J. (2014). Does expected future landscape condition support proposed population objectives for boreal birds? *Forest Ecology and Management*, *312*, 28–39. doi: 10.1016/j.foreco.2013.10.025

Marra, P. P., Francis, C. M., Mulvihill, R. S., & Moore, F. R. (2005). The influence of climate on the timing and rate of spring bird migration. *Oecologia, 142*(2),307 315. doi: 10.1007/s00442-004-1725-x

Matsuoka, S. M., Shaw, D., Sinclair, J., Johnson, R., Corcoran, N., Meyers, P. & Rojek, N. (2010). Nesting ecology of the Rusty Blackbird in Alaska and Canada. *The Condor*, *112*, 810-824.

McClure, C. J. W., Rolek, B. W., McDonald, K., & Hill, G. E. (2012). Climate change and the decline of a once common bird. *Ecology and Evolution, 2*(2), 370-378. doi: 10.1002/ece3.95.

McDaniel, C. N., & Borton, D. N. (2002). Increased human energy use causes biological diversity loss and undermines prospects for sustainability. *BioScience, 52,* 926-936.

McGarigal, K., & McComb, W. C. (1995). Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs*, *65*, 235 260

Meehan, T. D. & George, T. L. (2003). Short-term effects of moderate- to high-severity wildfire on a disturbance dependent flycatcher in northwest California. *The Auk*, *120*, 1102-1113.

Meiklejohn, K., Ament, R., & Tabor, G. (2010). *Habitat Corridors & Landscape Connectivity: Clarifying the Terminology*. Available from The Wildlands Network: http://www.wildlandsnetwork.org/sites/default/files/terminology%20CLLC.pdf

Merow, C., Smith, M. J., & Silander, J. A. (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*, *36*, 1058-1069. doi: 10.1111/j.1600-0587.2013.07872.x

Millenium Ecosystem Assessment. (2005). *Millenium Ecosystem Assessment : Ecosystems and Human Well-Being: Biodiversity Synthesis Report*. Washington, DC: Island Press.

Miller, J. (2014). Virtual species distribution models: Using simulated data to evaluate aspects of model performance. *Progress in Physical Geography 38*(1), 117-128. doi: 10.1177/0309133314521448

Morales, N. S., Fernandez, I. C., & Baca-Gonzalez, V. (2017). MaxEnt's parameter configuration and small samples: are we paying attention to recommendations: a systematic review. *PeerJ, 5,* e3093. doi: 10.7717/peerj.3093

Moreno-Amat, E., Mateo, R. G., Nieto-Lugilde, D., Morueta-Holme, N., Svenning, J. C., & Garcia-Amorena, I. (2015). Impact of model complexity on cross-temporal transferability in Maxent species distribution models: An assessment using paleobotanical data. *Ecological Modelling*, *312*, 308-317. doi: 10.1016/j.ecolmodel.2015.05.035

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Bessinger, S. R. (2016). Managing Climate Change Refugia for Climate Adaptation. *PloS ONE*, *11*(8). doi: 10.1371/journal.pone.0159909

Murphy, J. M., Sexton, D. M. H., Barnett, G. S., Jones, M., Webb, J., Collins, M., & Stainforth, D. A. (2004). Quantification of modelling uncertainties in a large ensemble of climate change simulations. *Nature*, *430*, 768-772.

National Audubon Society. (2014). *The Climate Report*. Available from Audubon: http://climate.audubon.org/all-species

Natural Resources Canada. (2009). *Land Cover* [map]. Scale not given. Available from Natural Resources Canada: http://geogratis.gc.ca/api/en/nrcan-rncan/ess sst/dc6c73e1-8893-11e0-9aa7-6cf049291510.html.

Neave, H. M., Cunningham, R. B., Norton, T. W. & Nix, H. A. (1996). Biological inventory for conservation evaluation III: Relationships between birds, vegetation, and environmental attributes in southern Australia. *Forest Ecology & Management*, *8,* 197-297.

Neily, P. D., Quigley, E., Benjamin, L., Stewart, B., & Duke, T. (2005). *Ecological Land Classification for Nova Scotia*. Retrieved from the Nova Scotia Department of Natural Resources: http://novascotia.ca/natr/forestry/ecological/pdf/ELCrevised2.pdf

Noss, R. (1983). A Regional Landscape Approach to Maintain Diversity. *BioScience* *33*(11), 700-706. doi: 10.2307/1309350

Noss, R. (1987). From plant communities to landscapes in conservation inventories: a look at The Nature Conservancy (USA). *Biological Conservation, 41,* 11-37. doi: 10.1016/00063207(87)90045-0

Noss, R. & Cooperrider, A. (1994). *Saving Nature's Legacy*. Washington, DC: Island Press.

Nova Scotia Department of Natural Resources (2006). Enhanced Digital Elevation Model, Nova Scotia, Canada (DP ME 55, version 2) [Raster GIS dataset]. Available from the Nova Scotia Department of Natural Resources: http://novascotia.ca/natr/meb/download/dp055.asp

Nova Scotia Department of Natural Resources (n.d.). Forest Inventory – Geographic Information Systems [Vector GIS dataset]. Available from the Nova Scotia Department of Natural Resources: http://novascotia.ca/natr/forestry/gis/forest inventory.asp

Nova Scotia Department of Natural Resources (n.d.). *Forest Inventory – Current Forest Data* [Metadata document for the Nova Scotia Forest Resource Inventory]. Available from the Nova Scotia Department of Natural Resources: http://novascotia.ca/natr/forestry/gis/forest inventory.asp

Nova Scotia Department of Natural Resources (2008). *State of the Forest: Report 1995 - 2005.* (Report No. FOR 2008-3). Halifax, NS: Nova Scotia Department of Natural Resources

Nova Scotia Department of Natural Resources (2007a). Wet Areas Mapping – Geographic Information Systems [Raster GIS dataset]. Available from the Nova Scotia Department of Natural Resources: https://novascotia.ca/natr/forestry/gis/wamdownload.asp

Nova Scotia Department of Natural Resources (2007b). *Nova Scotia Wet Areas Mapping* [Metadata document for the Nova Scotia Wet Areas Mapping dataset]. Available from the Nova Scotia Department of Natural Resources: http://novascotia.ca/natr/forestry/gis/Wam_wtbl_2012.xml

Nova Scotia Department of Natural Resources (n.d.). Nova Scotia's Wetland Inventory [Vector GIS dataset]. Halifax, NS: Nova Scotia Department of Natural Resources.

Nova Scotia Geomatics Center (n.d.). Roads and Rails Network [Vector GIS file from the Nova Scotia Topographic Database]. Amherst, Nova Scotia: Nova Scotia Geomatics Center.

Nova Scotia Museum of Natural History (1996a). Climate. In D. Davis & S. Brown (Eds.) *Natural History of Nova Scotia* (Vol. 1). Available from the Nova Scotia Museum of Natural History: https://ojs.library.dal.ca/NSM/issue/view/349

Nova Scotia Museum of Natural History (1996b). Canadian Setting. In D. Davis & S. Brown (Eds.) *Natural History of Nova Scotia* (Vol. 1). Available from the Nova Scotia Museum of Natural History: https://ojs.library.dal.ca/NSM/issue/view/349

O'Callaghan, J. F. & Mark, D. M. (1984). The extraction of drainage networks from digital elevation data. *Computer Vision, Graphics and Image Processing*, *28*, 323-344.

Runge, C. A., Watson, J. E. M., Butchard, S. H. M., Hanson, J. O., Possingham, H. P., & Fuller, R. A. (2015). Protected areas and global conservation of migratory birds. *Science, 350*(6265), 1255-1258. doi: 10.1126/science.aac9180

Peterson, A. T. & Soberon, J. (2012). Species Distribution Modeling and Ecological Niche Modeling: Getting the Concepts Right. *Brazilian Journal of Nature Conservation*, 10(2), 102-106. doi:10.4322/natcon.2012.019.

Phillips, S. (2005). *A Brief Tutorial on Maxent*. Floram Park, New Jersey: AT&T Research.

Phillips, S. J., Anderson, R. P., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, *190*, 231-259. doi: 10.1016/j.ecolmodel.2005.03.026.

Phillips, S. J., & Dudik, M. (2008). Modeling of species distributions with Maxent. New extensions & a comprehensive evaluation. *Ecography*, *31*, 161-175. doi: 10.1111/j.2007.0906-7590.05203

Phillips, S. J., Dudik, M., Elith, J. Graham, C. H., Lehmann, A., Leathwick, J. & Ferrier, S. (2009). Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, *19*, 181-197. doi: 10.1980/07-2153.1

Potapov, P., Yaroshenko, A., Turubanova, S., Dubinin, M., Laestadius, L., Thies, C., Aksenov, D. (2008). Mapping the World's Intact Forest Landscapes by Remote Sensing. *Ecology and Society*, *13*(2): 51 [online]. Retrieved from http://www.ecologyandsociety.org/vol13/iss2/art51/

Powell, L. L., Glanz, W. E., & Hodgman, T. P. (2014). Habitat occupancy of Rusty Blackbirds (*Euphagus carolinus*) breeding in northern New England, USA. *The Condor*, *116*, 122-133. doi: 10.1650/CONDOR-13-033-R1.1

Powell, L. L., Glanz, W. E.., Hodgman, T. P.., Fisher, C., & Osenton, J. (2010). Nest-site selection and nest survival of the Rusty Blackbird: does timber management adjacent to wetlands create ecological traps? *The Condor*, *112*, 800-809.

Prentice, I. C., Bartlein, P. J., & Webb, T. (1991) Vegetation and climate changes in eastern North America since the last glacial maximum: A response to continuous climatic forcing. *Ecology*, *72*, 2038-2056.

Province of Nova Scotia. (2002). Wildlife Habitat and Watercourses Protection Regulations, made under section 40 of the Forests Act, R.S.N.S. 1989, c. 179: https://novascotia.ca/just/regulations/regs/fowhwp.htm

Province of Nova Scotia. (2014). Climate Data for Nova Scotia. Retrieved from the Province of Nova Scotia: https://climatechange.novascotia.ca/climate-data

Province of Nova Scotia. (2015). *Province Reaches Land Protection Goal* [Press release]. Retrieved from https://novascotia.ca/news/release/?id=20151229002

Reitsma, L., Hallworth, M. T., & Benham, P. M. (2008). Does age influence territory size, habitat selection and reproductive success of male Canada Warblers in central New Hampshire? *Wilson Journal of Ornithology*, *120*, 446-459.

Reitsma, L. Goodnow, M. Hallworth, M. T., & Conway, C. J. (2010) Canada Warbler (*Cardellina Canadensis*). In A. Poole (Ed.) *Birds of North America Online*, Ithica: Cornell Lab of Ornithology. Available from Cornell Lab of Ornithology: http://bna.birds.cornell.edu/bna/species/421. doi: 10.2173/bna.421

Robertson, B. A. & Hutto, R. L. (2007). Is Selectively Harvested Forest an Ecological Trap for Olive-Sided Flycatchers? *The Condor*, *109*, 109-121.

Radosavljevic, A. & Anderson, R. P. (2013). Maxing better MAXENT models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography, 41*(4), 629-643. doi: 10.1111/jbi.12227

Rodder, D. & Engler, J. O. (2011). Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. *Global Ecology and Biogeography 20*(6), 915-927. doi: 10.1111/j.1466-8238.2011.00659.x

Rodhe, A. & Seibert, J. (1999). Wetland occurrence in relation to topography: a test of topographic indices as moisture indicators. *Agricultural and Forest Meteorology*, *98-99*, 325-340.

Rowe, J. S. (1972). *Forest regions of Canada* (Report No. 1300). Ottawa, ON: Canada Department of the Environment, Canada Forestry Service.

Rubio, L. & Saura, S. (2012). Assessing the importance of individual habitat patches as irreplaceable connecting elements: an analysis of simulated and real landscape data. *Ecological Complexity, 11,* pp 28-37. doi: 10.1016/j.ecocom.2012.01.003

Runge, C. A., Watson, J. E. M., Butchart, S. H.M., Hanson, J. O., Possingham, H. P., & Fuller, R. A. (2015). Protected areas and global conservation of migratory birds. *Science, 350*(6265), 1255-1258. doi: 10.1126

Sala, O. E., Chapin III, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans,R., Lodge, D. M., Mooney, H. A., Oesterheld, M., LeRoy Poff, N., Sykes, M. T., Walker, B. H., Walker, M.., & Wall, D. H. (2000). Global Biodiversity Scenarios for the Year 2100. *Science, 287*(5459), 1770-1775. doi: 10.1126/science.287.54959.1770

Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). TheHuman Footprint and the Last of the Wild. *BioScience, 52*(10), 891-904.

Saura, S., Bodin, O., & Fortin, M-J. (2014). Stepping stones are crucial for species' long distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, *51*(1). doi: 10.1111/1365-2664.12179

Saura, S. & Rubio, L. (2010). A common currency for the different ways in which patches and links can contribute to habitat availability and connectivity in the landscape. *Ecography, 33*, 523-537. doi: 10.1111/j.1600-0587.2009.05760.x

Schloss, C. A., Lawler, J. J., Larson, E. R., Papendick, H. L., Case, M. J., Evans, D. M., DeLap, J. H., Langdon, J. G., Hall, S. A., & McRae, B. H. (2011). Systematic Conservation Planning in the Face of Climate Change: Bet-Hedging on the Columbia Plateau. *PLoS, 6*(12), e28788. doi: 10.1371/journal.pone.0028788.

Schoener, T. W. (1968). Anolis lizards of Bimini: resource partitioning in a complex fauna. *Ecology 49*, 704-726.

Snaith, T. V. & Beazley, K. F. (2004). The distribution, status and habitat associations of mainland moose in Nova Scotia. *Proceedings of the Nova Scotian Institute of Science, 42*, 263-317.

Species at Risk Act, Consolidated Acts [S. C. 2002, c. 29]. Retrieved from the Justice Laws website: http://laws-lois.justice.gc.ca/eng/acts/s15.3/FullText.html.

Statistics Canada. (2014). Focus on Geography Series, 2011 Census: Province of Nova Scotia. Retrieved from: Statistics Canada: http://www12.statcan.gc.ca/census recensement/2011/as-sa/fogs-spg/Facts-pr-eng.cfm?Lang=Eng&GK=PR&GC=12

Statistics Canada. (2016). *Population and Dwelling Count Highlight Tables, 2011 Census* [Data table]. Retrieved from Statistics Canada: http://www12.statcan.gc.ca/census recensement/2011/dp-pd/hlt-fst/pd-pl/Table-Tableau.cfm

Stralberg, D., Matsuoka, S. M., Hamann, E. M., Baybe, P. Solymos, F., Schmiegelow, K. A., Wang, X., Cumming, S. G., & Song, S. J. (2015). Projecting boreal bird responses to climate change: the signal exceeds the noise. *Ecological Applications*, *25*, 52–69. doi: 10.1890/13-2289.1

Synes, N. W. & Osborne, P. E. (2011). Choice of predictor variables as a source of uncertainty in continental-scale species distribution modelling under climate change. *Global Ecology and Biogeography 20,* 904-914. doi: 10.1111/j.1466 8238.2010.00635.x

Taylor, T. N., Taylor, E. L., & Krings, M. (2009). *Paleobotany, Second Edition: The Biology and Evolution of Fossil Plants.* Burlington, MA: Elsevier.

The Nature Conservancy. (2015). *Ecological Buffers, Reducing Ecological Impacts of Shale Development: Recommended Practices for the Appalachians* [pamphlet]. Retrieved from: https://www.nature.org/media/centralapps/recommended-shale practices-ecological-buffers.pdf

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L.J., Collingham, Y. C., Erasmus, B. F. N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature, 427*(6970), 145-148. doi: 10.1038/nature02121

United Nations Department of Economic and Social Affairs. (2015, July 29). *World population projected to reach 9.7 billion by 2050*. Retrieved from the United Nations: http://www.un.org/en/development/desa/news/population/2015 report.html

Van Proosdij, A. S. J., Sosef, M. S. M., Wieringa, J. J., Raes, N. (2015). Minimum required number of specimen records to develop accurate species distribution models. *Ecography, 39*(6), 542-552. doi: 10.1111/ecog01509

Veloz, S. D. (2009). Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *Journal of Biogeography, 36*(12), 2290 2299. doi: 10.1111/j.1365.2699.2009.02174.x

Visser, M. E. & Both, C. (2005). Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B, 272*(1581). doi: 10.1098/rspb.2005.3356

Wagler, R. (2011). The Anthropocene Mass Extinction: An Emerging Curriculum Theme for Science Educators. *The American Biology Teacher, 73*(2), 78-83.doi: 10.1525/abt.2011.73.2.5

Warren, D. L., Glor, R. E., & Turelli, M. (2008). Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. *Evolution*, *62*. doi: 10.1111/j.1558-5646.2008.00482.x

Warren, D. L., Glor, R. E., Turelli, M. (2010). ENMTools: a toolbox for comparative studies of environmental niche models. *Ecography, 33*(3), 607-611. doi: 10.1111/j.1600-0587.2009.06142.x

Warren, D. L. & Seifert, S. N. (2010). Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications 21,* 345-352. doi: 10.1891/10-1171.1

Wells, J., Childs, D., Reid, F., Smith, K., Darveau, M., & Courtois, V. (2014). *Boreal Birds Need Half: Maintaining North America's Bird Nursery and Why it Matters.* Seattle, Washington: Boreal Songbird Initiative; Memphis, Tennessee: Ducks Unlimited Inc.; Stonewall, Manitoba: Ducks Unlimited Canada, Stonewall, Manitoba.

Weisendaul, S. (2000). *Living on the Wind: Across the Hemisphere with Migratory Birds.* Union Square West, New York: North Point Press.

Weiss, A. D. (2001). Topographic Position and Landform Analysis. Poster presented at the 2001 ESRI International User Conference. Retrieved from http://www.jennessent.com/downloads/tpi-poster-tnc_18x22.pdf

Westwood, A. (2016). Conservation of Three Forest Landbird Species at Risk: Characterizing and Modelling Habitat at Multiple Scales to Guide Management Planning (Unpublished doctoral dissertation). Dalhousie University, Halifax, Nova Scotia.

Westwood, A., Solymos, P., Fontaine, T., & Bayne, E. (2015). Estimating population density of the Rusty Blackbird (*Euphagus carolinus*), Olive-Sided Flycatcher (*Contopus cooperi*), and Canada Warbler (*Cardellina canadensis*) in national parks in New Brunswick and Nova Scotia. Report prepared for Parks Canada on behalf of the Boreal Avian Modelling Project, University of Alberta: Edmonton. 63pp.

Williams, K. J., Belbin, L., Austin, M. P., Stein, J. L., & Ferrier, S. (2012). Which environmental variables should I use in my biodiversity model? *International Journal of Geographic Information Science, 26,* 2009-2047, doi: 10.1080/13658816.2012.688015

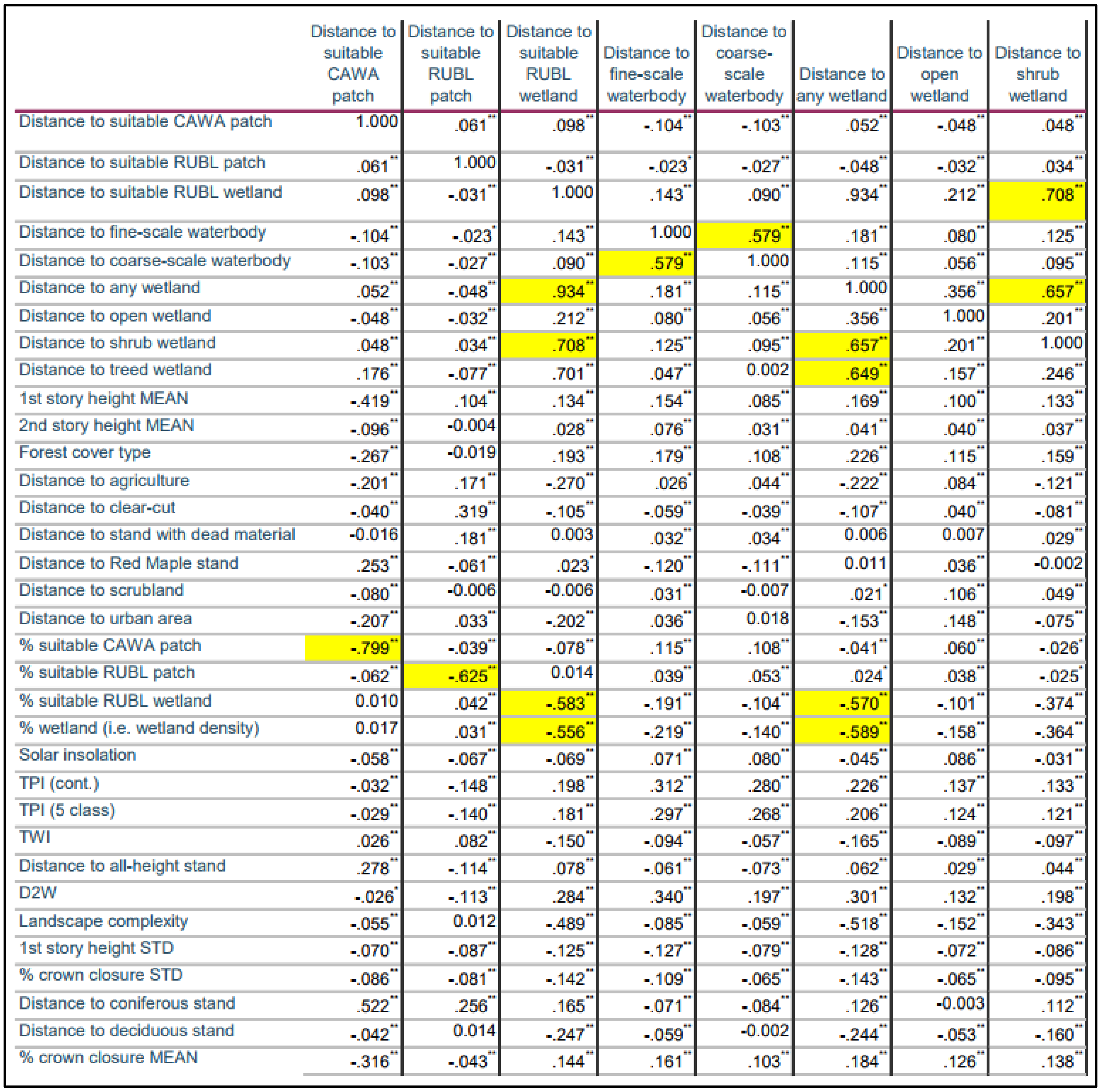
World Wildlife Federation. (2014). *Living Planet Report 2014: Species and spaces, people and places*. In R. McLellan, L. Iyengar, B. Jeffries, N. Oerlemans, M. Grooten, M. Guerraoui, & P. Sunters (Eds.). Gland, Switzerland: author

Yackulic, C. B., Chandler, R., Zipkin, E. F., Royle, A., Nichols, J. D., Campbell-Grant, E. H., & Veran, S. (2013). Presence-only modelling using MAXENT: when can we trust the inferences? *Methods in Ecology & Evolution, 4,* 236-243. doi: 10.1111/2041-210x.12004.

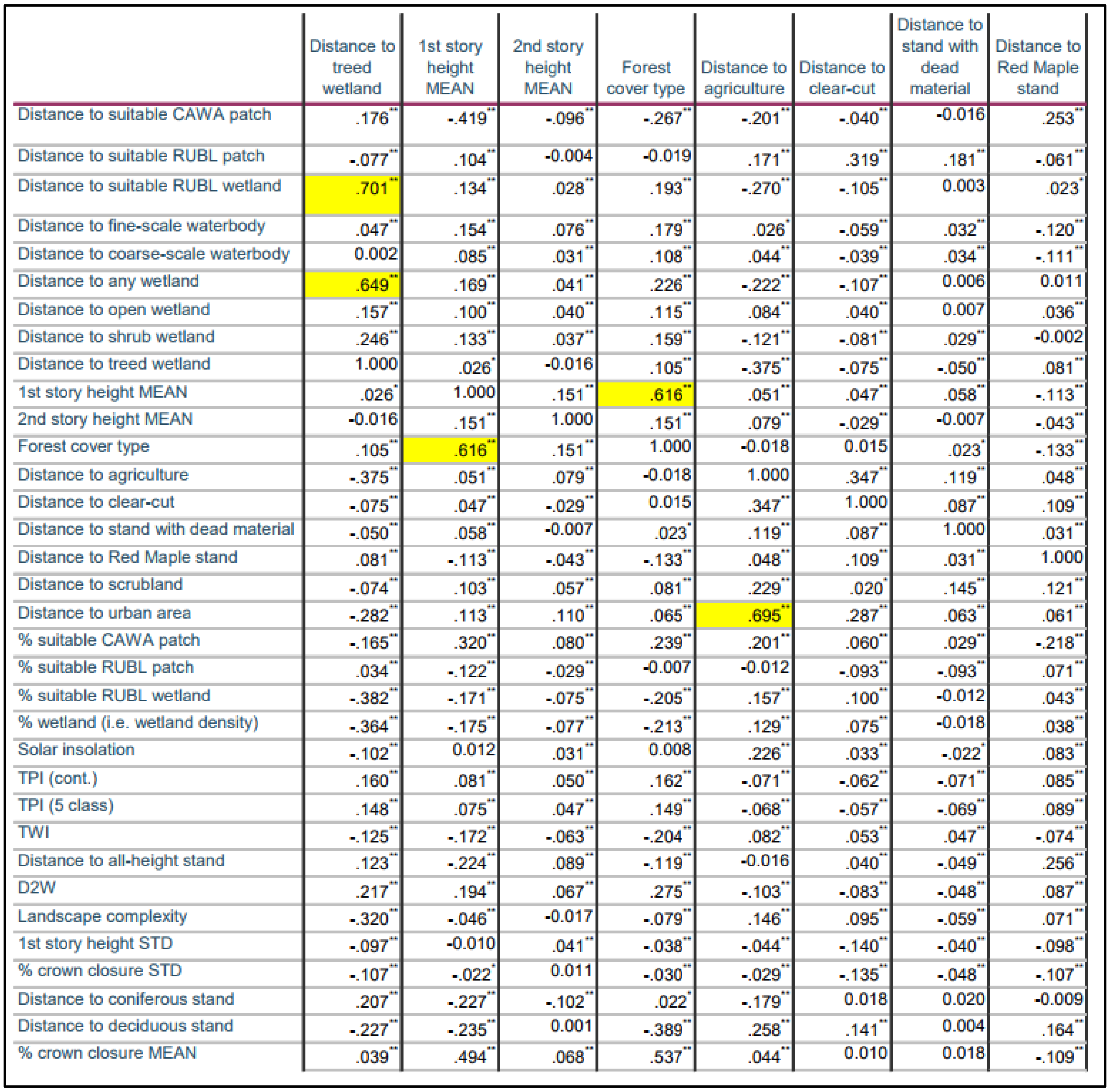
Yost, A. C., S. L. Petersen, M. Gregg, and M. Miller (2008). Predictive modeling and mapping sage grouse (*Centrocercus urophasianus*) nesting habitat using Maximum Entropy and a long-term dataset from Southern Oregon. *Ecological Informatics*, *3*, 375-386.

Zalasiewicz, J., Williams, M., Haywood, A., & Ellis, M. (2011). The Anthropocene: a new epoch of geological time? *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences, 369*(1938). doi: 10.1098/rsta/2010.0339

APPENDIX A: SPEARMAN CORRELATION COEFFICIENTS OF COVARIATES CONSIDERED IN PRE-MODELING TUNING EXPERIMENTS

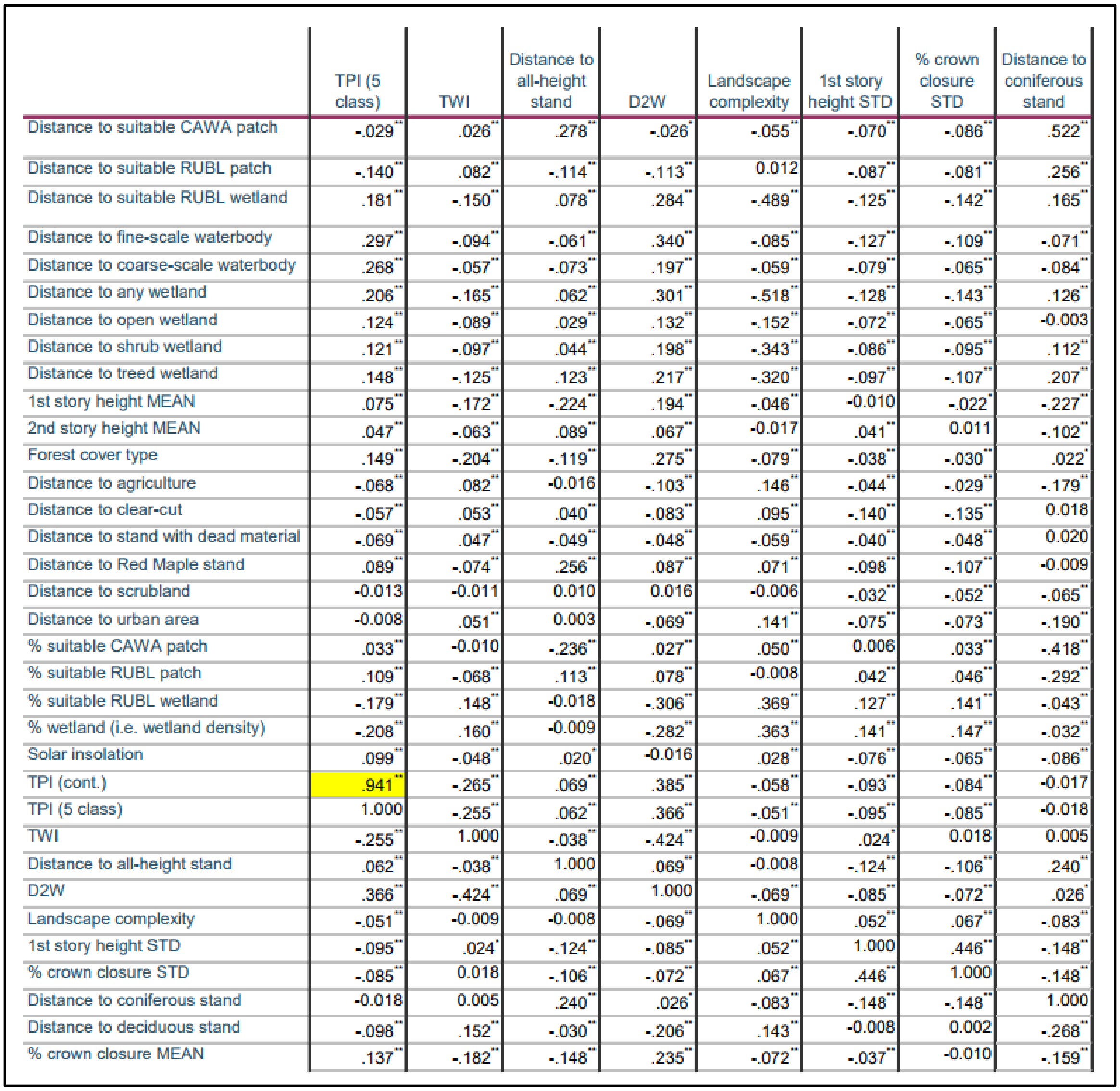


	Distance to suitable CAWA patch	Distance to suitable RUBL patch	Distance to suitable RUBL wetland	Distance to fine-scale waterbody	Distance to coarse-scale waterbody	Distance to any wetland	Distance to open wetland	Distance to shrub wetland
Distance to suitable CAWA patch	1.000	.061**	.098**	-.104**	-.103**	.052**	-.048**	.048**
Distance to suitable RUBL patch	.061**	1.000	-.031**	-.023*	-.027**	-.048**	-.032**	.034**
Distance to suitable RUBL wetland	.098**	-.031**	1.000	.143**	.090**	.934**	.212**	.708**
Distance to fine-scale waterbody	-.104**	-.023*	.143**	1.000	.579**	.181**	.080**	.125**
Distance to coarse-scale waterbody	-.103**	-.027**	.090**	.579**	1.000	.115**	.056**	.095**
Distance to any wetland	.052**	-.048**	.934**	.181**	.115**	1.000	.356**	.657**
Distance to open wetland	-.048**	-.032**	.212**	.080**	.056**	.356**	1.000	.201**
Distance to shrub wetland	.048**	.034**	.708**	.125**	.095**	.657**	.201**	1.000
Distance to treed wetland	.176**	-.077**	.701**	.047**	0.002	.649**	.157**	.246**
1st story height MEAN	-.419**	.104**	.134**	.154**	.085**	.169**	.100**	.133**
2nd story height MEAN	-.096**	-0.004	.028**	.076**	.031**	.041**	.040**	.037**
Forest cover type	-.267**	-0.019	.193**	.179**	.108**	.226**	.115**	.159**
Distance to agriculture	-.201**	.171**	-.270**	.026*	.044**	-.222**	.084**	-.121**
Distance to clear-cut	-.040**	.319**	-.105**	-.059**	-.039**	-.107**	.040**	-.081**
Distance to stand with dead material	-0.016	.181**	0.003	.032**	.034**	0.006	0.007	.029**
Distance to Red Maple stand	.253**	-.061**	.023*	-.120**	-.111**	0.011	.036**	-0.002
Distance to scrubland	-.080**	-0.006	-0.006	.031**	-0.007	.021*	.106**	.049**
Distance to urban area	-.207**	.033**	-.202**	.036**	0.018	-.153**	.148**	-.075**
% suitable CAWA patch	-.799**	-.039**	-.078**	.115**	.108**	-.041**	.060**	-.026*
% suitable RUBL patch	-.062**	-.625**	0.014	.039**	.053**	.024*	.038**	-.025*
% suitable RUBL wetland	0.010	.042**	-.583**	-.191**	-.104**	-.570**	-.101**	-.374**
% wetland (i.e. wetland density)	0.017	.031**	-.556**	-.219**	-.140**	-.589**	-.158**	-.364**
Solar insolation	-.058**	-.067**	-.069**	.071**	.080**	-.045**	.086**	-.031**
TPI (cont.)	-.032**	-.148**	.198**	.312**	.280**	.226**	.137**	.133**
TPI (5 class)	-.029**	-.140**	.181**	.297**	.268**	.206**	.124**	.121**
TWI	.026**	.082**	-.150**	-.094**	-.057**	-.165**	-.089**	-.097**
Distance to all-height stand	.278**	-.114**	.078**	-.061**	-.073**	.062**	.029**	.044**
D2W	-.026*	-.113**	.284**	.340**	.197**	.301**	.132**	.198**
Landscape complexity	-.055**	0.012	-.489**	-.085**	-.059**	-.518**	-.152**	-.343**
1st story height STD	-.070**	-.087**	-.125**	-.127**	-.079**	-.128**	-.072**	-.086**
% crown closure STD	-.086**	-.081**	-.142**	-.109**	-.065**	-.143**	-.065**	-.095**
Distance to coniferous stand	.522**	.256**	.165**	-.071**	-.084**	.126**	-0.003	.112**
Distance to deciduous stand	-.042**	0.014	-.247**	-.059**	-0.002	-.244**	-.053**	-.160**
% crown closure MEAN	-.316**	-.043**	.144**	.161**	.103**	.184**	.126**	.138**

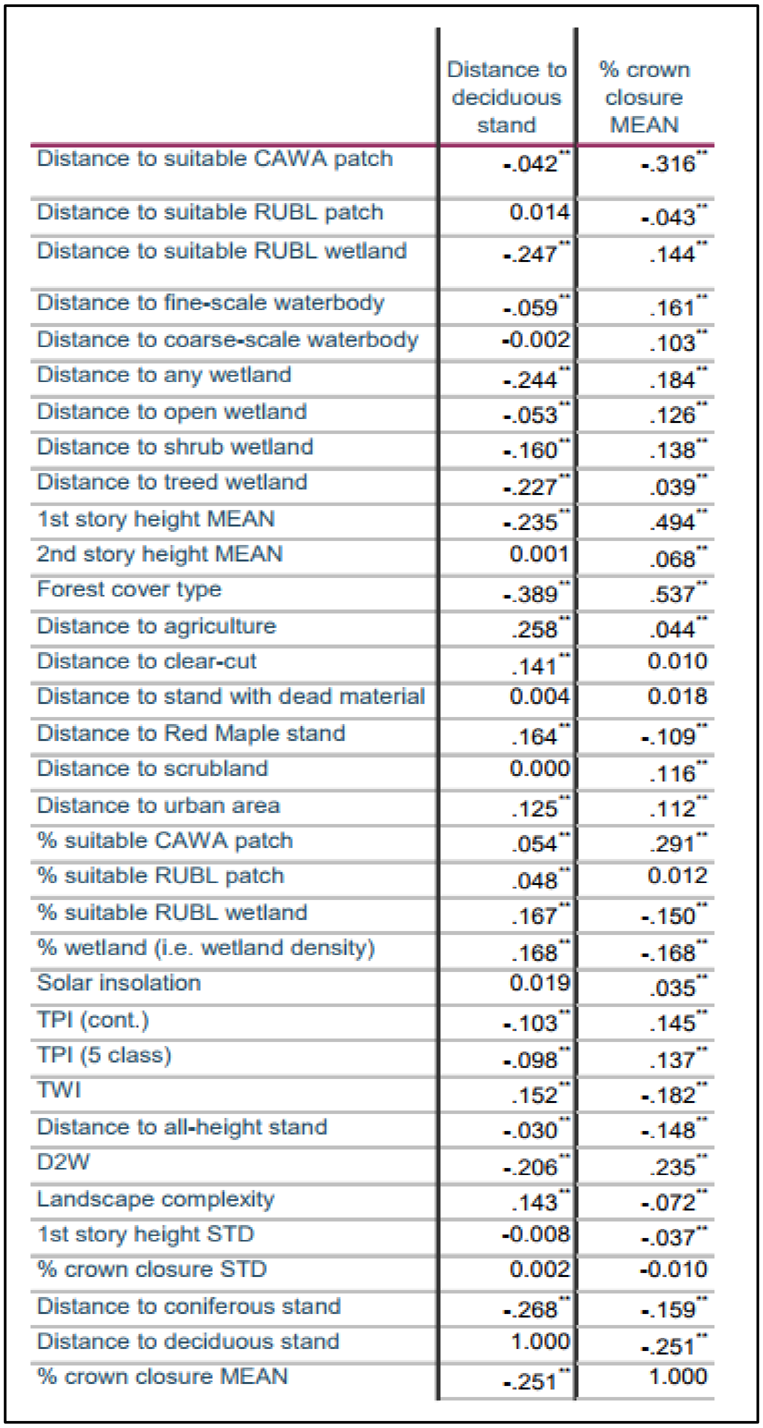


	Distance to treed wetland	1st story height MEAN	2nd story height MEAN	Forest cover type	Distance to agriculture	Distance to clear-cut	Distance to stand with dead material	Distance to Red Maple stand
Distance to suitable CAWA patch	.176**	-.419**	-.096**	-.267**	-.201**	-.040**	-0.016	.253**
Distance to suitable RUBL patch	-.077**	.104**	-0.004	-0.019	.171**	.319**	.181**	-.061**
Distance to suitable RUBL wetland	.701**	.134**	.028**	.193**	-.270**	-.105**	0.003	.023*
Distance to fine-scale waterbody	.047**	.154**	.076**	.179**	.026*	-.059**	.032**	-.120**
Distance to coarse-scale waterbody	0.002	.085**	.031**	.108**	.044**	-.039**	.034**	-.111**
Distance to any wetland	.649**	.169**	.041**	.226**	-.222**	-.107**	0.006	0.011
Distance to open wetland	.157**	.100**	.040**	.115**	.084**	.040**	0.007	.036**
Distance to shrub wetland	.246**	.133**	.037**	.159**	-.121**	-.081**	.029**	-0.002
Distance to treed wetland	1.000	.026*	-0.016	.105**	-.375**	-.075**	-.050**	.081**
1st story height MEAN	.026*	1.000	.151**	.616**	.051**	.047**	.058**	-.113**
2nd story height MEAN	-0.016	.151**	1.000	.151**	.079**	-.029**	-0.007	-.043**
Forest cover type	.105**	.616**	.151**	1.000	-0.018	0.015	.023*	-.133**
Distance to agriculture	-.375**	.051**	.079**	-0.018	1.000	.347**	.119**	.048**
Distance to clear-cut	-.075**	.047**	-.029**	0.015	.347**	1.000	.087**	.109**
Distance to stand with dead material	-.050**	.058**	-0.007	.023*	.119**	.087**	1.000	.031**
Distance to Red Maple stand	.081**	-.113**	-.043**	-.133**	.048**	.109**	.031**	1.000
Distance to scrubland	-.074**	.103**	.057**	.081**	.229**	.020*	.145**	.121**
Distance to urban area	-.282**	.113**	.110**	.065**	.695**	.287**	.063**	.061**
% suitable CAWA patch	-.165**	.320**	.080**	.239**	.201**	.060**	.029**	-.218**
% suitable RUBL patch	.034**	-.122**	-.029**	-0.007	-0.012	-.093**	-.093**	.071**
% suitable RUBL wetland	-.382**	-.171**	-.075**	-.205**	.157**	.100**	-0.012	.043**
% wetland (i.e. wetland density)	-.364**	-.175**	-.077**	-.213**	.129**	.075**	-0.018	.038**
Solar insolation	-.102**	0.012	.031**	0.008	.226**	.033**	-.022*	.083**
TPI (cont.)	.160**	.081**	.050**	.162**	-.071**	-.062**	-.071**	.085**
TPI (5 class)	.148**	.075**	.047**	.149**	-.068**	-.057**	-.069**	.089**
TWI	-.125**	-.172**	-.063**	-.204**	.082**	.053**	.047**	-.074**
Distance to all-height stand	.123**	-.224**	.089**	-.119**	-0.016	.040**	-.049**	.256**
D2W	.217**	.194**	.067**	.275**	-.103**	-.083**	-.048**	.087**
Landscape complexity	-.320**	-.046**	-0.017	-.079**	.146**	.095**	-.059**	.071**
1st story height STD	-.097**	-0.010	.041**	-.038**	-.044**	-.140**	-.040**	-.098**
% crown closure STD	-.107**	-.022*	0.011	-.030**	-.029**	-.135**	-.048**	-.107**
Distance to coniferous stand	.207**	-.227**	-.102**	.022*	-.179**	0.018	0.020	-0.009
Distance to deciduous stand	-.227**	-.235**	0.001	-.389**	.258**	.141**	0.004	.164**
% crown closure MEAN	.039**	.494**	.068**	.537**	.044**	0.010	0.018	-.109**

	Distance to scrubland	Distance to urban area	% suitable CAWA patch	% suitable RUBL patch	% suitable RUBL wetland	% wetland (i.e. wetland density)	Solar insolation	TPI (cont)
Distance to suitable CAWA patch	-.080**	-.207**	-.799**	-.062**	0.010	0.017	-.058**	-.032**
Distance to suitable RUBL patch	-0.006	.033**	-.039**	-.625**	.042**	.031**	-.067**	-.148**
Distance to suitable RUBL wetland	-0.006	-.202**	-.078**	0.014	-.583**	-.556**	-.069**	.198**
Distance to fine-scale waterbody	.031**	.036**	.115**	.039**	-.191**	-.219**	.071**	.312**
Distance to coarse-scale waterbody	-0.007	0.018	.108**	.053**	-.104**	-.140**	.080**	.280**
Distance to any wetland	.021*	-.153**	-.041**	.024*	-.570**	-.589**	-.045**	.226**
Distance to open wetland	.106**	.148**	.060**	.038**	-.101**	-.158**	.086**	.137**
Distance to shrub wetland	.049**	-.075**	-.026*	-.025*	-.374**	-.364**	-.031**	.133**
Distance to treed wetland	-.074**	-.282**	-.165**	.034**	-.382**	-.364**	-.102**	.160**
1st story height MEAN	.103**	.113**	.320**	-.122**	-.171**	-.175**	0.012	.081**
2nd story height MEAN	.057**	.110**	.080**	-.029**	-.075**	-.077**	.031**	.050**
Forest cover type	.081**	.065**	.239**	-0.007	-.205**	-.213**	0.008	.162**
Distance to agriculture	.229**	.695**	.201**	-0.012	.157**	.129**	.226**	-.071**
Distance to clear-cut	.020*	.287**	.060**	-.093**	.100**	.075**	.033**	-.062**
Distance to stand with dead material	.145**	.063**	.029**	-.093**	-0.012	-0.018	-.022*	-.071**
Distance to Red Maple stand	.121**	.061**	-.218**	.071**	.043**	.038**	.083**	.085**
Distance to scrubland	1.000	.285**	.075**	.029**	0.004	-0.015	.124**	-0.014
Distance to urban area	.285**	1.000	.209**	.052**	.133**	.106**	.267**	-0.012
% suitable CAWA patch	.075**	.209**	1.000	.058**	-.053**	-.031**	.065**	.033**
% suitable RUBL patch	.029**	.052**	.058**	1.000	-.036**	-.030**	.070**	.113**
% suitable RUBL wetland	0.004	.133**	-.053**	-.036**	1.000	.711**	.055**	-.190**
% wetland (i.e. wetland density)	-0.015	.106**	-.031**	-.030**	.711**	1.000	.028**	-.221**
Solar insolation	.124**	.267**	.065**	.070**	.055**	.028**	1.000	.101**
TPI (cont.)	-0.014	-0.012	.033**	.113**	-.190**	-.221**	.101**	1.000
TPI (5 class)	-0.013	-0.008	.033**	.109**	-.179**	-.208**	.099**	.941**
TWI	-0.011	.051**	-0.010	-.068**	.148**	.160**	-.048**	-.265**
Distance to all-height stand	0.010	0.003	-.236**	.113**	-0.018	-0.009	.020*	.069**
D2W	0.016	-.069**	.027**	.078**	-.306**	-.282**	-0.016	.385**
Landscape complexity	-0.006	.141**	.050**	-0.008	.369**	.363**	.028**	-.058**
1st story height STD	-.032**	-.075**	0.006	.042**	.127**	.141**	-.076**	-.093**
% crown closure STD	-.052**	-.073**	.033**	.046**	.141**	.147**	-.065**	-.084**
Distance to coniferous stand	-.065**	-.190**	-.418**	-.292**	-.043**	-.032**	-.086**	-0.017
Distance to deciduous stand	0.000	.125**	.054**	.048**	.167**	.168**	0.019	-.103**
% crown closure MEAN	.116**	.112**	.291**	0.012	-.150**	-.168**	.035**	.145**



	TPI (5 class)	TWI	Distance to all-height stand	D2W	Landscape complexity	1st story height STD	% crown closure STD	Distance to coniferous stand
Distance to suitable CAWA patch	-.029**	.026**	.278**	-.026*	-.055**	-.070**	-.086**	.522**
Distance to suitable RUBL patch	-.140**	.082**	-.114**	-.113**	0.012	-.087**	-.081**	.256**
Distance to suitable RUBL wetland	.181**	-.150**	.078**	.284**	-.489**	-.125**	-.142**	.165**
Distance to fine-scale waterbody	.297**	-.094**	-.061**	.340**	-.085**	-.127**	-.109**	-.071**
Distance to coarse-scale waterbody	.268**	-.057**	-.073**	.197**	-.059**	-.079**	-.065**	-.084**
Distance to any wetland	.206**	-.165**	.062**	.301**	-.518**	-.128**	-.143**	.126**
Distance to open wetland	.124**	-.089**	.029**	.132**	-.152**	-.072**	-.065**	-0.003
Distance to shrub wetland	.121**	-.097**	.044**	.198**	-.343**	-.086**	-.095**	.112**
Distance to treed wetland	.148**	-.125**	.123**	.217**	-.320**	-.097**	-.107**	.207**
1st story height MEAN	.075**	-.172**	-.224**	.194**	-.046**	-0.010	-.022*	-.227**
2nd story height MEAN	.047**	-.063**	.089**	.067**	-0.017	.041**	0.011	-.102**
Forest cover type	.149**	-.204**	-.119**	.275**	-.079**	-.038**	-.030**	.022*
Distance to agriculture	-.068**	.082**	-0.016	-.103**	.146**	-.044**	-.029**	-.179**
Distance to clear-cut	-.057**	.053**	.040**	-.083**	.095**	-.140**	-.135**	0.018
Distance to stand with dead material	-.069**	.047**	-.049**	-.048**	-.059**	-.040**	-.048**	0.020
Distance to Red Maple stand	.089**	-.074**	.256**	.087**	.071**	-.098**	-.107**	-0.009
Distance to scrubland	-0.013	-0.011	0.010	0.016	-0.006	-.032**	-.052**	-.065**
Distance to urban area	-0.008	.051**	0.003	-.069**	.141**	-.075**	-.073**	-.190**
% suitable CAWA patch	.033**	-0.010	-.236**	.027**	.050**	0.006	.033**	-.418**
% suitable RUBL patch	.109**	-.068**	.113**	.078**	-0.008	.042**	.046**	-.292**
% suitable RUBL wetland	-.179**	.148**	-0.018	-.306**	.369**	.127**	.141**	-.043**
% wetland (i.e. wetland density)	-.208**	.160**	-0.009	-.282**	.363**	.141**	.147**	-.032**
Solar insolation	.099**	-.048**	.020*	-0.016	.028**	-.076**	-.065**	-.086**
TPI (cont.)	.941**	-.265**	.069**	.385**	-.058**	-.093**	-.084**	-0.017
TPI (5 class)	1.000	-.255**	.062**	.366**	-.051**	-.095**	-.085**	-0.018
TWI	-.255**	1.000	-.038**	-.424**	-0.009	.024*	0.018	0.005
Distance to all-height stand	.062**	-.038**	1.000	.069**	-0.008	-.124**	-.106**	.240**
D2W	.366**	-.424**	.069**	1.000	-.069**	-.085**	-.072**	.026*
Landscape complexity	-.051**	-0.009	-0.008	-.069**	1.000	.052**	.067**	-.083**
1st story height STD	-.095**	.024*	-.124**	-.085**	.052**	1.000	.446**	-.148**
% crown closure STD	-.085**	0.018	-.106**	-.072**	.067**	.446**	1.000	-.148**
Distance to coniferous stand	-0.018	0.005	.240**	.026*	-.083**	-.148**	-.148**	1.000
Distance to deciduous stand	-.098**	.152**	-.030**	-.206**	.143**	-0.008	0.002	-.268**
% crown closure MEAN	.137**	-.182**	-.148**	.235**	-.072**	-.037**	-0.010	-.159**



	Distance to deciduous stand	% crown closure MEAN
Distance to suitable CAWA patch	-.042**	-.316**
Distance to suitable RUBL patch	0.014	-.043**
Distance to suitable RUBL wetland	-.247**	.144**
Distance to fine-scale waterbody	-.059**	.161**
Distance to coarse-scale waterbody	-0.002	.103**
Distance to any wetland	-.244**	.184**
Distance to open wetland	-.053**	.126**
Distance to shrub wetland	-.160**	.138**
Distance to treed wetland	-.227**	.039**
1st story height MEAN	-.235**	.494**
2nd story height MEAN	0.001	.068**
Forest cover type	-.389**	.537**
Distance to agriculture	.258**	.044**
Distance to clear-cut	.141**	0.010
Distance to stand with dead material	0.004	0.018
Distance to Red Maple stand	.164**	-.109**
Distance to scrubland	0.000	.116**
Distance to urban area	.125**	.112**
% suitable CAWA patch	.054**	.291**
% suitable RUBL patch	.048**	0.012
% suitable RUBL wetland	.167**	-.150**
% wetland (i.e. wetland density)	.168**	-.168**
Solar insolation	0.019	.035**
TPI (cont.)	-.103**	.145**
TPI (5 class)	-.098**	.137**
TWI	.152**	-.182**
Distance to all-height stand	-.030**	-.148**
D2W	-.206**	.235**
Landscape complexity	.143**	-.072**
1st story height STD	-0.008	-.037**
% crown closure STD	0.002	-0.010
Distance to coniferous stand	-.268**	-.159**
Distance to deciduous stand	1.000	-.251**
% crown closure MEAN	-.251**	1.000

Correlation co-efficients with a Spearman’s R value > 0.55 are highlighted in yellow. ‘Suitable CAWA patch’ included polygons in the FID with a primary species classification of Red Maple, Red Spruce, Black Spruce, Balsam Fir, Red & Black Spruce, Eastern Cedar, Other Softwood, or Tolerant Hardwood. ‘Suitable RUBL patch’ included polygons in the FID that were classified as softwood and had an average height of <6m. ‘Suitable RUBL wetland’ included polygons in the provincial wetland inventory with a primary vegetation code of low shrub, tall shrub, tree, or sphagnum.

APPENDIX B: CREATION OF GIS LAYERS USED IN RESEARCH CHAPTERS

Topographic Position Index. A topographic position index (TPI) that distinguished among 5 topographic positions (valleys, low-slopes, mid-slopes, up-slopes, and ridges) was included as a candidate covariate in the development of Maxent models (chapters 2 and 3) and was also used in the creation of the landscape complexity index (chapter 3) and the landscape resilience index (chapter 4). This TPI was created according to a methodology developed by Weiss (2001) and modified by Cooley (2014) and used the 20 m provincial digital elevation model (DEM) (Nova Scotia Department of Natural Resources [NSDNR], 2006) as a base layer.

In brief, to create the TPI, I ran the 'Focal Statistics' tool on the provincial DEM 3 times to generate layers delineating the minimum elevation (DEM_{min}), maximum elevation (DEM_{max}), and mean elevation (DEM_{mean}), respectively, in a 420 m^2 neighbourhood. A continuous TPI was then calculated by inputting the following equation into the 'Raster Calculator' tool: $(DEM_{mean} - DEM_{min}) / (DEM_{max} – DEM_{min})$

Next, I increased the cell size of the continuous TPI from 20 m to 150 m (using the 'Resample' tool) so that the resolution of the TPI was consistent with that of other environmental data layers. Finally, I used the 'Reclassify' tool to convert the continuous (150 m) index into a categorical one, For this, classes were defined according to standard deviation (STD), as follows: valleys (< -1 STD), low-slopes (-1 STD to -0.5 STD), mid-slopes (-0.5 STD to 0.5 STD), up-slope (0.5 STD to 1 STD), and ridges (>1 STD).

Depth to water-table index. A continuous index delineating the distance between the water-table and the soil surface was obtained from the Dalhousie University GIS Center, who in-turn received it from NSDNR (NSDNR, 2007a). (Note that this layer was originally created by researchers at the University of New Brunswick using a proprietary method (NSDNR, 2007b.) To ensure that the resolution of environmental data layers remained consistent, I increased the cell size of the depth to water-table (D2W) index from 10 m to 150 m using the ‘Reclassify’ tool. The 150 m D2W index was included as a candidate covariate in the development of Maxent models in chapters 2 and 3.

Solar insolation index. A solar insolation index was created using the provincial DEM (NSDNR, 2006) and included as a candidate covariate in Maxent models developed in chapter 2. To create this index, I first divided the DEM into 9 tiles (to increase computation efficiency) and ran the ‘Area Solar Radiation’ tool on each tile (with a multiday time configuration: days 105 – 288, to approximate the bird breeding season; all other parameters were left at default). The resultant output tiles were then combined into a single layer using the ‘Mosaic’ tool, and values were normalized between 0 and 1. The cell size of the final solar insolation index raster was increased from 20 m to 150 m to ensure that the resolutions of environmental data layers were consistent.

Layers describing forest canopy characteristics. To create GIS layers describing the general characteristics of forest canopy, I converted the vector provincial forest inventory database (FID) (NSDNR, n.d.) into 2 raster files which defined 2nd story height and percent crown closure, respectively. For this, I used the ‘Polygon to Raster’ tool with the ‘MAXIMUM AREA’ operator and an output cell size of 150 m. The resultant output layers (i.e. ‘2nd story height’ and ‘% crown closure’) were used as candidate covariates in the Maxent models developed in chapter 2).

To create GIS layers which characterized forest canopy characteristics according to various statistical values, I again converted the provincial FID (NSDNR, n.d.) from a vector file into 2 raster files which defined 1st story height and percent crown closure, respectively, at a 10 m cell size. I then ran the ‘Focal Statistics’ tool 4 times to create 4 layers delineating mean canopy height (‘1st story height MEAN’), mean canopy closure (‘% crown closure MEAN’), heterogeneity of canopy height (‘1st story height STD’), and heterogeneity of canopy closure (‘% crown closure STD’) in a 150 m^2 area. The cell sizes of all layers output by the ‘Focal Statistics’ tool were increased to 150 m. The layers ‘1st story height MEAN’ and ‘% crown closure MEAN’ were included as candidate covariates in the development of Maxent models in chapters 2 and 3; '1st story height STD' and '% crown closure STD' were only included as candidate covariates in the Maxent models developed in chapter 3.

Distance-based layers. Multiple layers were created to delineate distance from various types of forest stands, anthropogenic disturbance sites, and waterbodies. To delineate distance from forest stand types and anthropogenic disturbances, I first created 7 vector layers by extracting polygons representing (1) coniferous stands, (2) deciduous stands, (3) all-height stands, (4) brushland, (5) stands with dead material, (6) clear-cut areas, and (7) agricultural areas, respectively, from the provincial FID. The 'Euclidean Distance' tool was then run on each of these polygon layers to generate raster files (with a cell size of 150 m) delineating 'distance to coniferous stand', 'distance to deciduous stand', 'distance to all-height stand', 'distance to brushland', 'distance to stand with dead material', 'distance to clear-cut', and 'distance to agriculture', respectively.

We also created 2 layers which delineated distance from waterbodies: 'distance to wetland' and 'distance to river or lake'. To delineate distance from wetlands, we simply ran the 'Euclidean Distance' tool on all mapped wetlands contained in the provincial wetland inventory (NSDNR, n.d.), selecting 150 m as the output cell size. To delineate the distance to rivers and lakes, we converted 2 vector files (NSTDB, n.d.), respectively representing rivers and lakes, into 2 raster files and then merged them together. We subsequently ran the 'Euclidean Distance' tool on the merged raster file, again selecting an output cell size of 150 m.

The layers 'distance to coniferous stand', 'distance to deciduous stand', 'distance to all-height stand', 'distance to stand with dead material' were included as candidate covariates in the Maxent models developed in chapters 2 and 3. 'Distance to wetland' was included as a candidate covariate for the Maxent models developed in chapter 2 and also in the creation of the landscape complexity index (chapter 3) and the landscape resilience index (chapter 4). 'Distance to brushland', 'distance to clear-cut', and 'distance to agriculture' were only included as candidate covariates in the Maxent models developed in chapter 2.

Virtual species datasets with high- and low-roadside bias weightings. After synthesizing 5000 virtual presence points (according to methods described in section 2.2.2), I created 5 virtual species datasets with low roadside weight (LRW) and 5 virtual species datasets with high roadside weight (HRW). For this, I first calculated the distance of each virtual presence point to the nearest road contained in the 'Roads and Rails' network file (NSTDB, n.d.) using the 'Near' tool. Distance values were then normalized between 0 and 1 and reversed (using the 'Field Calculator' tool) to generate road distance scores, wherein points near roads received a road distance score that was closer to 1 and points far from roads received a road distance score that was closer to 0. Road distance scores were stored in an attribute table field. Next, I again used the 'Field Calculator' to generate and assign a random number between 0 and 1 to each of the 5000 virtual presence points, and these numbers (i.e. random scores) were also stored in an attribute table field. Following this, I used the 'Field Calculator' a final time to assign "sampling scores" by multiplying road distance scores with random scores. Finally, to create an LRW virtual species dataset, I extracted the 25% of points with the highest sampling scores (i.e. 1250 points); to create an HRW virtual species dataset, I extracted the 5% of points with the highest sampling scores (i.e. 250 points). This process was repeated 5 times in order to create 5 replicate LRW datasets and 5 replicate HRW datasets.

APPENDIX C: RESULTS OF VIRTUAL SPECIES REVERSE STEPWISE ELIMINATION TRIALS (TRIAL SERIES 1)[2]

LRW replicate dataset 1

Uncorrected model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4036	0.7497	35392.44	Distance to all height stand
Run 2	0.4036	0.7498	35392.33	Distance to stand with dead material
Run 3	0.4021	0.7484	35385.33	Distance to waterbody
Run 4	0.4016	0.7477	35388.1	Solar insolation
Run 5	0.3881	0.7421	35368.75	2nd story height
Run 6	0.3818	0.7401	35380.43	Distance to wetland
Run 7	*0.3813*	*0.7392*	*35366.6*	*D2W*
Run 8	0.3782	0.7354	35387.26	*Distance to scrubland*
Run 9	0.3765	0.7337	35379.57	*Distance to clear-cut*
Run 10	0.3791	0.7328	35383.11	*TPI*
Run 11	0.3894	0.7339	35459.24	*Distance to agriculture*
Run 12	0.4016	0.7266	35574.03	*Distance to coniferous stand*
Run 13	0.346	0.7078	35719.32	*** % crown closure*
Spatial Filter (SF) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4056	0.7514	33861.07	Distance to all height stand
Run 2	0.4056	0.7513	33852.05	Distance to waterbodies
Run 3	0.4051	0.7506	33842.47	Solar insolation
Run 4	0.4307	0.7449	33845.69	2nd story height
Run 5	0.3864	0.7436	33845.46	D2W
Run 6	0.3836	0.7398	33858.71	Distance to wetland
Run 7	0.3827	0.7385	33864.26	Distance to stand with dead material
Run 8	0.3799	0.7363	33849.92	Distance to scrubland
Run 9	*0.3773*	*0.7342*	*33842.57*	*Distance to clear-cut*
Run 10	0.3798	0.7334	33858.37	*TPI*
Run 11	0.3902	0.7345	33922.68	*Distance to coniferous stand*
Run 12	0.3597	0.7246	34046.75	*Distance to agriculture*
Run 13	0.3469	0.708	34160.99	*** % crown closure*

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[2] For all virtual species reverse stepwise elimination summaries, the final "best" model (as selected according to AIC$_c$ score) as well as the covariates it contained are shown in italics.

Background Manipulation (BM) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.3722	0.7501	35398.15	Distance to all height stand
Run 2	0.3721	0.75	35387.66	Distance to waterbody
Run 3	0.3712	0.7489	35379.94	Solar insolation
Run 4	0.3635	0.7427	35394.6	2nd story height
Run 5	0.3693	0.745	35376.84	D2W
Run 6	0.3792	0.7476	35376.65	Distance to stand with dead material
Run 7	0.3786	0.7468	35377.19	Distance to wetland
Run 8	0.3779	0.7462	35373.99	Distance to scrubland
Run 9	*0.3753*	*0.7426*	*35370.8*	*Distance to clear-cut*
Run 10	0.3707	0.739	35386.43	*TPI*
Run 11	0.3371	0.7219	35476.61	*Distance to agriculture*
Run 12	0.305	0.7006	35577	*Distance to coniferous stand*
Run 13	0.2595	0.6801	35722.38	*** % crown closure*
SF+BM model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.3752	0.7511	33854	Distance to all height stand
Run 2	0.3752	0.7512	33844.44	Distance to waterbody
Run 3	0.3743	0.75	33841.46	Solar insolation
Run 4	0.3668	0.7445	33840.77	2nd story height
Run 5	*0.3728*	*0.7466*	*33833.75*	*D2W*
Run 6	0.3824	0.7493	33845.24	*Distance to wetland*
Run 7	0.3816	0.7482	33852.74	*Distance to stand with dead material*
Run 8	0.3805	0.7474	33859.03	*Distance to scrubland*
Run 9	0.3766	0.7432	33839.16	*Distance to clear-cut*
Run 10	0.3721	0.7398	33855.98	*TPI*
Run 11	0.3388	0.7232	33928.48	*Distance to agriculture*
Run 12	0.3071	0.7015	34033.84	*Distance to coniferous stand*
Run 13	0.262	0.6817	34167.52	*** % crown closure*

LRW replicate dataset 2

Uncorrected model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4277	0.7563	35220.38	Distance to all height stand
Run 2	0.4276	0.7562	35217.32	Distance to composite wetland
Run 3	0.4273	0.7553	35223.82	Distance to stand with dead material
Run 4	0.4266	0.7547	35203.95	2nd story height
Run 5	0.4143	0.7512	35197.58	Distance to fine-scale waterbody
Run 6	0.4127	0.7502	35200.92	Depth to watertable
Run 7	0.4192	0.7503	35195.58	Solar insolation
Run 8	0.4037	0.7448	35200.66	Distance to scrubland
Run 9	*0.4021*	*0.7434*	*35189.07*	*Distance to clear-cut*
Run 10	0.4078	0.743	35191.14	*TPI*
Run 11	0.4125	0.7422	35298.58	*Distance to agriculture*
Run 12	0.4225	0.7374	35430.83	*Distance to coniferous stand*
Run 13	0.3693	0.719	35567.33	*** % crown closure*
Spatial Filter (SF) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4245	0.7556	33807.65	Distance to wetland
Run 2	0.4244	0.7551	33813.87	Distance to all height stand
Run 3	0.4241	0.7546	33798.55	Distance to stand with dead material
Run 4	0.4232	0.7538	33803.19	Distance to waterbody
Run 5	0.4213	0.7528	33809.95	2nd story height
Run 6	0.4092	0.7497	33806.94	Solar insolation
Run 7	*0.4039*	*0.747*	*33800.13*	*D2W*
Run 8	0.4002	0.744	33811.04	*Distance to clear-cut*
Run 9	0.3987	0.7423	33801.55	*Distance to scrubland*
Run 10	0.4046	0.7425	33801.01	*TPI*
Run 11	0.4083	0.7417	33891.93	*Distance to agriculture*
Run 12	0.4188	0.7379	34010.99	*Distance to coniferous stand*
Run 13	0.3665	0.7201	34139.48	*** % crown closure*

Background Manipulation (BM) model run #	**Training gain**	**AUC score**	**AIC_c score**	**Covariate removed**
Run 1	0.3926	0.754	35220.38	Distance to wetland
Run 2	0.3924	0.7538	35217.32	Distance to all height stand
Run 3	0.3924	0.7535	35223.82	Solar insolation
Run 4	0.3837	0.7494	35203.95	D2W
Run 5	0.3905	0.751	35197.58	Distance to waterbody
Run 6	0.3897	0.7506	35200.92	Distance to clear-cut
Run 7	0.3886	0.7496	35195.58	2^{nd} story height
Run 8	0.4014	0.7538	35200.66	Distance to stand with dead material
Run 9	*0.4006*	*0.7525*	*35189.07*	*Distance to scrubland*
Run 10	0.3981	0.7504	35191.14	*TPI*
Run 11	0.3543	0.7289	35298.58	*Distance to agriculture*
Run 12	0.3172	0.7076	35430.83	*Distance to coniferous stand*
Run 13	0.2738	0.6898	35567.33	*** % crown closure*
SF+BM model run #	**Training gain**	**AUC score**	**AIC_c score**	**Covariate removed**
Run 1	0.3906	0.7541	33834.22	Distance to wetland
Run 2	0.3905	0.7539	33828.1	Distance to all height stand
Run 3	0.3905	0.7535	33823.19	Distance to stand with dead material
Run 4	0.3892	0.7521	33817.12	Solar insolation
Run 5	0.3806	0.7486	33796.3	2^{nd} story height
Run 6	0.3854	0.7478	33788.47	Distance to waterbody
Run 7	0.3845	0.7469	33814.17	D2W
Run 8	0.4007	0.7531	33797.62	Distance to clear-cut
Run 9	0.3988	0.7519	33788.22	Distance to scrubland
Run 10	*0.3964*	*0.7501*	*33787.01*	*TPI*
Run 11	0.3517	0.7288	33912.37	*Distance to agriculture*
Run 12	0.3168	0.7093	34020.55	*Distance to coniferous stand*
Run 13	0.2735	0.6918	34152.99	***Percent crown closure*

LRW replicate dataset 3

Uncorrected model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4148	0.7496	35172.63	Distance to all height stand
Run 2	0.4148	0.7496	35165.31	Distance to stand with dead material
Run 3	0.4141	0.7488	35152.66	Solar insolation
Run 4	0.3985	0.742	35163.2	D2W
Run 5	0.393	0.7401	35156.73	Distance to waterbody
Run 6	0.3929	0.74	35157.3	2nd story height
Run 7	0.3911	0.7379	35155.79	Distance to scrubland
Run 8	*0.3901*	*0.7367*	*35152.26*	*Distance to wetland*
Run 9	0.389	0.7347	35161.77	*Distance to clear-cut*
Run 10	0.3933	0.7341	35176.78	*TPI*
Run 11	0.4061	0.7408	35247.32	*Distance to agriculture*
Run 12	0.4128	0.7348	35378.43	*Distance to coniferous stand*
Run 13	0.3499	0.7144	35533.04	*** % crown closure*
Spatial Filter (SF) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4127	0.7484	33762.52	Distance to all height stand
Run 2	0.4127	0.7485	33783.04	Distance to waterbody
Run 3	0.4124	0.748	33758.5	2nd story height
Run 4	0.404	0.748	33752.35	D2W
Run 5	0.4072	0.7446	33769.7	Solar insolation
Run 6	0.3913	0.7391	33761.44	Distance to scrubland
Run 7	0.3902	0.7382	33760.79	Distance to stand with dead material
Run 8	0.4157	0.736	33752.04	Distance to wetland
Run 9	*0.3865*	*0.7336*	*33753.02*	*Distance to clear-cut*
Run 10	0.3911	0.7331	33766.77	*TPI*
Run 11	0.4275	0.7389	33830.84	*Distance to agriculture*
Run 12	0.4108	0.7339	33949.15	*Distance to coniferous stand*
Run 13	0.3485	0.7134	34101.43	*** % crown closure*

Background Manipulation (BM) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.3774	0.745	35192.89	Distance to all height stand
Run 2	0.3774	0.745	35193.33	Distance to scrubland
Run 3	0.3768	0.7441	35187.11	Distance to waterbody
Run 4	0.3765	0.7439	35186.46	Solar insolation
Run 5	0.3688	0.7391	35167.3	D2W
Run 6	0.3825	0.7457	35173.36	2nd story height
Run 7	0.392	0.7478	35161.53	Distance to stand with dead material
Run 8	*0.3917*	*0.7475*	*35151.78*	*Distance to wetland*
Run 9	0.3893	0.7455	35161.65	*Distance to clear-cut*
Run 10	0.3863	0.7426	35169.12	*TPI*
Run 11	0.3478	0.7265	35255.41	*Distance to agriculture*
Run 12	0.3121	0.7056	35372.76	*Distance to coniferous stand*
Run 13	0.2615	0.686	35531.32	*** % crown closure*

SF+BM model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.3767	0.7447	33781.68	Distance to waterbody & Distance to all height stand
Run 2	n/a	n/a	n/a	n/a
Run 3	0.3764	0.7444	33775.22	2nd story height
Run 4	0.3827	0.7449	33782.51	Solar insolation
Run 5	0.3769	0.7426	33779.92	D2W
Run 6	0.3918	0.7485	33751	Distance to stand with dead material
Run 7	0.3914	0.748	33783.69	Distance to wetland
Run 8	0.3885	0.7455	33766.35	Distance to scrubland
Run 9	*0.3872*	*0.7442*	*33747.42*	*Distance to clear-cut*
Run 10	0.3847	0.7417	33763.77	*TPI*
Run 11	0.3464	0.7255	33835.86	*Distance to agriculture*
Run 12	0.3131	0.7052	33946.16	*Distance to coniferous stand*
Run 13	0.2626	0.6859	34096.93	*** % crown closure*

LRW replicate dataset 4

Uncorrected model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4174	0.7521	35356.99	2nd story height
Run 2	0.4061	0.7487	35374.29	Distance to waterbody
Run 3	0.4055	0.7483	35383.82	D2W
Run 4	0.4088	0.7453	35364.03	Distance to scrubland
Run 5	0.4085	0.7449	35348.74	Distance to clear-cut
Run 6	0.4079	0.7444	35358.45	Distance to wetland
Run 7	0.4074	0.7433	35345.78	Distance to all height stand
Run 8	0.4066	0.7426	35346.36	Solar insolation
Run 9	0.3926	0.7364	35345.13	Distance to stand with dead material
Run 10	*0.3976*	*0.7372*	*35335.38*	*TPI*
Run 11	0.4028	0.737	35424.84	*Distance to agriculture*
Run 12	0.4183	0.7329	35531.39	*Distance to coniferous stand*
Run 13	0.3629	0.7144	35669.18	*** % crown closure*
Spatial Filter (SF) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4133	0.7511	33619.85	Distance to clear-cut
Run 2	0.4116	0.7497	33612.62	D2W
Run 3	0.4049	0.745	33613.16	Distance to scrubland
Run 4	0.4048	0.745	33600.66	2nd story height
Run 5	0.4055	0.7439	33626.17	Solar insolation
Run 6	0.3911	0.7387	33605.82	Distance to all height stand
Run 7	0.3898	0.7378	33603.15	Distance to waterbody
Run 8	0.389	0.737	33602.7	Distance to stand with dead material
Run 9	0.3875	0.7359	33595.46	Distance to wetland
Run 10	*0.3929*	*0.7357*	*33594.19*	*TPI*
Run 11	0.3998	0.7355	33669.85	*Distance to agriculture*
Run 12	0.414	0.7323	33773.95	*Distance to coniferous stand*
Run 13	0.3571	0.7119	33902.68	*** % crown closure*

Background Manipulation (BM) model run #	**Training gain**	**AUC score**	**AIC_c score**	**Covariate removed**
Run 1	0.3959	0.7492	35346.32	Distance to all height stand
Run 2	0.3957	0.7488	35275.12	Distance to scrubland
Run 3	0.3955	0.7488	35265.14	D2W
Run 4	0.4086	0.7505	35256.74	Distance to waterbody
Run 5	0.4079	0.749	35242.88	Distance to wetland
Run 6	0.407	0.7478	35223.4	2nd story height
Run 7	0.3903	0.7408	35233.42	Solar insolation
Run 8	0.3892	0.7411	35214.75	Distance to clear-cut
Run 9	0.3886	0.7406	35214.06	Distance to stand with dead material
Run 10	*0.3873*	*0.7386*	*35189.16*	*TPI*
Run 11	0.3758	0.7306	35272.16	*Distance to agriculture*
Run 12	0.3414	0.7103	35387.77	*Distance to coniferous stand*
Run 13	0.2995	0.6928	35537.51	*** % crown closure*

SF+BM model run #	**Training gain**	**AUC score**	**AIC_c score**	**Covariate removed**
Run 1	0.3927	0.7481	33621	Distance to all height stand
Run 2	0.3925	0.7478	33618.61	Distance to scrubland
Run 3	0.3922	0.7477	33607.05	D2W
Run 4	0.405	0.7488	33603.65	Distance to clear-cut
Run 5	0.4037	0.747	33606.66	Distance to wetland
Run 6	0.4026	0.7454	33609.87	Solar insolation
Run 7	0.3743	0.7353	33604.4	2nd story height
Run 8	0.386	0.7402	33600.19	Distance to waterbody
Run 9	0.3853	0.7393	33601.77	Distance to stand with dead material
Run 10	*0.384*	*0.7374*	*33580.92*	*TPI*
Run 11	0.3743	0.7299	33675.57	*Distance to agriculture*
Run 12	0.3412	0.7101	33770.86	*Distance to coniferous stand*
Run 13	0.2974	0.6921	33906.29	*** % crown closure*

LRW replicate dataset 5

Uncorrected model run #	**Training gain**	**AUC score**	**AIC_c score**	**Covariate removed**
Run 1	0.4111	0.7526	35327.21	Distance to waterbody
Run 2	0.411	0.7523	35322.38	Distance to all height stand
Run 3	0.4105	0.7517	35314.82	Distance to scrubland
Run 4	0.4092	0.7502	35301.8	Distance to wetland
Run 5	0.4087	0.7496	35287.33	2nd story height
Run 6	0.3975	0.7474	35273.43	D2W
Run 7	0.4036	0.7469	35283.89	Distance to stand with dead material
Run 8	0.402	0.746	35275.17	Solar insolation
Run 9	*0.3861*	*0.7387*	*35272.34*	*Distance to clear-cut*
Run 10	0.3903	0.7386	35292.89	*TPI*
Run 11	0.3967	0.7399	35363.46	*Distance to agriculture*
Run 12	0.4118	0.7366	35494.74	*Distance to coniferous stand*
Run 13	0.3551	0.7162	35630.54	*** % crown closure*
Spatial Filter (SF) model run #	**Training gain**	**AUC score**	**AIC_c score**	**Covariate removed**
Run 1	0.4109	0.7529	33616.99	Distance to waterbody
Run 2	0.4106	0.7526	33617.22	Distance to stand with dead material
Run 3	0.4098	0.7517	33603.34	Distance to all height stand
Run 4	0.4093	0.7509	33601.12	Distance to wetland
Run 5	0.4088	0.7504	33587.87	D2W
Run 6	0.4037	0.7477	33584.46	2nd story height
Run 7	*0.4037*	*0.748*	*33578.56*	*Distance to scrubland*
Run 8	0.4014	0.7464	33581.65	*Solar insolation*
Run 9	0.3843	0.7383	33587.34	*Distance to clear-cut*
Run 10	0.3882	0.738	33590.23	*TPI*
Run 11	0.3937	0.7389	33663.91	*Distance to agriculture*
Run 12	0.4088	0.7351	33780.89	*Distance to coniferous stand*
Run 13	0.3519	0.715	33912.36	*** % crown closure*

Background Manipulation (BM) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.404	0.7475	35330.95	Distance to all height stand
Run 2	0.3676	0.7469	35325.42	D2W
Run 3	0.3904	0.7541	35276.89	Distance to wetland
Run 4	0.3901	0.7533	35275.41	Distance to waterbody
Run 5	0.3899	0.7529	35270.06	2nd story height
Run 6	0.3719	0.7548	35311.14	Distance to stand with dead material
Run 7	0.371	0.7449	35303.36	Solar insolation
Run 8	0.3709	0.7444	35275.72	Distance to clear-cut
Run 9	*0.3693*	*0.7434*	*35266.93*	*Distance to scrubland*
Run 10	0.3668	0.7413	35277.37	*TPI*
Run 11	0.3572	0.7327	35367.51	*Distance to agriculture*
Run 12	0.3522	0.7145	35490.13	*Distance to coniferous stand*
Run 13	0.2832	0.6953	35632.45	*** % crown closure*
SF+BM model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.3689	0.7483	33625.68	Distance to waterbody
Run 2	0.3684	0.7479	33622.08	Distance to all height stand
Run 3	0.368	0.7474	33606.93	D2W
Run 4	0.392	0.7546	33580.54	Distance to wetland
Run 5	0.3915	0.7539	33580.84	2nd story height
Run 6	0.3724	0.7462	33597.97	Distance to stand with dead material
Run 7	0.3714	0.7452	33602.33	Solar insolation
Run 8	0.3711	0.7445	33568.63	Distance to clear-cut
Run 9	*0.3695*	*0.7431*	*33567.31*	*Distance to scrubland*
Run 10	0.3664	0.7409	33588.68	*TPI*
Run 11	0.3563	0.7319	33683.85	*Distance to agriculture*
Run 12	0.3265	0.7146	33781.24	*Distance to coniferous stand*
Run 13	0.2837	0.6953	33917.48	*** % crown closure*

HRW replicate dataset 1

Uncorrected model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.5124	0.8092	7316.00	Distance to-all height stand
Run 2	0.5124	0.8093	7288.49	Distance to river or lake
Run 3	0.5104	0.8076	7247.82	Solar insolation
Run 4	0.4947	0.8022	7210.08	2nd story height
Run 5	0.49	0.7987	7172.10	D2W
Run 6	0.4712	0.7923	7180.20	Distance to wetland
Run 7	0.4639	0.7873	7155.31	Distance to clear-cut
Run 8	0.4497	0.7816	7153.97	TPI
Run 9	0.4438	0.7779	7176.63	Distance to stand with dead material
Run 10	0.4326	0.771	7140.93	Distance to scrubland
Run 11	*0.4174*	*0.7589*	*7128.64*	*Distance to agriculture*
Run 12	0.3948	0.7353	7138.12	*Distance to coniferous stand*
Run 13	0.3288	0.7086	7170.67	*** % crown closure*
Spatial Filter (SF) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.5051	0.8078	7120.91	Distance to all height stand
Run 2	0.5048	0.8076	7096.06	Distance to river or lake
Run 3	0.5029	0.8054	7076.74	D2W
Run 4	0.4861	0.8003	7030.47	TPI
Run 5	0.4967	0.802	7060.75	Solar insolation
Run 6	0.4569	0.7881	7025.24	Distance to wetland
Run 7	0.4465	0.7813	7009.76	2nd story height
Run 8	0.4543	0.7813	7005.18	Distance to stand with dead material
Run 9	0.4445	0.7752	6984.78	Distance to clear-cut
Run 10	0.4266	0.7673	6975.59	Distance to scrubland
Run 11	*0.4113*	*0.7557*	*6962.08*	*Distance to coniferous stand*
Run 12	0.3532	0.7333	6998.81	*Distance to agriculture*
Run 13	0.3237	0.7062	7002.79	*** % crown closure*

Background Manipulation (BM) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4913	0.8069	7266.28	Distance to all height stand
Run 2	0.4907	0.8059	7262.92	D2W
Run 3	0.5036	0.8068	7236.10	Solar insolation
Run 4	0.4716	0.795	7204.79	Distance to waterbody
Run 5	0.469	0.793	7179.16	2nd story height
Run 6	0.468	0.7917	7175.16	Distance to wetland
Run 7	0.4597	0.7865	7164.36	Distance to stand with dead material
Run 8	0.4477	0.7808	7135.72	TPI
Run 9	0.4447	0.777	7131.53	Distance to scrubland
Run 10	*0.4321*	*0.7704*	*7129.14*	*Distance to clear-cut*
Run 11	0.4166	0.761	7133.12	*Distance to agriculture*
Run 12	0.3831	0.7347	7137.60	*Distance to coniferous stand*
Run 13	0.3197	0.7081	7167.70	*** % crown closure*

SF+BM model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4842	0.8076	7094.15	Distance to waterbody
Run 2	0.4804	0.804	7076.04	Distance to all height stand
Run 3	0.48	0.8034	7063.43	Solar insolation
Run 4	0.473	0.7969	7065.85	TPI
Run 5	0.4891	0.8017	7043.73	2nd story height
Run 6	0.476	0.7961	7028.24	Distance to wetland
Run 7	0.4659	0.7904	7006.70	D2W
Run 8	0.4508	0.7833	6991.94	Distance to stand with dead material
Run 9	0.4399	0.7755	6962.46	Distance to scrubland
Run 10	*0.4276*	*0.7694*	*6956.57*	*Distance to clear-cut*
Run 11	0.411	0.7594	6967.43	*Distance to agriculture*
Run 12	0.3776	0.7314	6969.03	*Distance to coniferous stand*
Run 13	0.315	0.7063	6999.89	*** % crown closure*

HRW replicate dataset 2

Uncorrected model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.629	0.831	7051.34	Distance to waterbody
Run 2	0.6199	0.8283	7056.33	Distance to scrubland
Run 3	0.6151	0.825	7041.78	Distance to wetland
Run 4	0.6123	0.8229	7011.66	Solar insolation
Run 5	0.591	0.8171	7006.32	D2W
Run 6	0.5716	0.8092	7020.37	Distance to all-height stand
Run 7	0.5642	0.8042	7030.13	2nd story height
Run 8	0.5503	0.7981	6999.79	Distance to clear-cut
Run 9	0.5385	0.7936	6990.62	Distance to stand with dead material
Run 10	*0.5169*	*0.7849*	*6986.36*	*Distance to coniferous stand*
Run 11	0.4722	0.7672	7013.02	*Distance to agriculture*
Run 12	0.451	0.756	7018.13	*TPI*
Run 13	0.4026	0.7213	7046.42	*** % crown closure*
Spatial Filter (SF) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.6312	0.8314	6987.57	Distance to composite wetland
Run 2	0.6289	0.8297	6973.97	Solar insolation
Run 3	0.6092	0.8266	6990.87	Distance to waterbody
Run 4	0.6005	0.8229	6978.48	2nd story height
Run 5	0.5808	0.8152	6989.38	Distance to scrubland
Run 6	0.5715	0.81	6954.09	Distance to all-height stand
Run 7	0.5702	0.8082	6941.46	Depth to watertable
Run 8	0.5496	0.798	6944.55	Distance to clearcut
Run 9	0.5381	0.7935	6932.31	Distance to stand with dead material
Run 10	*0.5166*	*0.7853*	*6932.72*	*Distance to coniferous stand*
Run 11	0.4721	0.7674	6963.37	*Distance to agriculture*
Run 12	0.4503	0.7555	6959.42	*TPI*
Run 13	0.4015	0.7201	6991.87	*** % crown closure*

Background Manipulation (BM) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.6021	0.8326	7111.21	Distance to wetland
Run 2	0.5977	0.8298	7089.75	Solar insolation
Run 3	0.585	0.8223	7058.22	Distance to waterbody
Run 4	0.5743	0.8174	7038.65	Distance to scrubland
Run 5	0.5664	0.8137	7002.74	Distance to all height stand
Run 6	0.5601	0.8085	6993.57	2nd story height
Run 7	0.5409	0.8016	6994.30	Distance to clear-cut
Run 8	*0.5269*	*0.7971*	*6995.23*	*D2W*
Run 9	0.5333	0.7978	6997.22	*Distance to stand with dead material*
Run 10	0.5163	0.7871	6996.74	*Distance to coniferous stand*
Run 11	0.4632	0.7667	7018.82	*Distance to agriculture*
Run 12	0.4238	0.7485	7014.95	*TPI*
Run 13	0.3874	0.7181	7050.78	*** % crown closure*
SF+BM model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.6022	0.8328	7042.03	Distance to scrubland
Run 2	0.5965	0.8294	7011.08	Solar insolation
Run 3	0.5824	0.821	6968.5	Distance to wetland
Run 4	0.5791	0.8198	6954.88	Distance to waterbody
Run 5	0.5673	0.8139	6948.03	Distance to all height stand
Run 6	0.5612	0.8089	6944.53	2nd story height
Run 7	0.5402	0.801	6934	Distance to clear-cut
Run 8	0.527	0.7965	6940.01	Distance to stand with dead material
Run 9	*0.5127*	*0.7885*	*6929.72*	*D2W*
Run 10	0.5159	0.7872	6937.99	*Distance to agriculture*
Run 11	0.4746	0.7731	6938.49	*Distance to coniferous stand*
Run 12	0.4233	0.7488	6960.7	*TPI*
Run 13	0.3867	0.718	6992.04	*** % crown closure*

HRW replicate dataset 3

Uncorrected model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.5806	0.8217	7163.23	Distance to all height stand
Run 2	0.5788	0.8206	7140.73	Distance to waterbody
Run 3	0.5741	0.8185	7113.49	2^{nd} story height
Run 4	0.5616	0.8176	7103.10	Distance to scrubland
Run 5	0.5567	0.815	7089.31	Solar insolation
Run 6	*0.544*	*0.8101*	*7066.51*	*D2W*
Run 7	0.5279	0.7974	7084.09	*Distance to wetland*
Run 8	0.5148	0.7892	7084.83	*Distance to stand with dead material*
Run 9	0.4892	0.7788	7068.75	*TPI*
Run 10	0.4765	0.7772	7086.35	*Distance to clear-cut*
Run 11	0.4677	0.7666	7088.83	*Distance to agriculture*
Run 12	0.4336	0.7365	7099.80	*Distance to coniferous stand*
Run 13	0.375	0.7076	7125.83	*** % crown closure*
Spatial Filter (SF) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.5051	0.8078	7137.75	Distance to all height stand
Run 2	0.5756	0.8202	7110.85	Solar insolation
Run 3	0.5576	0.8153	7104.81	2^{nd} story height
Run 4	0.5471	0.814	7085.33	Distance to scrubland
Run 5	0.5417	0.811	7044.88	Distance to waterbody
Run 6	0.5399	0.8093	7038.23	D2W
Run 7	0.5244	0.7969	7048.65	Distance to clear-cut
Run 8	0.5092	0.7894	7049.46	Distance to stand with dead material
Run 9	0.4857	0.7787	7037.98	Distance to wetland
Run 10	*0.475*	*0.7673*	*7031.43*	*TPI*
Run 11	0.4671	0.7665	7060.50	*Distance to coniferous stand*
Run 12	0.4133	0.7478	7090.88	*Distance to agriculture*
Run 13	0.3744	0.7073	7097.23	*** % crown closure*

Background Manipulation (BM) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.5612	0.8195	7165.61	Distance to all height stand
Run 2	0.5566	0.818	7173.85	Distance to waterbody
Run 3	0.5518	0.816	7147.32	Distance to scrubland
Run 4	0.547	0.8135	7126.73	Solar insolation
Run 5	0.5367	0.8102	7097.83	2nd story height
Run 6	0.5238	0.8035	7101.76	D2W
Run 7	0.5292	0.8025	7083.15	Distance to wetland
Run 8	0.5136	0.7936	7073.08	Distance to stand with dead material
Run 9	0.4966	0.7834	7074.54	Distance to clear-cut
Run 10	*0.4839*	*0.7756*	*7068.31*	*TPI*
Run 11	0.4657	0.7654	7087.86	*Distance to agriculture*
Run 12	0.4223	0.7386	7101.06	*Distance to coniferous stand*
Run 13	0.365	0.7061	7125.12	*** % crown closure*

SF+BM model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.5581	0.8193	7126.26	Distance to all height stand
Run 2	0.5534	0.8179	7147.81	2nd story height
Run 3	0.5549	0.8177	7070.60	Solar insolation
Run 4	0.5264	0.8075	7092.32	Distance to waterbody
Run 5	0.5245	0.806	7098.44	Distance to scrubland
Run 6	0.52	0.8029	7076.37	Distance to clear-cut
Run 7	0.5039	0.7956	7065.84	D2W
Run 8	0.5133	0.795	7044.75	Distance to stand with dead material
Run 9	0.4971	0.7865	7039.74	Distance to composite wetland
Run 10	*0.4818*	*0.7751*	*7040.80*	*Distance to agriculture*
Run 11	0.4358	0.7516	7051.75	*Distance to coniferous stand*
Run 12	0.3734	0.7237	7081.54	*TPI*
Run 13	0.0607	0.582	7248.81	*** % crown closure*

HRW replicate dataset 4

Uncorrected model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.5044	0.8151	7247.57	2nd story height
Run 2	0.4884	0.8104	7163.31	Distance to all height stand
Run 3	0.4856	0.8087	7158.43	Distance to waterbody
Run 4	0.4815	0.8065	7137.78	Distance to wetland
Run 5	0.4719	0.8008	7114.32	Distance to scrubland
Run 6	0.4617	0.7936	7079.41	Solar insolation
Run 7	0.4414	0.7834	7081.70	Distance to stand with dead material
Run 8	0.4227	0.7749	7069.76	D2W
Run 9	*0.4131*	*0.7683*	*7049.72*	*Distance to clear-cut*
Run 10	0.4013	0.7617	7057.77	*TPI*
Run 11	0.3913	0.7584	7079.28	*Distance to coniferous stand*
Run 12	0.3648	0.7511	7088.26	*Distance to agriculture*
Run 13	0.3125	0.713	7095.22	*** % crown closure*
Spatial Filter (SF) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.5053	0.8153	7169.02	Distance to all height stand
Run 2	0.5028	0.814	7134.64	Distance to waterbody
Run 3	0.4976	0.8126	7121.76	2nd story height
Run 4	0.4815	0.8064	7090.39	Solar insolation
Run 5	0.4616	0.7989	7057.47	Distance to wetland
Run 6	0.4551	0.7921	7041.93	D2W
Run 7	0.443	0.7865	7011.75	Distance to clear-cut
Run 8	0.4291	0.7808	7005.90	Distance to scrubland
Run 9	*0.4195*	*0.7705*	*6994.88*	*Distance to stand with dead material*
Run 10	0.4002	0.7611	6996.95	*Distance to coniferous stand*
Run 11	0.3679	0.7495	7009.61	*TPI*
Run 12	0.3621	0.7498	7030.71	*Distance to agriculture*
Run 13	0.3108	0.7127	7038.35	*** % crown closure*

Background Manipulation (BM) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.5018	0.8176	7149.62	2nd story height
Run 2	0.4988	0.8183	7192.61	Distance to wetland
Run 3	0.4886	0.8125	7168.24	Distance to waterbody
Run 4	0.4827	0.8092	7126.47	Distance to all height stand
Run 5	0.4765	0.8071	7127.02	D2W
Run 6	0.4511	0.7915	7079.46	Solar insolation
Run 7	0.4337	0.7848	7064.98	Distance to scrubland
Run 8	0.4251	0.7757	7049.62	Distance to clear-cut
Run 9	*0.4119*	*0.7697*	*7050.78*	*Distance to stand with dead material*
Run 10	0.3982	0.7603	7056.43	*TPI*
Run 11	0.3925	0.758	7073.31	*Distance to coniferous stand*
Run 12	0.3654	0.7494	7080.09	*Distance to agriculture*
Run 13	0.3034	0.7107	7092.49	*** % crown closure*

SF+BM model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.5035	0.8182	7079.33	Distance to all height stand
Run 2	0.4974	0.8156	7075.45	Distance to waterbody
Run 3	0.4897	0.8135	7057.46	Distance to wetland
Run 4	0.4806	0.8088	7043.30	Solar insolation
Run 5	0.4592	0.8001	7044.69	2nd story height
Run 6	0.4424	0.7902	7041.18	D2W
Run 7	0.4335	0.7856	7004.87	Distance to stand with dead material
Run 8	0.4205	0.7783	7010.05	Distance to scrubland
Run 9	*0.4096*	*0.7664*	*6998.78*	*Distance to clear-cut*
Run 10	0.3996	0.7598	7003.23	*TPI*
Run 11	0.39	0.7569	7013.15	*Distance to coniferous stand*
Run 12	0.3634	0.7483	7019.86	*Distance to agriculture*
Run 13	0.3018	0.7102	7035.65	*** % crown closure*

HRW replicate dataset 5

Uncorrected model run #	Training gain	AUC score	AIC$_c$ score	Covariate removed
Run 1	0.4963	0.8048	7328.00	Distance to waterbody
Run 2	0.4902	0.8031	7272.27	Distance to all height stand
Run 3	0.4862	0.8004	7275.27	2nd story height
Run 4	0.465	0.7949	7225.93	Distance to stand with dead material
Run 5	0.456	0.7904	7184.53	Distance to wetland
Run 6	0.4496	0.7846	7170.53	Distance to clear-cut
Run 7	0.4394	0.7804	7165.11	Distance to scrubland
Run 8	0.431	0.7734	7146.96	Solar insolation
Run 9	0.4201	0.767	7167.18	TPI
Run 10	0.427	0.7677	7159.59	D2W
Run 11	*0.4196*	*0.7575*	*7143.00*	*Distance to coniferous stand*
Run 12	0.3754	0.7443	7154.03	*Distance to agriculture*
Run 13	0.3238	0.7085	7173.86	*** % crown closure*
Spatial Filter (SF) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4941	0.8046	7221.79	Distance to waterbody
Run 2	0.4884	0.802	7205.08	2nd story height
Run 3	0.4568	0.7946	7175.38	Distance to all height stand
Run 4	0.4629	0.7945	7167.07	Distance to scrubland
Run 5	0.4545	0.7906	7146.41	Distance to wetland
Run 6	0.4475	0.7837	7129.89	Solar insolation
Run 7	0.4344	0.7757	7144.51	Distance to stand with dead material
Run 8	0.4221	0.7719	7118.15	Distance to clear-cut
Run 9	0.4186	0.7666	7096.81	TPI
Run 10	0.4253	0.7673	7109.02	D2W
Run 11	*0.4128*	*0.7573*	*7083.95*	*Distance to coniferous stand*
Run 12	0.3744	0.7455	7099.25	*Distance to agriculture*
Run 13	0.3218	0.7102	7119.35	*** % crown closure*

Background Manipulation (BM) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4745	0.8035	7276.17	Distance to clear-cut
Run 2	0.4671	0.7993	7245.09	Distance to wetland
Run 3	0.4635	0.7974	7240.63	2nd story height
Run 4	0.4691	0.7951	7215.03	Distance to all height stand
Run 5	0.4613	0.7926	7177.46	TPI
Run 6	0.436	0.7859	7202.62	Distance to waterbody
Run 7	0.4296	0.7865	7193.56	D2W
Run 8	0.4305	0.7778	7175.90	Solar insolation
Run 9	0.4316	0.7739	7157.52	Distance to stand with dead material
Run 10	0.4234	0.7667	7145.16	Distance to scrubland
Run 11	*0.4134*	*0.7541*	*7135.10*	*Distance to coniferous stand*
Run 12	0.3705	0.7403	7152.07	*Distance to agriculture*
Run 13	0.3117	0.7102	7174.00	*** % crown closure*
SF+BM model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4725	0.8032	7227.59	Distance to wetland
Run 2	0.4681	0.8003	7200.49	Distance to waterbody
Run 3	0.4575	0.7955	7165.69	2nd story height
Run 4	0.4638	0.7938	7147.28	Distance to all height stand
Run 5	0.4595	0.7939	7145.86	Distance to stand with dead material
Run 6	0.4528	0.7911	7119.38	Distance to clear-cut
Run 7	0.4459	0.788	7117.34	TPI
Run 8	0.4178	0.7793	7116.24	Solar insolation
Run 9	0.4239	0.7748	7117.23	D2W
Run 10	0.4219	0.7669	7083.84	Distance to scrubland
Run 11	*0.4122*	*0.7545*	*7081.21*	*Distance to coniferous stand*
Run 12	0.3698	0.7424	7097.43	*Distance to agriculture*
Run 13	0.3326	0.7083	7121.51	*** % crown closure*

APPENDIX D: RESULTS OF REAL SPECIES (CANADA WARBLER) REVERSE STEPWISE ELIMINATION TRIALS (TRIAL SERIES 2)[3]

Canada Warbler Models

Uncorrected model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.4865	0.7994	12335.66	Distance to all height stand
Run 2	0.4821	0.7988	12372.96	TPI
Run 3	0.4734	0.7942	12315.39	Distance to waterbody
Run 4	0.4685	0.7926	12302.19	2nd story height
Run 5	0.4459	0.7878	12323.46	Solar insolation
Run 6	*0.4551*	*0.7853*	*12273.26*	*Distance to coniferous stand*
Run 7	0.4375	0.7793	12286.94	*% crown closure*
Run 8	0.4215	0.7785	12293.05	*Distance to stand with dead material*
Run 9	0.4013	0.7664	12296.54	*Distance to deciduous stand*
Run 10	0.3792	0.7599	12311.23	*Distance to scrubland*
Run 11	0.3316	0.7491	12339.64	*Distance to agriculture*
Run 12	0.3026	0.7372	12360.65	*D2W*
Run 13	0.2417	0.7115	12428.71	*Distance to clear-cut*
Run 14	0.116	0.6423	12525.42	***Distance to wetland*

Spatial Filter (SF) model run #	**Training gain**	**AUC score**	**AIC$_c$ score**	**Covariate removed**
Run 1	0.3648	0.7819	9158.32	Distance to all height stand
Run 2	0.364	0.7807	9170.31	Distance to agriculture
Run 3	0.358	0.7761	9116.08	Distance to waterbody
Run 4	0.35	0.7717	9110.09	2nd story height
Run 5	0.3528	0.769	9123.00	TPI
Run 6	0.3227	0.7598	9078.39	Solar insolation
Run 7	0.3293	0.7559	9084.43	Distance to stand with dead material
Run 8	*0.3088*	*0.7493*	*9071.19*	*Distance to scrubland*
Run 9	0.2892	0.7414	9080.39	*% Crown closure*
Run 10	0.2702	0.7339	9083.30	*Distance to deciduous stand*
Run 11	0.2514	0.7248	9088.73	*Distance to wetland*
Run 12	0.1983	0.7031	9073.31	*Distance to coniferous stand*
Run 13	0.1611	0.6825	9096.11	*Distance to clear-cut*
Run 14	0.1095	0.6398	9160.79	***D2W*

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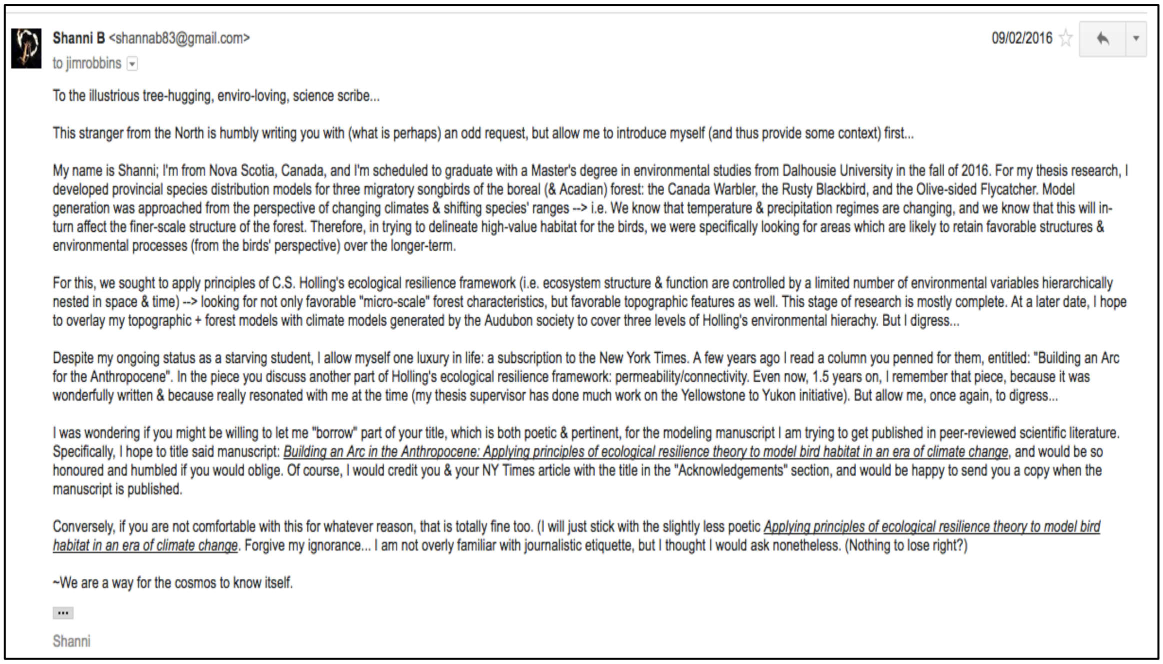
[3] For all Canada Warbler reverse stepwise elimination summaries, the final "best" model (as selected according to AIC$_c$ score) as well as the covariates it contained are shown in italics.

Background Manipulation (BM) model run #	**Training gain**	**AUC score**	**AIC_c score**	**Covariate removed**
Run 1	0.3755	0.8007	12355.27	Distance to waterbody
Run 2	0.375	0.8002	12347.14	Distance to all height stand
Run 3	0.3725	0.7986	12342.82	TPI
Run 4	0.38	0.801	12370.13	2nd story height
Run 5	0.371	0.7952	12323.78	Solar insolation
Run 6	0.3446	0.7858	12356.17	% crown closure
Run 7	*0.3349*	*0.7841*	*12288.16*	*Distance to stand with dead material*
Run 8	0.3189	0.7754	12309.40	*Distance to scrubland*
Run 9	0.2971	0.7643	12330.94	*Distance to agriculture*
Run 10	0.2837	0.755	12360.26	*Distance to deciduous stand*
Run 11	0.2605	0.745	12372.17	*Distance to coniferous stand*
Run 12	0.2344	0.7314	12390.55	*Distance to wetland*
Run 13	0.1803	0.2172	12443.63	*Distance to clear-cut*
Run 14			12525.20	***D2W*
SF+BM model run #	**Training gain**	**AUC score**	**AIC_c score**	**Covariate removed**
Run 1	0.348	0.7818	9120.42	Distance to all height stand
Run 2	0.3471	0.781	9121.98	Distance to waterbody
Run 3	0.3466	0.7798	9095.11	Distance to agriculture
Run 4	0.3421	0.7746	9072.54	TPI
Run 5	0.3459	0.7755	9130.85	Solar insolation
Run 6	0.3157	0.7604	9065.46	Distance to stand with dead material
Run 7	0.2956	0.7544	9065.00	2nd story height
Run 8	0.2857	0.7486	9071.71	% crown closure
Run 9	0.268	0.742	9064.70	Distance to scrubland
Run 10	*0.2476*	*0.7344*	*9046.86*	*Distance to deciduous stand*
Run 11	0.2227	0.7219	9054.25	*Distance to coniferous stand*
Run 12	0.1892	0.7033	9091.20	*Distance to wetland*
Run 13	0.1444	0.6786	9123.10	*Distance to clear-cut*
Run 14	0.0963	0.6347	9153.36	***D2W*

Target Group (TG) model run #	**Training gain**	**AUC score**	**AIC_c score**	**Covariate removed**
Run 1	0.5063	0.7993	12341.05	TPI
Run 2	0.5014	0.7972	12302.94	2nd story height
Run 3	0.4821	0.7926	12304.29	Distance to waterbody
Run 4	0.4745	0.7896	12308.47	Solar insolation
Run 5	*0.4679*	*0.789*	*12235.15*	*Distance to all height stand*
Run 6	0.4584	0.7875	12254.23	*% crown closure*
Run 7	0.4597	0.7807	12255.34	*Distance to stand with dead material*
Run 8	0.4406	0.7732	12261.16	*Distance to deciduous stand*
Run 9	0.4091	0.7663	12281.99	*Distance to coniferous stand*
Run 10	0.3847	0.7582	12287.84	*Distance to scrubland*
Run 11	0.335	0.7491	12333.83	*Distance to agriculture*
Run 12	0.3005	0.7359	12379.34	*Distance to wetland*
Run 13	0.2319	0.7084	12435.10	*Distance to clear-cut*
Run 14	0.1385	0.6525	12530.19	***D2W*
SF+TG model run #	**Training gain**	**AUC score**	**AIC_c score**	**Covariate removed**
Run 1	0.3793	0.7792	9158.16	Distance to all height stand
Run 2	0.3782	0.778	9128.75	TPI
Run 3	0.3652	0.7733	9127.66	2nd story height
Run 4	0.3455	0.7679	9147.11	Distance to waterbody
Run 5	0.34	0.7634	9153.62	Distance to agriculture
Run 6	0.3318	0.7561	9133.71	Solar insolation
Run 7	0.3277	0.754	9066.88	Distance to scrubland
Run 8	*0.3102*	*0.747*	*9057.85*	*% Crown closure*
Run 9	0.2999	0.7413	9073.89	*Distance to stand with dead material*
Run 10	0.2782	0.734	9085.80	*Distance to deciduous stand*
Run 11	0.2499	0.7225	9091.65	*Distance to coniferous stand*
Run 12	0.2146	0.7062	9079.26	*D2W*
Run 13	0.1638	0.68	9100.41	*Distance to clear-cut*
Run 14			9144.08	*Distance to wetland*

APPENDIX E: COPYRIGHT PERMISSION LETTER

The following is a copy of the e-mail with New York Times writer Jim Robbins, who kindly granted permission for use of the phrase “Building an Arc in the Anthropocene” as the title to chapter 4 and of the thesis itself. This phrase was originally used as the title to an article published in the New York Times on September 27th, 2014.



Shanni B <shannab83@gmail.com>
09/02/2016
to jimrobbins

To the illustrious tree-hugging, enviro-loving, science scribe...

This stranger from the North is humbly writing you with (what is perhaps) an odd request, but allow me to introduce myself (and thus provide some context) first...

My name is Shanni; I'm from Nova Scotia, Canada, and I'm scheduled to graduate with a Master's degree in environmental studies from Dalhousie University in the fall of 2016. For my thesis research, I developed provincial species distribution models for three migratory songbirds of the boreal (& Acadian) forest: the Canada Warbler, the Rusty Blackbird, and the Olive-sided Flycatcher. Model generation was approached from the perspective of changing climates & shifting species' ranges --> i.e. We know that temperature & precipitation regimes are changing, and we know that this will in-turn affect the finer-scale structure of the forest. Therefore, in trying to delineate high-value habitat for the birds, we were specifically looking for areas which are likely to retain favorable structures & environmental processes (from the birds' perspective) over the longer-term.

For this, we sought to apply principles of C.S. Holling's ecological resilience framework (i.e. ecosystem structure & function are controlled by a limited number of environmental variables hierarchically nested in space & time) --> looking for not only favorable "micro-scale" forest characteristics, but favorable topographic features as well. This stage of research is mostly complete. At a later date, I hope to overlay my topographic + forest models with climate models generated by the Audubon society to cover three levels of Holling's environmental hierachy. But I digress...

Despite my ongoing status as a starving student, I allow myself one luxury in life: a subscription to the New York Times. A few years ago I read a column you penned for them, entitled: "Building an Arc for the Anthropocene". In the piece you discuss another part of Holling's ecological resilience framework: permeability/connectivity. Even now, 1.5 years on, I remember that piece, because it was wonderfully written & because really resonated with me at the time (my thesis supervisor has done much work on the Yellowstone to Yukon initiative). But allow me, once again, to digress...

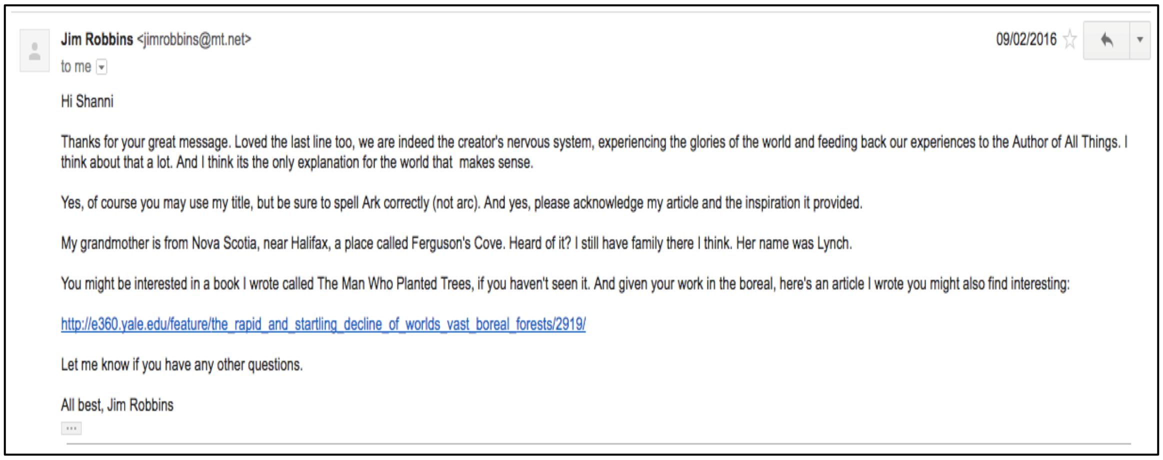
I was wondering if you might be willing to let me "borrow" part of your title, which is both poetic & pertinent, for the modeling manuscript I am trying to get published in peer-reviewed scientific literature. Specifically, I hope to title said manuscript: *Building an Arc in the Anthropocene: Applying principles of ecological resilience theory to model bird habitat in an era of climate change*, and would be so honoured and humbled if you would oblige. Of course, I would credit you & your NY Times article with the title in the "Acknowledgements" section, and would be happy to send you a copy when the manuscript is published.

Conversely, if you are not comfortable with this for whatever reason, that is totally fine too. (I will just stick with the slightly less poetic *Applying principles of ecological resilience theory to model bird habitat in an era of climate change*. Forgive my ignorance... I am not overly familiar with journalistic etiquette, but I thought I would ask nonetheless. (Nothing to lose right?)

~We are a way for the cosmos to know itself.

...

Shanni



Jim Robbins <jimrobbins@mt.net>
09/02/2016
to me

Hi Shanni

Thanks for your great message. Loved the last line too, we are indeed the creator's nervous system, experiencing the glories of the world and feeding back our experiences to the Author of All Things. I think about that a lot. And I think its the only explanation for the world that makes sense.

Yes, of course you may use my title, but be sure to spell Ark correctly (not arc). And yes, please acknowledge my article and the inspiration it provided.

My grandmother is from Nova Scotia, near Halifax, a place called Ferguson's Cove. Heard of it? I still have family there I think. Her name was Lynch.

You might be interested in a book I wrote called The Man Who Planted Trees, if you haven't seen it. And given your work in the boreal, here's an article I wrote you might also find interesting:

http://e360.yale.edu/feature/the_rapid_and_startling_decline_of_worlds_vast_boreal_forests/2919/

Let me know if you have any other questions.

All best, Jim Robbins

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